

**NESTS AND BROOD BALLS OF *COPROPHANAEUS* (*COPROPHANAEUS*)
CYANESCENS (OLSOUFIEFF, 1924) (COLEOPTERA:
SCARABAEIDAE: SCARABAEINAE)**

L. F. CANTIL, M. V. SÁNCHEZ, L. SARZETTI
CONICET-Museo Argentino de Ciencias Naturales, División Icnología
Av. Ángel Gallardo 470, 1405 Buenos Aires, ARGENTINA
cantil@macn.gov.ar

A. MOLINA
CONICET-Instituto Superior de Entomología, Facultad de Ciencias Naturales
Miguel Lillo 205, 4000 S. M. de Tucumán, ARGENTINA

AND

J. F. GENISE
CONICET-Museo Argentino de Ciencias Naturales, División Icnología
Av. Ángel Gallardo 470, 1405 Buenos Aires, ARGENTINA

ABSTRACT

Twenty nests of *Coprophanaeus* (*Coprophanaeus*) *cyanescens* (Olsoufieff) were studied in the field and described herein for the first time. They are paracoprid, subterranean (simple), and basically L-shaped. Nine pear-shaped brood balls were obtained *in situ*. The brood balls display a protuberance that is separated from the provision chamber by a partition of soil material. However, no constriction between them is externally recognizable. The brood balls exhibit a thick wall composed of soil material. In the upper part of the brood ball, the wall is wide enough to include the complete spherical egg chamber. The egg chamber lacks an organic lining. Between the top of the protuberance and the egg chamber, there is an aeration conduit connecting the egg chamber to the exterior via a filter of loose soil. The provision chambers are filled with carnivore/omnivore feces or carrion, mainly pig fat, which originated from remains discarded from a nearby slaughterhouse. The brood balls are surrounded and penetrated by roots. The wall shows traces (pits) produced by the appendages of the brood ball constructor and borings and fecal pellets attributed to earthworms.

Key Words: behavior, dung beetles, necrophagy, nest structure, brood ball morphology

Species of *Coprophanaeus* Olsoufieff, 1924 use carrion and, in some cases, carnivore/omnivore feces as the provision required for the development of the larva, which occurs inside brood balls (Halfpeter and Edmonds 1982; Edmonds and Zidek 2010). There is scant literature on the behavior and larval development of the species of *Coprophanaeus*, and even less is known about their nests and brood balls (Edmonds and Zidek 2010). The detailed descriptions by Fabre (1899) and Judulien (1899) on the nesting behavior and brood balls of *Coprophanaeus* (*Coprophanaeus*) *milon* (Blanchard), later enriched by the observations of Barattini and Sáenz (1953) and Morelli and González Vainer (1990), are the major contributions to this subject. Some data and photographs have been published on brood balls of *Coprophanaeus* (*Coprophanaeus*) *cyanescens* (Olsoufieff) as *Phanaeus jasius* Oliver, *Coprophanaeus* (*Metallophanaeus*) *saphirinus* (Sturm), and *Coprophanaeus* (*Megaphanaeus*) *bonariensis* (Gory) (Frenguelli 1938; Pessôa and Lane

1941; Sauer 1955; Edmonds 1967; Edmonds and Zidek 2010; Cantil *et al.* 2012). No detailed descriptions on the structure of the nests of *Coprophanaeus* species have been published so far.

Field observations on the structure of the nests of *C. cyanescens* and new aspects on the structure of their brood balls are described herein.

MATERIAL AND METHODS

Twenty nests and nine brood balls were found in January 2012 at Paraje La Florida, near Rosario de Lerma, Salta province, Argentina (S 25°00'50", W 65°33'32"). The study area was located near a pig slaughterhouse. The entrances of the nests were associated with pieces of pig remains, feces from dogs that fed on wastes, and corpses of small vertebrates (Fig. 1A). The nests ($n = 20$) were studied *in situ*, and some of them ($n = 7$) consisted of nesting chambers that contained brood balls. Only two studied brood balls, probably old and

