The Brood Ball of *Canthon* (*Canthon*) *Lituratus* Germar (Coleoptera: Scarabaeidae: Scarabaeinae) and Its Fossil Counterpart *Coprinisphaera cotiae* Sánchez and Genise New Ichnospecies, with a Brief Review of South American Fossil Brood Balls

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The Brood Ball of *Canthon* (*Canthon*) *lituratus* Germar (Coleoptera: Scarabaeidae: Scarabaeinae) and its Fossil Counterpart *Coprinisphaera cotiae* Sánchez and Genise New Ichnospecies, with a Brief Review of South American Fossil Brood Balls

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Abstract

The brood ball of *Canthon* (*Canthon*) *lituratus* Germar is an elongated ovoid covered by a thin lining of soil and dung fibers. The provision is mostly composed of dung and scattered flakes of organic matter. The egg chamber, which is located in the upper part of the provision, shows no evidence of lining and is connected to the exterior through an elongated aeration conduit. This conduit, which acts as a filter, is filled with interlaced dung fibers. These brood ball features are compared with those reported for several coprophagous species of *Canthon* Hoffmansegg. The brood ball of *C. lituratus* is also compared with a similar new fossil brood ball from the Cenozoic of Patagonia: *Coprinisphaera cotiae* Sánchez and Genise, **new ichnospecies.** A brief review of South American fossil brood balls in the ichnogenera *Coprinisphaera* Sauer and *Quirogaichnus* Laza is also provided with illustrations of the types.

Key Words: morphology, brood ovoids, elongated aeration conduit, trace fossil, Canthonini

Knowledge of the nesting behavior, nests, and brood balls of species of *Canthon* Hoffmansegg is uneven. The biology, physiology, and behavior of the necrophagous *Canthon cyanellus cyanellus* LeConte has been widely studied (*e.g.*, Halffter 1977; Halffter and Edmonds 1982; Halffter *et al.* 1983; Bellés and Favila 1983; Favila 1993, 2001; Favila and Díaz 1996; Favila *et al.* 2012). Recently, detailed reports on two other necrophagous species have been published: *Canthon quinquemaculatus* Laporte (Halffter *et al.* 2013; Cantil *et al.* 2014a) and *Canthon* (*Canthon*) *virens* aff. *paraguayanus* Balthasar (Cantil *et al.* 2014b).

Various aspects of the coprophagous species of *Canthon* have been studied also, with different degrees of detail, including mentions or descriptions of the nests and the morphology of the brood balls of *Canthon* (*Pseudopilissus*) *muticus muticus* Harold (Judulien 1899; González Vainer *et al.* 2012; Halffter *et al.* 2013), *Canthon edentulus* Harold (Judulien 1899), *Canthon* (*Canthon*) *obliquus* Horn (Halffter and Halffter 1989; González Vainer *et al.* 2012), *Canthon* (*Canthon*) *pilularius* (L.) (Halffter 1961; Matthews 1963), *Canthon* (*Glaphyrocanthon*) *viridis* Palisot de Beauvois (Blume 1981), *Canthon* (*Glaphyrocanthon*) *leechi* (Martinez, Halffter, and Halffter) (Edmonds and Halffter 1972), and *Canthon* (*Glaphyrocanthon*) *femoralis femoralis* (Chevrolat) (Martínez and Halffter 1972; Rivera-Cervantes and Halffter 1999; Cortez Gallardo 2007).

Macro- and micromorphological features of the brood ball of *Canthon* (*Canthon*) *lituratus* Germar from La Rioja province (Argentina) are described herein and compared with those published for the above mentioned species of *Canthon*. A new fossil brood ball from the Cenozoic of Patagonia (Argentina), comparable with those of *C. lituratus* and other coprophagous species of *Canthon*, is described herein. Additionally, a brief review of South American fossil brood balls is provided to exemplify their differences from the new ichnospecies.

Material and Methods

Adults of *C. lituratus* were found active during the afternoon (3:30 pm) as they were cutting and rolling horse dung on a road in Antinaco (S 28°49′09.93″, W 67°18′50.59″), La Rioja on 11 February 2008. Their behavior was recorded *in situ* by photographs and video. Eleven dung beetles were collected and taken to the Centro Regional de Investigaciones La Rioja (CRILAR), Anillaco, La Rioja to be studied in the laboratory.

