

Food Relocation Behavior, Nests, and Brood Balls of *Canthon quinquemaculatus* Laporte de Castelnau (Coleoptera: Scarabaeidae: Scarabaeinae)

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**FOOD RELOCATION BEHAVIOR, NESTS, AND BROOD BALLS OF *CANTHON*
QUINQUEMACULATUS LAPORTE DE CASTELNAU
(COLEOPTERA: SCARABAEIDAE: SCARABAEINAE)**

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ABSTRACT

Individuals of *Canthon quinquemaculatus* Laporte de Castelnau rolled balls up to 4 m from the food source. Stealing balls was common. Male headstand position was observed at the entrance of chambers containing a rolled ball and a female. Nests were shallow, telecoprid, and compound. Male and female cooperate, and parental care is performed (Nesting Pattern V). A total of 23 brood balls from five nesting chambers were obtained from terraria. The brood balls display a protuberance that is separated from the provision chamber by a partition of soil material. An egg chamber that lacks an organic lining is located at the base of the protuberance. At the roof of the egg chamber, there is an aeration conduit that ends in a filter composed of loose soil. The carrion provisions contain a high percentage of soil material. Some brood balls have larval fecal pellets in the external surface of the wall. Egg chamber separated from provisions, lack of an organic lining coating the egg chambers, ejection of larval fecal pellets, and loose soil filters are typical characters of brood balls made by necrophagous Scarabaeinae. The first three characters might reflect a set of adaptive characters of the necrophagous species to their food. These characters might be useful to distinguish fossil brood balls constructed by necrophagous Scarabaeinae from those constructed by coprophagous species.

Key Words: dung beetles, rolling behavior, ball construction, micromorphology, necrophagy, ball characters

In South American rainforests, necrophagy is more important than coprophagy among species of the genus *Canthon* Hoffmannsegg (Halffter and Matthews 1966). However, little is known about the food relocation behavior, nests, and brood ball structure of the necrophagous species that inhabit this region (Judulien 1899; Luederwaldt 1911; Morelli and González Vainer 1990; Sánchez 2009; Rueda *et al.* 2012). Only *Canthon cyanellus cyanellus* LeConte has been broadly studied, mainly due to the contributions by G. Halffter, M. E. Favila, and coworkers (Halffter and Edmonds 1982; Bellés and Favila 1983; Halffter *et al.* 1983; Favila 1988a, b, 1993, 2001; Favila and Díaz 1996; Ortiz-Dominguez *et al.* 2006; Chamorro-Florescano and Favila 2008, 2009; Chamorro-Florescano *et al.* 2011; Favila *et al.* 2012). Since this genus consti-

tutes a polyphyletic group (Medina *et al.* 2003; Monaghan *et al.* 2007), the study of behavioral traits, such as nesting behavior and brood ball construction, might be an important contribution for phylogenetic analyses.

Canthon quinquemaculatus Laporte de Castelnau is a common necrophagous beetle in forests from Peru to Argentina (Medina *et al.* 2003; Silva *et al.* 2012). It has been proposed that, like *C. cyanellus cyanellus* and several South American species of this genus, this roller beetle may be included in Nesting Pattern V (Halffter and Edmonds 1982; Morelli and González Vainer 1990; Rueda *et al.* 2012). However, no detailed studies have been published so far. Field observations on food relocation behavior, together with terrarium observations on the nests and the brood balls, are described

herein. The descriptions of the brood balls include macro- and micromorphological characters, the latter useful to interpret behavioral traits more accurately (Sánchez and Genise 2008; Sánchez *et al.* 2012). The study of brood balls in different stages of construction allowed us to propose a sequence of ball construction by *C. quinquemaculatus*.