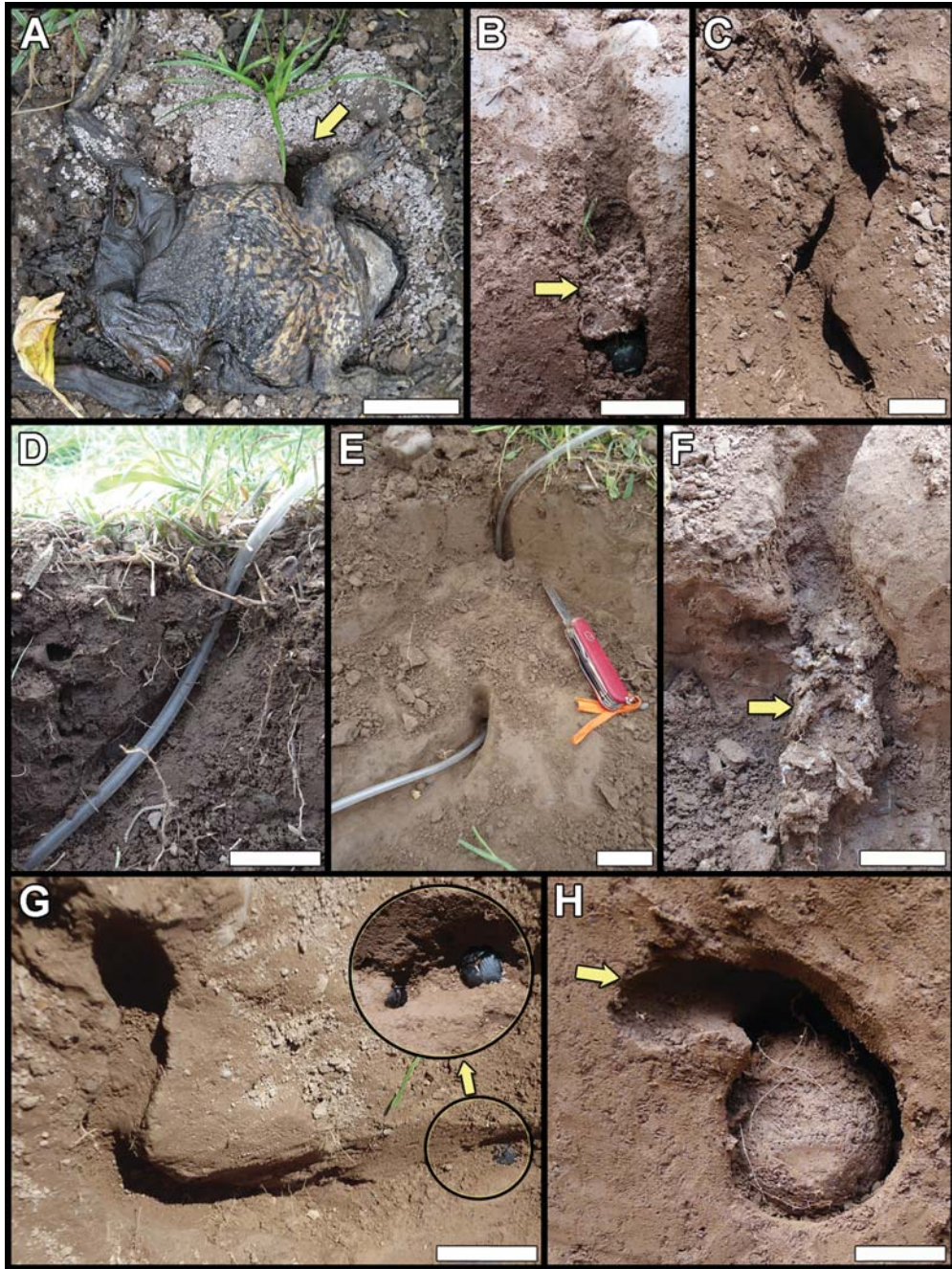


Fig. 1. Nests of *Coprophanaeus cyanescens*. A) Entrance of the nests (arrow) associated with the corpse of a toad, scale bar = 5 cm, B) Straight, vertical tunnel containing a male and pig fat at the end (arrow), scale bar = 2.5 cm, C) Sinuous, vertical tunnel, scale bar = 2.5 cm, D) Oblique tunnel, scale bar = 5 cm, E) L-shaped tunnel, scale bar = 5 cm, F) Bifurcation with one branch filled with a mixture of fat and soil material (arrow), scale bar = 2.5 cm, G) Nest with a male-female pair (detail) at the end of the tunnel, scale bar = 5 cm, H) Isolated nesting chamber containing a brood ball in a vertical position; note that the chamber is connected on top to an empty fragment of tunnel (arrow), scale bar = 2.5 cm.

poorly preserved, lacked any remains of nesting chambers. The height of the pear-shaped brood balls was measured along the vertical axis. The diameter was measured perpendicular to the height. A longitudinal section was made to determine the internal structure and measure the wall thickness and the size of the egg chamber. Data presented below are expressed as mean values \pm standard deviations.