All the adults collected were placed in a transparent plastic cube (each side: 30 cm) with 15 cm of slightly moistened local soil and provided with one-day-old cow dung. They were observed for four days. On the first day, the beetles were exposed to daylight from 1:30 pm to 7:30 pm. However, they were only active on the surface from 3:30 pm to 6:30 pm, corresponding with

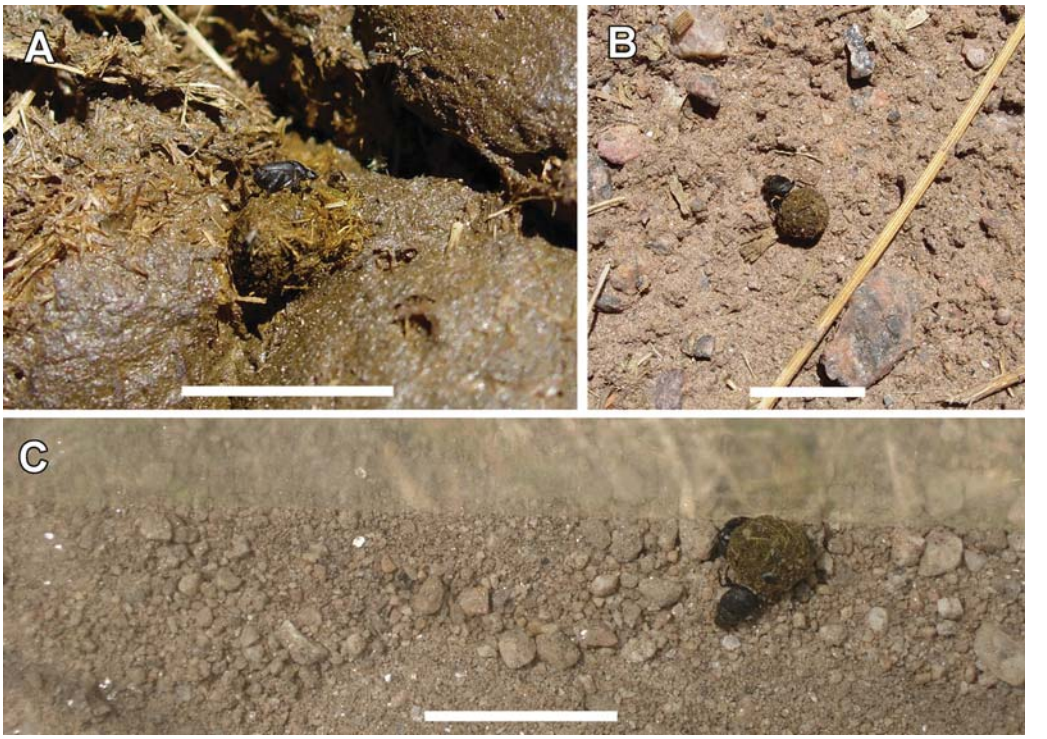

Fig. 1. Behavior of *Canthon lituratus* recorded *in situ* (A, B), and in a plastic container (C). A) An adult making a ball from horse dung, B) Ball rolling by a single adult, C) Ball rolling by a pair. Scale bar = 1 cm.

their activity recorded in the field. Accordingly, during the three successive days observations were carried out during that lapse of time. Soil moisture was checked, and food relocation and nesting behaviors were recorded daily (Fig. 1). The dung supply was changed only once in the middle of the observation period. On the fourth day, rolled balls left on the soil surface were collected, and the soil of the container was carefully removed and sieved to recover any buried balls and the beetles that made them.

The only brood ball collected was cut along its long axis to observe its internal features, particularly those related to the egg chamber. One half of the ball was used to make a thin section that was prepared by impregnating it with blue-stained polyester resin (Murphy 1986). The thin section then was observed under a Nikon HFX-DX Optiphot-pol petrographic microscope to analyze the micromorphology of the brood ball. Micromorphological features were observed under transmitted plain light, whereas the iso- and anisotropism and the birefringence fabric of the fine material were observed under polarized light. Terminology used in the micromorphological descriptions follows previously published nomenclature from similar studies (Sánchez and Genise 2008). The rolled balls, the remains of the unique brood ball found and its thin section, and the dung beetles were deposited in the Museo Argentino de Ciencias Naturales (MACN), Buenos Aires.

Results

When the soil was removed from the container, no defined nests were recognized and only one brood ball was found (Fig. 2A–C). From the soil surface, eight rolled balls were collected (Fig. 2D, E), half with a deep cut in the middle (Fig. 2E). The cuts were made by the adults during and after rolling and just before abandoning the ball.