MATERIAL AND METHODS

The field study was carried out in March and December 2012 at the Karadya Bioreserve (S25°52'14", W53°58'10"), a remnant of Atlantic forest in northeastern Misiones province, Argentina. Twenty-five *C. quinquemaculatus* were found in a bird carcass (*Tachyphonus coronatus* Vieillot) in early stages of decomposition and in dog feces, or were attracted to baits using tuna or remains of rattlesnakes (*Rhinocerophis alternatus* Duméril, Bibron and Duméril and *Crotalus durissus* L.) that were found dead in the field. The behavioral observations were recorded by photographs and videos *in situ*. Then, the adults were collected and placed inside plastic rectangular or cylindrical terraria (23.0 × 13.5 cm or 12.5 cm in diameter, respectively). The terraria contained bird remains or tuna on the surface of a 6–7 cm deep layer of humid soil taken from the forest. The provisions were renewed regularly when they became too decayed or dry. Water was sprayed daily onto the soil to maintain moisture.

After several days, in the facilities of the Centro de Investigaciones Antonia Ramos (CIAR, S27°26'40", W54° 56' 23") in Misiones, or then in the División Icnología of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires, the nesting chambers were opened. The superficial layers of soil material were removed from the terraria to expose brood balls in chambers, interrupting the nesting activities. Brood balls in different stages of construction were found inside the chambers. These brood balls had a protuberance that contained an egg chamber, which was separated from the provision chamber by a constriction. The diameter of the brood balls was measured along an axis that corresponds with the largest width of the protuberance and the provision chamber. Orthogonal to the former, the height was measured along an axis that runs through the protuberance and the provision chamber, and the brood balls were cut along this axis. Longitudinal sections were carried out to measure the egg chamber and the wall thickness, as well as describing the internal structure. The nesting chambers and the entire and sectioned brood balls were photographed with unaided eyes and/or under a stereoscopic microscope. Data presented below are expressed as the mean value ± standard deviation.

Thin sections were prepared with undisturbed and vacuumed samples impregnated with polyester resin (Murphy 1986). They were observed and photographed under a stereoscopic microscope Olympus SZ61 and a petrographic microscope Nikon HFX-DX Optiphot-pol. The micromorphological features were observed in transmitted plain light, whereas the iso- and anisotropism and the birefringence fabrics of the fine material were observed under polarized light. Terminology and micromorphological descriptions follow the nomenclature of soil micromorphology proposed by Bullock *et al.* (1985), which has been utilized for descriptions of brood balls (Sánchez and Genise 2008; Sánchez *et al.* 2010, 2012).

The brood balls and the dung beetles were deposited in Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina).

RESULTS

Food Relocation Behavior. Individuals of *C. quinquemaculatus* arrived at the area with baits by flying in zigzag and circular patterns about 30–40 cm above the ground. They landed 30–40 cm from the bait and walked toward it. The beetles cut a piece of bait that soon took the shape of a ball by using mostly their head as a shovel. They moved their forelegs alternately to compress the ball and complete its separation from the source. They occasionally added new material to the ball during the shaping process, avoiding tendons and bones (Fig. 1A, B). The beetles cut balls from the same bait started rolling them away in similar directions, along an arc of about 45°. After some distance, each beetle took a different direction. The beetles attempted to step over obstacles rather than avoid them. During rolling, the balls (5–10 mm in diameter) became passively covered by a thin layer of soil. Along their way, single beetles paused the rolling, climbed and turned around on top of the ball and moved their antennae, and descended to continue rolling. In some cases, they stopped rolling and buried the ball shallowly for a while. They walked away up to 8 cm from the buried ball and usually returned by the same path. In rolling pairs, while the male walked backward in the rolling position, the female remained clinging onto the ball (Fig. 1C). In some cases, the male left the ball with the female and disappeared beneath the litter. Later, the male emerged and located the ball with the clinging female beneath the litter. Five male-female pairs buried the balls up to 4 m from the food source, but in two cases the rolling did not follow a straight path and the ball was rolled for 20 m changing direction several times. In two cases, we observed that a male adopted a headstand position with the



Fig. 1. Food relocation and nests of *Canthon quinque maculatus*. A) Individuals (arrows) in *Tachyphonus coronatus* remains, scale bar = 10 mm, B) An individual making a ball with rattlesnake remains, scale bar = 5 mm; note the avoidance of ribs (arrows), C) Rolling positions of male (lower beetle) and female (upper beetle), scale bar = 5 mm, D) Male in headstand position with the hind legs (arrows) extended in the air, scale bar = 5 mm, E) Nesting chamber that contains five brood balls and a female, scale bar = 5 mm, F) Nesting chamber that contains a rolled ball and an incomplete brood ball (arrow), scale bar = 5 mm.

hind legs extended in the air at the entrance of a shallow chamber (Fig. 1D). The males retracted their hind legs under the abdomen for a while, and later extended them again. The shallow chambers, 3.0–4.5 cm long and 3 cm high, contained the rolled ball and the female.