The collected brood balls were deposited in the División Icnología of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina.

RESULTS

Nest Structure. The nests reflected different stages of construction, from those in their initial stages (A) to finished ones (D). Five stage A nests consisted of a vertical shaft, 2.2–2.5 cm wide, which reached 13–28 cm in depth. In two nests, the tunnel was straight, and one of these nests held a male and carrion provision, mainly fat, at the end of the tunnel (Fig. 1B). In two nests, the vertical tunnel was sinuous and 14–28 cm deep (Fig. 1C). One of these nests showed a soil plug 2 cm long occluding the tunnel. In the remaining nest, the tunnel was oblique and 13 cm deep (Fig. 1D). Three stage B nests displayed a vertical shaft, 2.0–2.6 cm wide, which within 10–23 cm deep ended in a curved section. One of these nests had fat packed into the end of the tunnel.

Five stage C nests showed L-shaped tunnels (Fig. 1E, G) with three distinguishable sections: 1) a vertical shaft, 2.0–2.6 cm wide and 6.5–25 cm deep, which in one case had a plug of soil 3 cm long; 2) a curved section, which in one nest exhibited a bifurcation with one branch filled with a fat-soil mixture (Fig. 1F, arrow); and 3) a horizontal section 8–20 cm long that was located at 12–30 cm depth. One of these nests was empty at the end of the tunnel; another one contained a male-female couple (Fig. 1G). The remaining three nests had fat at the end of the tunnel, and two of them contained a plug of soil located before the provisions.

The most advanced stage of construction (stage D) was represented by seven nests, each one containing one pear-shaped brood ball vertically oriented (Fig. 1H). The nests consisted of prolate spheroid nesting chambers, 5–6 cm in diameter and 6–7 cm in height, which were found deeper (30–49 cm) than the incomplete nests. Four of the seven nesting chambers were connected on top to an unfilled and short tunnel about 2 cm in diameter (Fig. 1H, arrow). No other tunnels were connected to the chambers. Six of the seven nesting chambers were found within an area of 45 cm in diameter. The remaining one was found about 5 m from the others.

Brood Ball Structure. The pear-shaped brood balls ($n = 9$) are 46.8 ± 1.6 mm in diameter and 52.2 ± 1.8 mm in height (Fig. 2A, B). The spherical provision core, 25.7 ± 2 mm in diameter, consists of carnivore/omnivore feces or carrion, mainly fat, and remains of soil material (Fig. 2C, D). The thick wall, which is composed of soil material, is slightly thinner along the sides of the brood balls (7.5–11.7 mm) than in the base and the upper part of them (10.7–15.6 mm) (Fig. 2C, D, black arrows). In the upper part, the wall is wide enough to include the complete spherical egg chamber, which is isolated from the provisions (Fig. 2C, arrow). The egg chambers are 11.7 ± 1.2 mm in diameter ($n = 7$), their inner surface is ridged and lacks an organic lining. In six cases, the brood balls preserved the exuviae from the larvae that excavated the base of the egg chamber and moved to the provision chamber (Fig. 2D, yellow arrow). At the roof of the egg chambers, there is a narrow, cylindrical conduit (3 mm in diameter) that connects to the exterior and is plugged on top with loose soil (Fig. 2E–F, arrows).

The walls of the brood balls are surrounded and penetrated by roots (Fig. 2G, H). Most of the brood balls show pits produced by the appendages of the brood ball constructor on the external surface of the wall (Fig. 2B). Some brood balls have small circular borings across the wall, 2.5–3.5 mm in diameter (Fig. 2A, I, arrows). These brood balls also have fecal pellets attached to the external surface of the wall (Fig. 2J). One of them (Fig. 2I, J) was located inside a nesting chamber that housed identical pellets and an earthworm (Fig. 2K).

DISCUSSION

Nests of *C. cyanescens* are paracoprid, subterranean (simple), and the structure of the tunnels is basically L-shaped. Edmonds (1967) was the first to briefly describe the brood balls of *C. cyanescens*, which he identified as those of *P. jasius*. He described them as pear-shaped brood balls with a very thick wall and carrion provisions. He also mentioned that the brood balls of *C. saphirinus* were similar to those of *C. cyanescens*. Since pear-shaped brood balls were also found for *C. milon* (Fabre 1899; Judulien 1899, fig. 9), it is reasonable to assume that pear-shaped brood balls are a common morphology for the genus.