Brood Ball Structure. The brood ball can be defined as an elongated ovoid (Fig. 2A), 10 mm long and 7 mm in equatorial diameter. The tapered pole, 2 mm wide, had a tiny open pore. A longitudinal section (Fig. 2B) of the ball revealed a thin external lining, up to 0.5 mm thick, composed of soil material and dung fibers. The provision, which to the naked eye was mostly composed of dung, had an external, more compact zone and a core formed by more porous material. A spherical egg chamber, 2 mm in equatorial diameter, was located

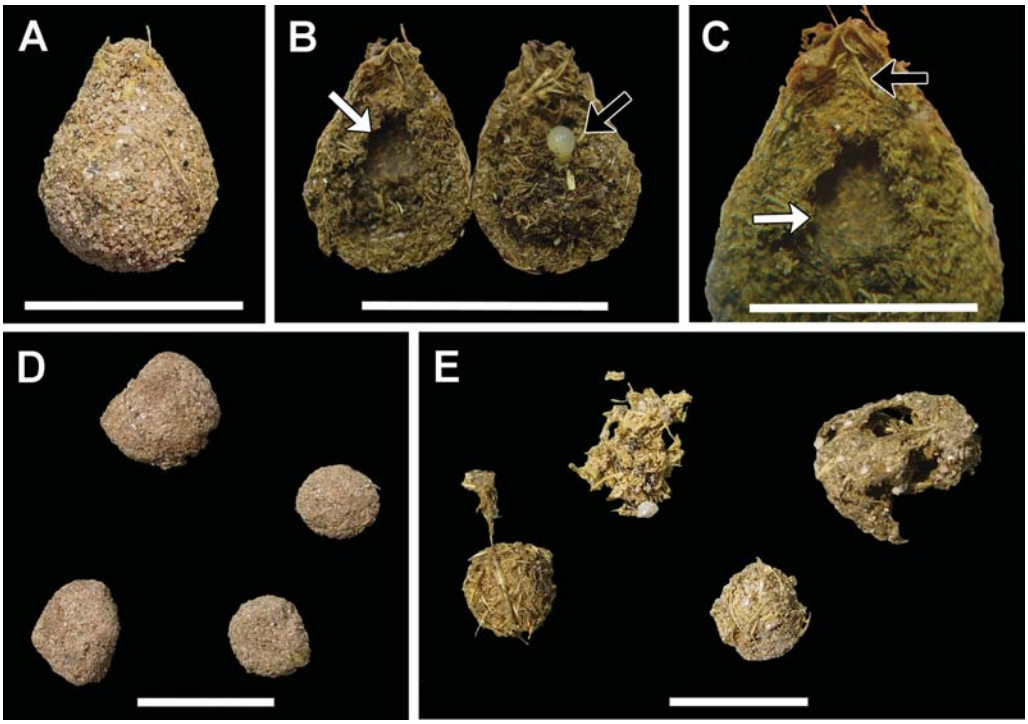

Fig. 2. Brood and rolled balls of *Canthon lituratus*. A) External view of the brood ball showing its elongated ovoid shape, B) Longitudinal section of the brood ball showing the egg chamber (white arrow) located in the upper part of the provision and the egg (black arrow), C) Detail of the egg chamber (white arrow) with no lining and interlaced dung fibers in the aeration conduit (black arrow), D) Rolled brood balls slightly covered with soil, E) Rolled brood balls not covered with soil and partially consumed. Scale bar = 1 cm.

in the upper part of the provision (Fig. 2B, C). This chamber had a smooth surface with no discrete lining. It opened to an upper conduit exhibiting interlaced dung fibers that emerged from the internal part of the brood ball's lining (Fig. 2C). A tiny pore connected this conduit to the outside. An elongated, pale yellow egg, 2.0 mm long and 1.2 mm wide, was located in a horizontal position inside the chamber (Fig. 2B).

Brood Ball Micromorphology. The external lining ranged from 425 μ to 500 μ in thickness (Fig. 3). Its microstructure was single grain, with 15% porosity. The coarse fraction represented 70% of the wall and was composed of mineral grains from silt to fine sand-sized quartz, K-feldspar, lithic fragments, mica (muscovite), and birefringent dung fibers (Fig. 3). There were also a few medium sand-sized grains, and scattered, reddish brown flakes of organic matter (approximately 50 μ long).