Frequently, a beetle (robber) stole the ball that was being rolled by another beetle (owner). In one case, the owner cut the ball into two fragments and both owner and robber acquired a fragment. In another case, the robber attacked from behind an owner that was rolling a ball with the female

over it. The robber, which finally remained with the ball and the female, held the male with its legs until the owner released and abandoned the ball.

Nest Structure. In terraria, five nesting chambers were found at 4–6 cm from the soil layer surface. They were spheroidal-oblate, 3.0–4.5 cm long, and 2.5–3.5 cm high. When opened, each nesting chamber contained 2–5 brood balls that showed vertical, inclined, and horizontal orientation (Fig. 1E). Three additional brood balls, two having dry eggs and another with a healthy egg, were found at the surface of the terraria. A total of 23 brood balls were obtained. Two nesting chambers that contained a single female showed four and five complete brood balls, respectively (Fig. 1E). The other three nesting chambers contained a male-female pair each. Two of them had a ball in the condition it was rolled and four or five complete brood balls, respectively. The third nesting chamber was opened twice. The first time, the nesting chamber contained a ball as it was rolled and an incomplete egg chamber with an egg, which was removed (Fig. 1F). The second time it was opened, after two days during which the terrarium was provisioned with tuna, the same nesting chamber lacked the rolled ball and held a complete brood ball together with a ball showing a crater-like depression at one pole (Fig. 2A).

Brood Ball Structure. Brood balls ($n = 23$) have a protuberance that is separated from the provision chamber by a constriction (Fig. 2). The protuberances, which are from spherical to conical, are 7.2 ± 0.4 mm in diameter and 5.4–10.5 mm high (Fig. 2B–D). The provision chambers range from 10 to 13 mm in diameter. In sections, brood balls have an egg chamber located at the base of the protuberance, separated from the provisions by a partition of soil material (Fig. 2C, E). These egg chambers are 4.3 ± 0.4 mm in diameter and 3.3 ± 0.2 mm high. Their inner surface is ridged, and lacks an organic lining. They are connected to the exterior by a cylindrical and narrow conduit that is located in the upper pole of the protuberance, ending in a plug of loose soil (Fig. 2F, G). The yellow eggs, 3.5 ± 0.3 mm long and 2.2 ± 0.3 mm wide ($n = 9$), are oriented horizontally (Fig. 2C) or inclined inside the egg chambers. The wall thickness ranges from 1.3 to 2 mm ($n = 18$).

Seven of the 23 collected brood balls housed larvae in different stages of development, from a pharate larva located inside the egg (Fig. 2C) to those that had broken the soil partition and moved to the provision chamber (Fig. 2H). In some cases, the larvae ejected small fecal pellets to the external surface of the brood ball (Fig. 2B). Only one brood ball contained a pupa that continued its development to adult (Fig. 2I, J) in the laboratory.

The balls abandoned inside the nesting chambers in the condition they were rolled ($n = 3$, Fig. 1F) were 12.75 ± 1.1 mm in diameter. The only ball with a crater-like depression at one pole was about 9.6 mm in diameter (Fig. 2A). The depression was shaped on the external surface of the wall, so it was not open to the provision.

Brood Ball Micromorphology. The wall is composed of soil material and shows a massive microstructure with 5–7% porosity (Fig. 3). The pores are equidimensional to elongate; in the latter case, they are oriented parallel to the wall. The coarse fraction represents 10–20% of the wall and is mostly composed of medium silt grains, including quartz, feldspar, clay aggregates, lithic fragments, mica, and scarce heavy minerals and volcanic glass yards. Organic components are present in this fraction, too. The fine fraction is composed of iron oxide-stained clay material. The oxidation is more intense towards the internal zone of the wall. The wall also shows Mn-Fe nodules. The egg chamber shows no organic lining (Fig. 3A). The provision chamber has patchy contents composed of elongated, birefringent muscle fibers (30–60%) and soil material similar to that of the wall (70–40%) (Fig. 3B).