The pear-shaped brood balls of *C. cyanescens* result from a spherical provision chamber and a protuberance, which contains the egg chamber. No deep neck or constriction between them is recognizable. The provision chamber contains carrion or carnivore/omnivore feces, mixed with soil. The egg chamber is completely included inside the

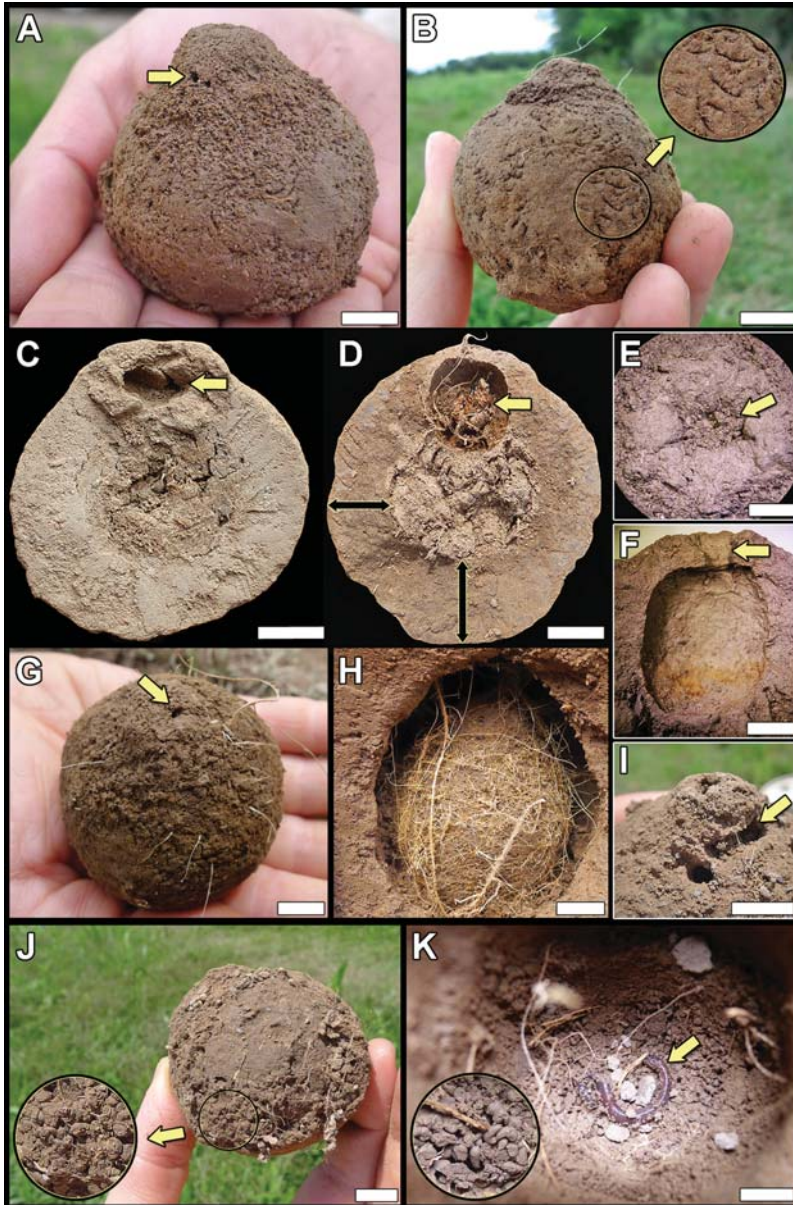


Fig. 2. Brood balls of *Coprophanaeus cyanescens*. A) External view of a pear-shaped brood ball; note the borings on the wall of the brood ball (arrow), scale bar = 1 cm, B) Pits produced by the appendages of the brood ball constructor (detail) on the external surface of the wall, scale bar = 1 cm, C) Internal view of a brood ball showing the egg chamber (arrow) completely included in the thick wall, scale bar = 1 cm, D) Internal view of a brood ball showing the base of the egg chamber excavated by the larva; note the differences in wall thickness in that area (black arrows) and the exuvia from the larva (yellow arrow), scale bar = 1 cm, E) Plug of loose soil (arrow) seen from the top of a brood ball, scale bar = 3 mm, F) Aeration conduit (arrow) in longitudinal section; the plug of loose soil is not preserved in this case, scale bar = 5 mm, G) Opening of the aeration conduit (arrow) seen from the top of a brood ball; note the roots surrounding and penetrating the wall of a brood ball that is located inside a nesting chamber, scale bar = 1 cm, H) Roots surrounding and penetrating the wall of a brood ball that is located inside a nesting chamber, scale bar = 1 cm, I) Borings in the wall of a brood ball (arrow), scale bar = 1 cm, J) Pellets from earthworms (detail) on the external surface of a brood ball, scale bar = 1 cm, K) Nesting chamber housing an earthworm (arrow) and its pellets (detail), scale bar = 1 cm.