The provision was less porous than the wall (10%), and its microstructure was mostly massive. The coarse fraction represented 80% of the provision, and was mostly composed of dung fibers and scattered, reddish brown flakes of organic matter (Fig. 3). This fraction also had soil material in the form of dispersed mineral grains, from silt to fine sand-sized plagioclase, K-feldspar, quartz, and lithic fragments. The fine fraction was composed of light brown, shredded dung fibers, and scattered, reddish brown, small flakes (approximately 30 μ long) of organic matter. In the external compact zone of the provision, dung fibers were oriented in parallel toward the lining (Fig. 3). Such orientation was absent in the inner part.

Coprinisphaera cotiae Sánchez and Genise, new ichnospecies
(Fig. 4A)

Etymology. Dedicated to the first daughter *Constantina*, nicknamed *Coti*, of the first author.

Diagnosis. *Coprinisphaera* with an elongated protuberance at one pole with an internal conduit connecting the main chamber to the outside. The wall is of uniform thickness throughout the structure. There are no remains of a secondary chamber or additional structures. It is passively filled.

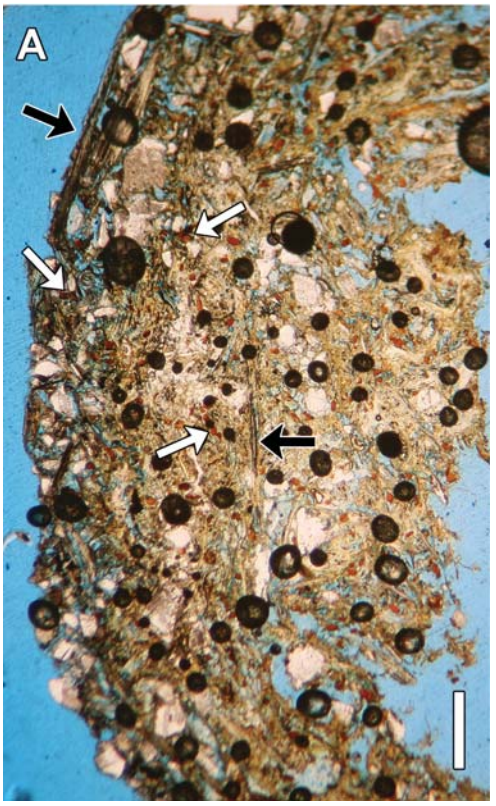

Fig. 3. Brood ball micromorphology. Longitudinal section showing the external wall and the infilling that is mostly composed of dung fibers. Note that both dung fibers (black arrows) and reddish brown flakes (white arrows) are found in the wall and infilling but in different amounts. Scale bar = 450 μ.

Comments. This ichnospecies differs from the other nine described to date (Laza 2006; Krell and Schawaller 2011; Cantil *et al.* 2013; Sánchez *et al.* 2013) by the elongated protuberance that is internally crossed by a conduit that ends in a very tiny pore. On the outside, it resembles *Coprinisphaera ndolanyana* Krell, 2011, but in the latter the protuberance is shorter and truncated and lacks internal cavities (*i.e.*, main chamber, conduit).

Holotype. One specimen (MACN-Icn 2169) collected by J. H. Laza, J. C. Quiroga, and F. Perez in 1984 and deposited in the Colección de Icnología of the Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina).

Description. The holotype is 42 mm long and its main chamber, with a discrete wall of 3–5 mm thick, is 27 mm in equatorial diameter. The elongated protuberance is 15 mm long, 13 mm wide at its base, and 8 mm wide at the most distal part, which is open to the exterior by a rounded hole, 1 mm in diameter. Its wall is 2.7–5.0 mm thick. The external surface is slightly irregular, and the protuberance contains fragments of the rock matrix.

Occurrence. The holotype and only known specimen comes from the Puesto Almendra Member of the Middle Eocene–Lower Miocene Sarmiento Formation, Bajada del Diablo, Sierra de Talquino (Chubut province, Argentina). This Formation is a continental pyroclastic succession, 320 m thick, exposed in the center and north of Patagonia, Argentina (Bellosi 2010). It has been extensively studied, particularly at Gran Barranca, the type locality of the Formation (Madden *et al.* 2010). It is a classic locality for South American fossil mammals and also is rich in insect trace fossils including several *Coprinisphaera* ichnospecies (Sánchez *et al.* 2010).

Discussion

Brood Balls of Coprophagous *Canthon* Species. *Canthon* Hoffmannsegg is a large genus distributed throughout the Americas and has about 180 species adapted to different habitats and with different feeding strategies (*e.g.*, Halffter and Martinez 1968, 1977; Rivera-Cervantes and Halffter 1999; Vaz de Mello 1999; Solis and Kohlmann 2002; Medina *et al.* 2003; Halffter *et al.* 2013; Cantil *et al.* 2014a, b). Most species are diurnal and good representative rollers (Halffter and Martínez 1966). Habitat, food preferences, and rolling behavior are well described for a number of species, but nests and brood balls have received less study.