DISCUSSION

Several individuals of *C. quinque maculatus* that came to the same bait started to roll balls away in similar directions, thus providing new observations on preferential directions of rolling in Scarabaeinae. Matthews (1963) suggested that in the absence of stronger guiding stimuli *Canthon pilularius* (L.) tends to roll the balls toward (0°) or directly away (180°) from the position of the sun. Similarly, cessation of rolling and turning around on top of the ball observed herein for *C. quinque maculatus* was also associated with the sun orientation in *C. pilularius* (Matthews 1963). However, the position of the sun seems to be an inconclusive factor to explain the orientation of *C. cyanellus cyanellus* inhabiting closed forests (Favila and Díaz 1996). These authors suggested that chemical and/or visual mechanisms of orientation might also be involved. The conditions at Misiones were intermediate, alternating shaded areas with open patches with direct sun radiation. A preferential direction in which a ball is rolled away from the resource was also recorded for *Gymnopleurus miliaris* (F.), *Scarabaeus sacer* L., and *Geotrupes sylvaticus* Panzer (Hingston 1923; Geisler 1961).

Rolling might have evolved to reduce inter-specific and intraspecific competition by quickly transporting the ball away from the food source (Halffter and Matthews 1966; Scholtz *et al.* 2009). The distance that male-female pairs of