thick wall, above the provision chamber and separated from it by a partition of soil material. Neonate larvae must break through the partition to access the provision (Fabre 1899; Halffter and Matthews 1966). This isolation of the egg chamber from the provision was mentioned for *C. cyanescens* by Edmonds (1967) and described for *C. milon* by Fabre (1899), Frenguelli (1938), and Barattini and Sáenz (1953). The fossil brood balls included in the ichnospecies *Coprinisphaera tonnii* Laza (Cantil *et al.* 2013) show a similar pear-shaped morphology and the egg chamber located inside the wall. Accordingly, this ichnospecies could be attributable to a necrophagous species.

Between the top of the protuberance and the egg chamber there is an aeration conduit (Fig. 2F). This conduit connects the egg to the exterior through a plug of loose soil, which acts like a filter. Similar aeration structures were described for *C. milon* and some necrophagous species of *Canthon* Hoffmannsegg (Fabre 1899; Judulien 1899; Frenguelli 1938; Cantil *et al.* 2014a, b). Together with the lack of an organic lining in the egg chamber, these characters are considered typical of Scarabaeinae that provision their brood balls with carrion (Cantil *et al.* 2014a, b).

The size of the brood balls described herein (46.8 ± 1.6 mm in diameter and 52.2 ± 1.8 mm in height) is smaller than those described by Edmonds (1967) for *C. cyanescens* (about 60 mm in diameter and 80 mm in height). However, these sizes fall within the range from 38 mm to 65 mm in diameter reported for the brood balls of *C. milon* (Fabre 1899; Judulien 1899; Frenguelli 1938; Barattini and Sáenz 1953; Morelli and González Vainer 1990).

Barattini and Sáenz (1953) reported that the full-grown larva of *C. milon* obliterates the protuberance and modifies the brood ball until it shows lumps on the outside and an alveolar structure connected to a thin layer of feces (laminar structure) on the inside (Barattini and Sáenz 1953; Morelli and González Vainer 1990). The external lumps may be interpreted as fecal pellets from the larvae in advanced stages of development, according to observations on other species of necrophagous dung beetles (Favila 2001; Cantil *et al.* 2014a, b). The interior alveolar and laminar structures are interpreted as the "roof" and the wall of the pupation chamber, respectively (Sánchez *et al.* 2010). Edmonds (1967), who followed the development of *C. cyanescens* from larva to pupa, reported the presence of the laminar structure but remarked that no significant modifications of the apical area of the brood ball, such as the lumps and the alveolar structures, were observed. In addition, the brood balls of *C. cyanescens* illustrated by Pessôa and Lane

(1941, fig. B) show emergence holes and lack structures like those described by Barattini and Sáenz (1953). In our study, no modifications of the shape of the brood ball of *C. cyanescens* were observed, probably because of the absence of full-grown larvae.

The wall shows traces (pits) produced by the appendages of the brood ball constructor on their external surface, particularly from their tarsi and tibiae, which are also mentioned for *C. milon* (Fabre 1899; Barattini and Sáenz 1953; Morelli and González Vainer 1990). The brood ball shows roots surrounding and penetrating the wall, which continue through the nesting chamber and the soil. Borings and fecal pellets in the wall may be attributed to earthworms, which were mentioned as cleptoparasites of brood balls (Halffter *et al.* 1996; Huerta and Halffter 2000; Sánchez and Genise 2009). In our study, earthworms were found inside one nesting chamber.

ACKNOWLEDGMENTS

We thank Fernando Z. Vaz-de-Mello for confirming the identification of the dung beetles and Mr. Luis Torino from Frigorífico La Florida for allowing us to carry out the study on his property. This research was supported by grants from FONCYT-PICT 07/1972 and 12/022 to Jorge F. Genise, and FONCYT-PICT 10/2463 and 13/2025 to M. Victoria Sánchez.

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(Received 4 September 2014; accepted 21 December 2014.
Publication date 18 March 2015.)