Judulien (1899) was the first to describe the brood balls of three species of *Canthon*, one being necrophagous, *Canthon* (*Canthon*) *bispinus* Germar, and two coprophagous, *C. muticus muticus* and *C. edentulus*. He defined the brood ball shape of the former species as resembling the number "8", and the brood balls of the two latter species as pear-shaped. From Judulien's illustrations, it is possible to recognize that the brood balls of *C. muticus muticus* are more ovoid in external shape than those of *C. edentulus*. González Vainer *et al.* (2012) redescribed the brood balls of *C. muticus muticus* as ovoid or pear-shaped and covered by a thin layer of dry dung. This description and the accompanying pictures confirm that the brood balls of *C. muticus muticus* are more ovoid than pear-shaped. Recently, Halffter *et al.* (2013) described the brood balls of *C. edentulus* as pear-shaped with a very small apical protuberance where the egg chamber is housed. These balls have no external layer of soil. Halffter and Halffter (1989) described the brood balls made by *C. obliquus* as pear-shaped, composed of a spherical mass of dung covered with soil (1 mm

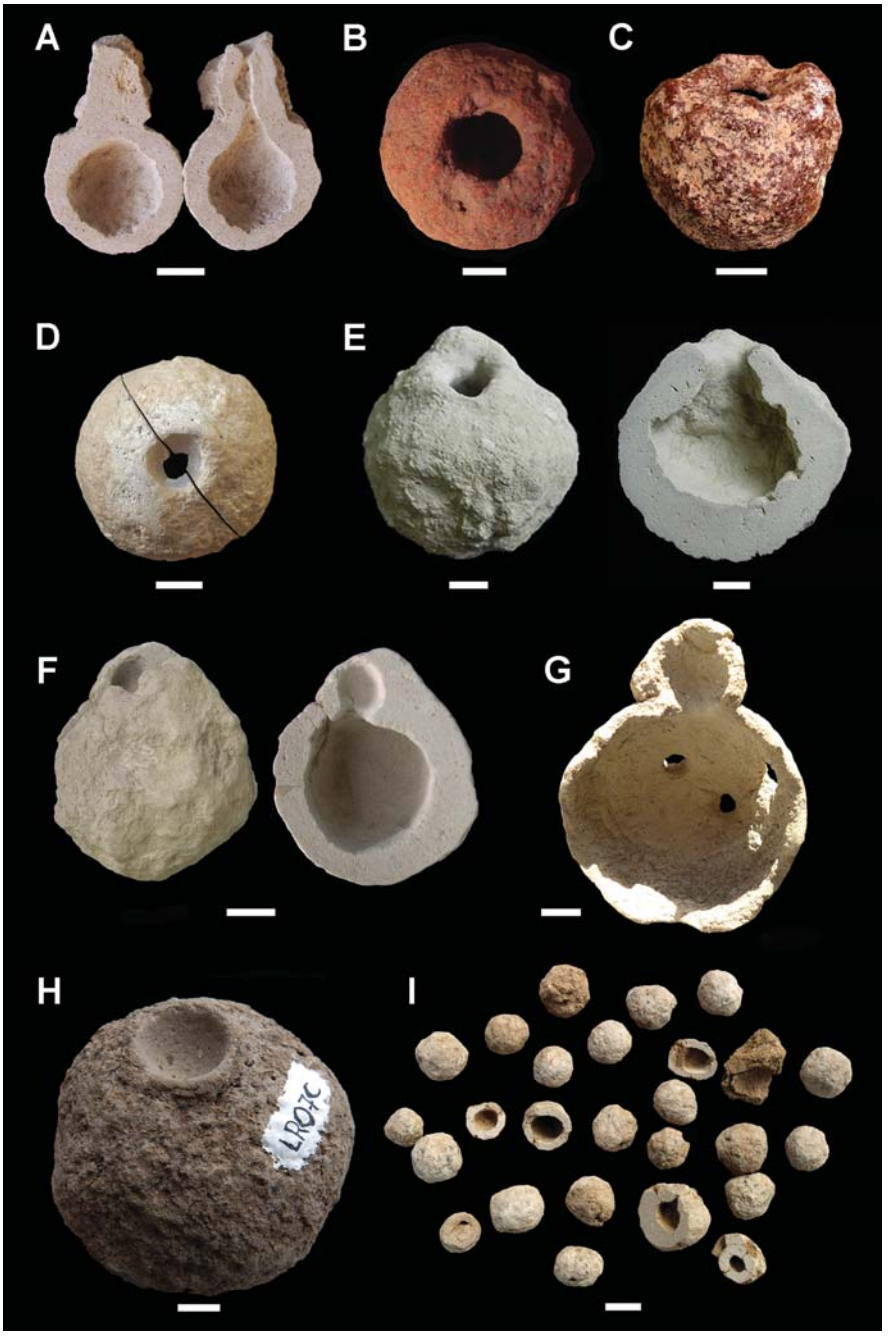

Fig. 4. Fossil brood balls *Coprinisphaera cotiae*, other South American *Coprinisphaera* ichnospecies, and *Quirogaichnus coniunctus*. A) Internal view of the sectioned holotype of *C. cotiae* (MACN-Icn 2169), B) Top view of the lectotype of *C. murguiai* (MLR 479b), C) Top-lateral view of a paratype of *C. kraglievichi* (MLR 319), D) Top view of the holotype of *C. lazai* (MACN-Icn 2058), E) External view (left) of the holotype of *C. kheprii* (MACN-Icn 1670) and internal view (right) of one half of a sectioned specimen (MACN-Icn 1417), F) External (left) and internal (right) views of the holotype of *C. tonnii* (MACN-Icn 1769), G) Internal view of the holotype of *C. akatanka* (MMP 4046), H) Top-lateral view of the holotype of *C. kitu* (EPN-Icn 003), I) Holotype of *Q. coniunctus* (MACN-Icn 2252). Scale bar = 1 cm.