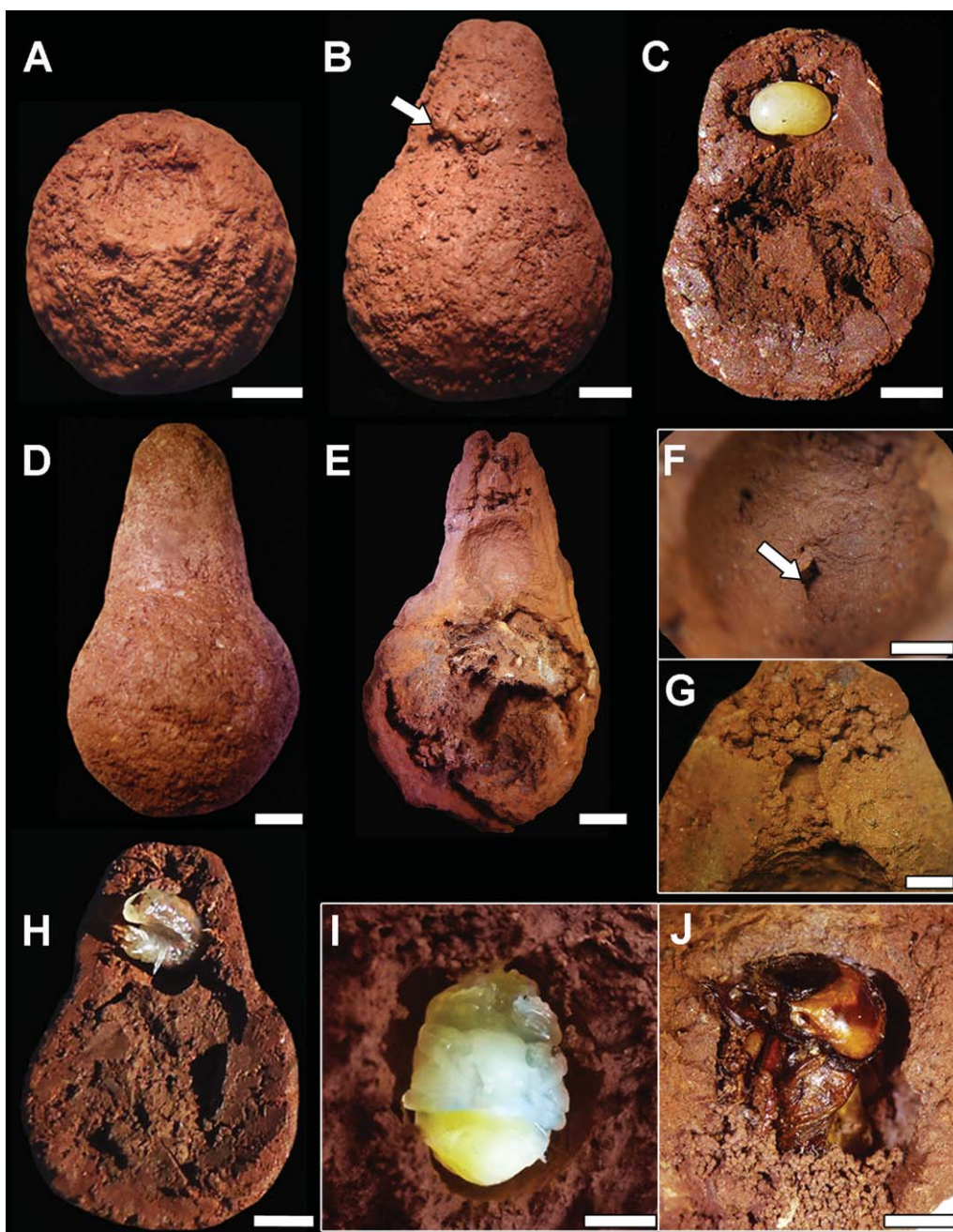


Fig. 2. Brood balls and larval development of *Canthon quinquemaculatus*. A) Ball with a crater-like depression at one pole, scale bar = 2.5 mm, B) External view of a brood ball with a conical protuberance, scale bar = 2.5 mm; note the larval fecal pellets (arrow) with high content of soil material, ejected outside the ball, C) Internal view of a brood ball showing a pharate larva inside the egg chamber, scale bar = 2.5 mm; note that the egg chamber is completely located inside the spherical protuberance, D) External view of a brood ball with a conical, elongate protuberance, scale bar = 2.5 mm, E) Internal view of a brood ball showing the location of the egg chamber at the base of the protuberance, scale bar = 2.5 mm, F) Aeration conduit opening (arrow) seen from the egg chamber, scale bar = 1 mm; note the absence of organic lining, G) Aeration conduit in longitudinal section and the filter of loose soil, scale bar = 1 mm, H) Internal view of a brood ball showing a larva in contact with the provisions, scale bar = 2.5 mm, I) Pupa, scale bar = 2.5 mm, J) Adult, scale bar = 2.5 mm.

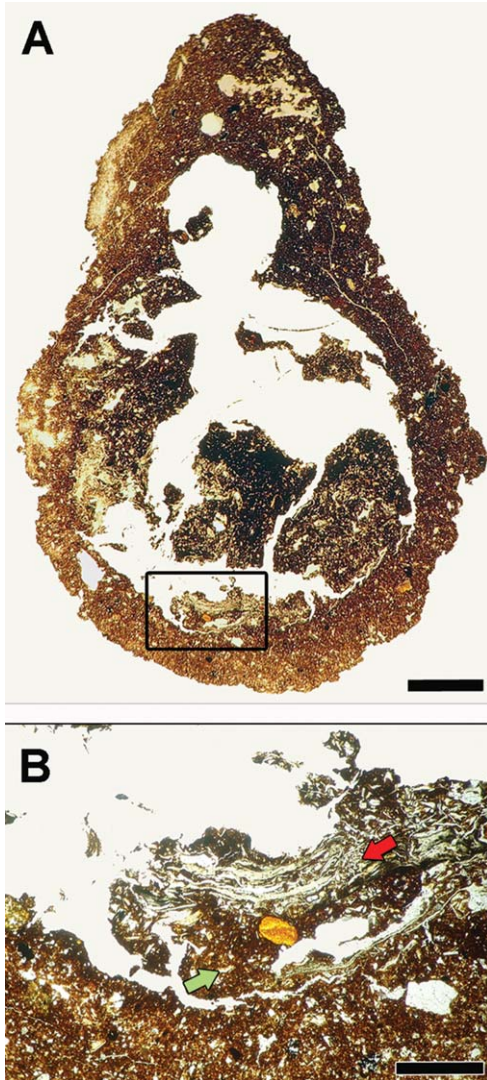


Fig. 3. Micromorphology of a brood ball of *Canthon quinquemaculatus*. A) Longitudinal section showing the wall (note the internal zone stained with iron oxide), the egg and provision chambers, and the provisions distributed in patches; note the amount of soil material (dark brown) in provisions, scale bar = 2 mm, B) Detail of the provisions containing muscle fibers (dark red arrow) and soil material (light green arrow), scale bar = 500 μ .