thick), or dry dung mixed with soil, and a protuberance that they refer to as a papilla. The egg chamber is located below this protuberance, under the provisions, and is connected to the exterior by a well-defined conduit containing loose pieces of straw, which acts as an aeration conduit. Halffter (1961) and Matthews (1963) reported that *C. pilularius*, like other coprophagous species of *Canthon*, constructs simple nests composed of only one pear-shaped brood ball. Blume (1981) described the brood balls of *C.viridis* as similar in external shape to a narcissus bulb, coated with a thin layer of soil. An egg chamber lacking a soil lining is included in the provision. These brood balls also exhibit an external ovoid shape. According to Blume (1981), the brood balls of *C. viridis* are similar to those of *C. leechi* described in detail by Edmonds and Halffter (1972) as elongated pears. These balls show an extensive fibrous plug in the narrowed protuberance, composed of carefully arranged fibers that run parallel to the longitudinal axis of the ball. G. Halffter and V. Halffter (in Rivera-Cervantes and Halffter 1999) also recorded pear-shaped brood balls of *C. leechi*, covered by a layer of soil and showing a well-defined aeration conduit. Martínez and Halffter (1972), Rivera-Cervantes and Halffter (1999), and Cortez Gallardo (2007) described different aspects of the nests and brood balls of *C. femoralis femoralis*. Cortez Gallardo (2007) reported that adults construct simple nests composed of only one pear-shaped brood ball covered by a thick layer of soil (5 mm thick). These balls display a particularly pronounced protuberance, 7 mm long, and open to the exterior by a rounded hole. Pictures show that this ball has an external elongated ovoid shape. The egg chamber is included in the provision at the base of this protuberance. Rivera-Cervantes and Halffter (1999) also mentioned that the central chamber of dung, where the larva develops, is connected to the outside by an internal, well-defined conduit which passes through the protuberance and opens at its distal end.