C. quinquemaculatus rolled the balls from the resource (4 m) was similar to distances mentioned for *Canthon curvipes* Harold (about 5–6 m), *C. pilularius* (1–3 m), *C. cyanellus cyanellus* (about 2 m), and *Canthon indigaceus chevrolati* Harold (1–3 m) (Luederwaldt 1911; Matthews 1963; Montes de Oca *et al.* 1991; Favila and Díaz 1996).

The headstand position of the male (Fig. 1D) was also observed in *Scarabaeus catenatus* (Gerstaecker), *Kheper aegyptiorum* (Latreille), *Kheper nigroaeneus* (Boheman), *Kheper platynotus* (Bates), *Kheper lamarcki* (MacLeay), *Kheper bonellii* (MacLeay), *Kheper subaeneus* (Harold), and *C. cyanellus cyanellus* (Tribe 1975; Bellés and Favila 1983; Sato and Imamori 1986, 1987; Edwards and Aschenborn 1988; Favila and Díaz 1996; Sato 1998; Burger *et al.* 2002, 2008; Favila *et al.* 2012). The advantage of this behavior remains uncertain in *S. catenatus* and *K. platynotus* (Sato 1998). In the other cases, this behavior was associated with the releasing of sex pheromones from the abdominal glands of males to attract females near the resource, after or before ball making. The headstand position of the male in *C. quinquemaculatus* occurs at the entrance of a chamber that already contains a female. Therefore, it is unlikely that this behavior plays a sexual-attraction purpose. In *C. cyanellus cyanellus*, the male headstand position was also attributed to the releasing of chemical secretions with repulsive properties against cleptoparasites and predators (Bellés and Favila 1983; Favila *et al.* 2012), which is more compatible with the observations presented herein.

This study confirms that *C. quinquemaculatus* falls in Nesting Pattern V: the nest is shallow, telecoprid, and compound; male and female cooperate; and parental care is conducted (Halfpter and Edmonds 1982) (Fig. 1C, E, F). The brood balls have the egg chamber located in a superior protuberance that may be spherical or conical. This egg chamber is isolated from the provisions by a partition of soil material (Fig. 2). Similar structures of brood balls have been already described for the necrophagous *C. cyanellus cyanellus* (Halfpter *et al.* 1983; Favila 2001; Hernández-Martínez and Martínez 2003) and *Canthon bispinus* Germar (Judulien 1899; Fabre 1899; Halfpter and Matthews 1966). The complete isolation of the egg chamber from the provision chamber by a partition of soil material is also present in necrophagous species of *Coprophanaeus* Olsoufieff (Fabre 1899; Judulien 1899; Barattini and Sáenz 1953; Cantil *et al.* 2012) and preserved in Pleistocene brood balls from Argentina named as *Coprinisphaera akatanka* Cantil *et al.* (2013). This isolation was proposed as a mechanism to avoid contact between the egg and possible cleptoparasites, parasitoids, and fungi brought with the provisions (Laza 2006; Sánchez 2009). The isolation would be maximum in the case of brood balls constructed by necrophagous species (Cantil *et al.* 2012, 2013).

Another two characters, also present in *C. quinquemaculatus*, are recurrent in necrophagous balls. One character is the lack of an organic

lining coating the egg chamber (Fig. 3A). This organic lining is typical in brood balls of most coprophagous species (Halffter and Matthews 1966; Halffter and Edmonds 1982). In contrast, the lack of an organic lining seems to be typical of necrophagous species since it was also recorded in brood balls of *Coprophanaeus milon* Blanchard (Fabre 1899), *Coprophanaeus cyanescens* (Olsoufieff) (Cantil *et al.* 2012), and in other species of *Canthon* (L. F. Cantil, personal observation). According to Fabre (1899) and Halffter and Matthews (1966), the organic lining is regurgitated by the female and constitutes the first food for the newly hatched larvae. The second character is the ejection of small fecal pellets that remain attached to the external surface of the brood ball (Fig. 2B). This behavior was also mentioned for the necrophagous *C. milon*, *C. cyanellus cyanellus*, and *Deltochilum gibbosum* (F.) (Howden and Richter 1952; Barattini and Sáenz 1953; Favila 2001). In contrast, larvae of coprophagous beetles deposit fecal pellets in the internal surface of the brood ball and ingest and excrete them several times, increasing the bacterial content in the gut's fermentation chamber every time and improving the nutritional quality of the dung (Scholtz *et al.* 2009).