From a comparison of all these descriptions, along with the available images and figures, it is possible to infer that the expression "pear-shaped brood balls" is not the most appropriate for precisely describing the brood ball shape for the aforementioned species of *Canthon*. These balls lack an external constriction between the main chamber and the protuberance as seen in typical pears. Rather, they are geometrical ovoids, with a continuous outline and no constriction and with a more or less elongated protuberance. The brood balls of *C. lituratus*, as described in detail above, are elongated ovoids, 10 mm long, covered by a thin lining of soil material and dung fibers, 0.5 mm thick (Fig. 1). Despite original descriptions mentioning pear-shaped balls for *C. muticus muticus*, *C. leechi*, and *C. femoralis femoralis*, all of them exhibit the same ovoid shape as that of *C. lituratus*. Also, they are covered by a layer of dry dung (*C. muticus muticus*) or soil (*C. leechi* and *C. femoralis femoralis*), a feature also described for *C. obliquus* (soil or dry dung and soil) and *C. viridis* (soil). The tapered pole is elongated in the brood balls of *C. lituratus* and *C. leechi* and is longer yet in those of *C. femoralis femoralis,* forming a more distinct protuberance. Internally, this protuberance contains a conduit that begins in the egg chamber, extends through the protuberance, and ends at a pore that connects the chamber to the outside. In *C. lituratus*, the conduit is filled with interlaced dung fibers that emerge from the internal surface of the wall, forming a dung fiber filter described here for the first time. The brood balls of *C. obliquus* and *C. leechi* also have a filter, but it is formed by a conduit that is filled with loose pieces of straw in the former and with fibers parallel oriented to the long axis of the ball in the latter. In *C. femoralis*, the elongated conduit is completely empty. The egg chamber in the upper part of the provision, with no lining, and connected to the exterior by the aeration conduit is present in *C. lituratus*, *C. obliquus*, *C. viridis*, and *C. femoralis femoralis.*

Ichnospecies *C. cotiae*, the new brood ball from the Cenozoic of Patagonia, seems to be the fossil counterpart of the brood balls of the coprophagous species of *Canthon* we have reviewed. *Coprinisphaera cotiae* is a spherical chamber with an elongated protuberance, internally crossed by a long conduit (aeration conduit) and lacking an egg chamber located in or that intersects with the wall (Fig. 4A). As discussed above, most of the species analyzed exhibit all or some of these features. It is particularly more similar to the brood balls of *C. femoralis* because of the internal and external features of its remarkably long conduit.

South American Fossil Brood Balls (*Coprinisphaera* and *Quirogaichnus*) and their Possible Producers. Dung beetle fossil brood balls are grouped into two ichnogenera, *Coprinisphaera* Sauer for isolated balls and *Quirogaichnus* Laza for clustered ones. The latter has only one ichnospecies, *Quirogaichnus coniunctus* Laza, whereas the former has 10, including the new one described here. *Quirogaichnus coniunctus* and eight ichnospecies of *Coprinisphaera* come from Cenozoic deposits in South America (Roselli 1939, 1987; Sauer 1955, 1956; Laza 2006; Sánchez *et al.* 2010, 2013; Cantil *et al.* 2013; Genise *et al.* 2013). These eight ichnospecies can be recognized as follows:

Coprinisphaera murguiai (Roselli) (Fig. 4B) is a spherical to subspherical chamber with a discrete wall and a medium-sized hole (about one-quarter of its diameter) at one pole but no remains of a secondary chamber or additional structures. The hole is interpreted as made by the emergent adult.

Many extant species in different taxa leave similar holes when the new adult emerges, resulting in the morphology of this ichnospecies. It has been widely recorded from the Cenozoic of Argentina, the Paleogene of Uruguay, and the Pleistocene of Ecuador (Roselli 1939, 1987; Sauer 1955, 1956; Laza 2006; Sánchez *et al.* 2010, 2013; Genise *et al.* 2013).

Coprinisphaera kraglievichi (Roselli) (Fig. 4C) is a spherical to subspherical chamber with a relatively thick discrete wall and a hole pierced in the middle of a more or less flattened surface at one pole, which is externally surrounded by a rim. Until now, no extant dung beetles have been found to construct brood balls similar to *C. kraglievichi*, which may resemble brood balls under construction. For instance, in some dung beetles, such as *Cephalodesmius armiger* Westwood (Halffter and Edmonds 1982, fig. 98), the female hollows out the ball, forming a lipped cup that looks similar to the flattened surface of *C. kraglievichi*. Some brood balls under construction by *Scarabaeus sacer* L. and *Copris hispanus* (L.) show a comparable shape (Fabre 1897, 1899). However, the emergence hole pierced in the flattened surface of *C. kraglievichi* suggests that the shape may be the definite one, rather than a particular stage of construction. This ichnospecies has been recorded from the Cenozoic of Argentina and from the Paleogene of Uruguay (Roselli 1939, 1987; Laza 2006; Sánchez *et al.* 2010).