In combination, the complete isolation of the egg from the provision chamber, the lack of an organic lining to nourish the newly hatched larvae, and the ejection of larval fecal pellets outside the ball seem to be a set of adaptive characters of the necrophagous species to their food. Is it possible that carrion contains some harmful elements for eggs or newly hatched larvae? Is the ejection of larval feces outside the ball reflecting that provisions cannot be re-ingested several times or, on the contrary, that provisions are more efficiently exploited? The acquisition of necrophagous habits in South America was prompted by the Pleistocene extinction of dung providers (Halffter 1959, 1991; Halffter and Matthews 1966; Cantil *et al.* 2013). Fresh carrion is considered a higher quality food than dung because of its content of proteins and nitrogen, which results in faster larval development (Scholtz *et al.* 2009). Are the adaptive characters shown by brood balls of necrophagous species reflecting the benefit of a higher quality food or the cost of a behavioral shift forced by dung scarcity?

At the roof of the egg chamber, there is an aeration conduit which ends in a plug of loose soil that acts as a filter (Fig. 2F, G). This aeration filter composed of loose soil was already described for other necrophagous species, such as *C. cyanellus cyanellus* (Halffter *et al.* 1983) and *C. milon* (Fabre 1899; Barattini and Sáenz 1953). In contrast, the aeration filters in brood balls of coprophagous Scarabaeinae are typically made with dung fibers (Halffter and

Edmonds 1982; Cabrera Walsh and Gandolfo 1996; Sánchez and Genise 2008; Sánchez *et al.* 2012).

The nesting chambers studied herein showed brood balls in different stages of construction (Figs. 1E-F, 2). This scenario yields clues to how *C. quinque maculatus* females might construct their brood balls. The female adds a covering of soil to the rolled ball and, in one pole, makes a crater-like depression in the soil lining (Fig. 2A). This depression would be the base of the egg chamber. Then, the female would extend upwards the rim of the crater with soil material, constructing a spherical to conical protuberance, laying the egg before completing the egg chamber, and constructing the aeration conduit and the filter. This construction behavior was already mentioned for several Scarabaeinae species such as *Copris armatus* Harold, *Copris hispanus* L., *Homocopris torulosus* (Eschscholtz), *Gymnopleurus geoffroyi* (Fuessly), *Sisyphus schaefferi* L., *Phanaeus palliatus* Sturm, *Megathopa villosa* Eschscholtz, *Sulcophanaeus carnifex* L., *S. sacer*, and *K. platynotus* (Fabre 1897; Joseph 1929; Prasse 1957; Halffter and Matthews 1966; Ovalle and Solervicens 1980; Klemperer 1983; Anduaga *et al.* 1987; Sato and Imamori 1987).

Two micromorphological characters of brood balls of *C. quinque maculatus* deserve some comments. The wall is composed of soil material without any other materials, but the interior zone is more stained with iron oxide (Fig. 3), which is a common character in insect trace fossils and interpreted as a higher concentration of original organic matter (Genise *et al.* 2002). The other character is the high percentage of soil material in the provisions, which reaches up to 70% (Fig. 3) and is reflected in the aspect of the larval feces (Fig. 2B). This soil material might reduce the efficiency of provisions and, on the other hand, increase the potential of preservation of fillings in fossil brood balls.

The characters present in *C. quinque maculatus* brood balls, although not exclusive for balls of necrophagous species, are widespread among them and relatively rare in those of coprophagous species. Further studies are likely to confirm whether or not these characters will aid in the possibility of distinguishing fossil brood balls made from necrophagous beetles from those made by coprophagous ones.

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