Coprinisphaera lazai Sánchez, Genise, Bellosi, Román-Carrión, and Cantil (Fig. 4D) is a spherical to subspherical chamber with a discrete wall and a hemispherical, concave, small depression at one of its poles. This depression occupies the whole wall thickness and shows a narrow passage in the center connecting with the main chamber. The *C. lazai* specimen can be interpreted as the result of the interruption of the brood ball construction in which the hemispherical structure represents the floor of an incomplete egg chamber. Brood balls under construction resembling *C. lazai* have been reported and illustrated for *Homocopris torulosus* (Eschscholtz) (Joseph 1929), *S. sacer* and *C. hispanus* (Fabre 1897, 1899), *Copris armatus* Harold (Anduaga *et al.* 1987), *Phanaeus palliatus* Sturm (Halffter and Matthews 1966), *Sulcophanaeus carnifex* (L.) (Klemperer 1983), *Kheper platynotus* Bates (Sato and Imamori 1987), *Megathopa villosa* Eschscholtz (Ovalle and Solervicens 1980), and *Gymnopleurus geoffroyi* Fuessly and *Sisyphus shaefferi* (L.) (Prasse 1957). The unfinished brood balls of Argentine species also have hemispherical chambers in the wall as is found in *C. lazai* (unpublished observations). This ichnospecies has been recorded from the Cenozoic of Argentina (Laza 2006; Sánchez *et al.* 2010; Genise *et al.* 2013).

Coprinisphaera kheprii Laza (Fig. 4E) is a subspherical to pear-shaped chamber with a thick discrete wall and a small protuberance at one pole that has a hemispherical secondary chamber inside, the concavity of which is opened to the main one. The hemispherical chamber was interpreted by Laza (2006) as half of the egg chamber whose roof is included in the wall. Recently, Sánchez *et al.* (2012) reported that some Phanaeini, such as *Sulcophanaeus imperator* (Chevrolat), construct brood balls similar to *C. kheprii*. This ichnospecies has been recorded from the Cenozoic of Patagonia, Argentina (Laza 2006; Sánchez *et al.* 2010).

Coprinisphaera tonnii Laza (Fig. 4F) is a pear-shaped, thick-walled structure, internally composed of a main chamber and a secondary smaller one, located in the wall of the upper protuberance. Neither chamber is externally separated by a deep neck or constriction, but internally they are clearly separate though they may be connected by a small passage. The secondary chamber of *C. tonnii* represents a complete egg chamber entirely isolated from the provisions (Laza 2006). Extant brood balls reported to date share no similarities with *C. tonnii*. This ichnospecies has been recorded from the Cenozoic of Patagonia, Argentina (Laza 2006; Sánchez *et al*. 2010; Cantil *et al.* 2013).

Coprinisphaera akatanka Cantil, Sánchez, Bellosi, González, Sarzetti, and Genise (Fig. 4G) is a bispherical, thin-walled structure composed of a main larger chamber and a secondary smaller one, externally separated by a deep neck or constriction and sometimes internally connected by a small open passage. The smaller chamber is interpreted as the egg chamber and is completely separated from the main one where the larval food was originally provisioned. Cantil *et al.* (2013) reported that this particular brood ball shape and the egg chamber location are observed in the brood balls of some necrophagous species of *Canthon*, suggesting that *C. akatanka* is the only *Coprinisphaera* that can be attributed to necrophagous dung beetles. This ichnospecies has been recorded from the Lower Pleistocene of Buenos Aires province, Argentina (Laza 2006; Cantil *et al.* 2013; Genise *et al.* 2013).

Coprinsphaera kitu Sánchez, Genise, Bellosi, Román-Carrión, and Cantil (Fig. 4H) is a spherical to subspherical chamber which has a hemispherical, concave structure at one pole that is partially included in the wall and externally surrounded by a rim. This structure is considered more as an ornament rather than a half-constructed egg chamber (Sánchez *et al.* 2013). Recently, Zunino (2013) described a new fossil dung beetle, *Phanaeus violetae* Zunino, whose remains were found inside a specimen of *C. murguiai* from the Pleistocene Cangahua Formation of Ecuador. In that formation, only this ichnospecies and *C. kitu* have been

recorded (Sauer 1955, 1956; Laza 2006; Sánchez *et al.* 2013), suggesting that *P. violetae* may be the producer of *C. kitu*. No extant dung beetles construct brood balls similar to those of this ichnospecies.

Quirogaichnus coniunctus Laza (Fig. 4I) is a cluster of spherical to subspherical, small chambers located in a main cavity contained in the paleosol. The individual chambers have a discrete wall and some of them an emergence hole. The spherical to subspherical morphology of the individual chambers that conforms the cluster, and the type of nest, resembles those of *Eurysternus* Dalman (Halffter and Edmonds 1982; Huerta *et al*. 2003). Only two specimens have been recorded from the Miocene of Buenos Aires province and from the late Pleistocene of Entre Ríos province (Argentina) (Laza 2006).

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