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Nests and Brood Balls of Two South American Species of *Sulcophanaeus* Olsoufieff, 1924 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini)

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Abstract

Nests of *Sulcophanaeus menelas* (Laporte) and *Sulcophanaeus imperator* (Chevrolat) are composed of single or branched, vertical to horizontal tunnels, empty or partially filled with dung, and at most one nesting chamber bearing a brood ball. Horizontal, branched nests were found made only by *S. imperator*, whereas branched nests of *S. menelas* were vertical. Brood balls of *S. menelas* are drop-shaped with a conical upper pole and a plug of dung fibers. The egg chamber, inside the provisions, is lined with organic matter, probably adult feces. Brood balls of *S. imperator* are pear-shaped, showing a protuberance composed of soil material, which contains the upper half of the egg chamber. The lower half is located in the provisions. The egg chamber has an upper pore and its wall, relatively thick, is made of soil material and dung fibers, like the external wall. These observations are analyzed considering previous reports, behavioral plasticity, adaptations to different environmental conditions, and phylogeny. Brood balls of *S. imperator* are similar to the ichnofossil *Coprinisphaera kheprii* Laza from the Cenozoic of Argentina.

Key Words: *Sulcophanaeus menelas*, *Sulcophanaeus imperator*, dung beetles, behavior, micromorphology

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Several aspects of the nesting behavior, nest architecture, and brood balls of *Sulcophanaeus menelas* (Laporte) and *Sulcophanaeus imperator* (Chevrolat) have been published by Judulien (1899), Cabrera Walsh and Gandolfo (1996), and Morelli *et al.* (1996). Nevertheless, some of these articles either are in conflict with each other, or lack details of brood ball structure. The understanding of behavior and brood ball construction of dung beetles is critical to phylogenetic analysis of this group, and also for interpreting fossil brood balls as physical evidence of the evolution of dung beetle behavior (Sánchez *et al.* 2010a).

Nests and macro- and micromorphological characters of brood balls of *S. menelas* and *S. imperator* are described herein. Micromorphological descriptions provide new characters to interpret behavioral traits difficult to observe (Sánchez and Genise 2008), which may be useful for phylogenetic analyses (Sánchez *et al.* 2010a). Differences between the brood balls of *S. menelas* and *S. imperator* are analyzed considering previous reports, behavioral plasticity, adaptations to different environmental conditions, and phylogeny.

Material and Methods

Nests and brood balls of *S. menelas* and *S. imperator* were collected and studied at five Argentine localities on various dates from December 2006 to April 2008. All nests were measured *in situ* and recorded by photographs and videos. Collected parts of nests and brood balls, along with dung beetles, were deposited in the Colección de Icnología of the Museo Argentino de Ciencias Naturales. Those of *S. menelas* (n = 18) were studied at Navarro (35°6′27.32″ S, 59°25′46.29″ W), Buenos Aires province, in an establishment with cows and horses, and where the soil was uniformly covered by grasses. Fifteen nests contained adults, whereas the three nests without adults contained the three collected brood balls. These latter three nests are attributed to this species because nests and balls of *Ontherus sulcator* (F.), the other only ball-constructing dung beetle in this area, are completely different (Sánchez and Genise 2008). Nests of *S. imperator* (n = 14), 13 containing only adults and one containing only a brood ball, were studied at three localities in La Rioja province. Six of the 14 nests were found at Chuquis, adjacent to provincial Route 1 (28°53′32.4″ S, 66°56′50.4″ W), in a patch of shrubland with scattered trees, where the soil was poorly covered by sparse grasses and herbs. The dung came from cows and horses. From one of these nests was collected one brood ball, whereas a second brood ball was collected in the soil where no nest could be recognized. The former was attributed to *S. imperator* because the full-grown larva, reared in the laboratory, was identified to genus level using Edmonds and Halffter (1978) and because there is no other species of the genus known in this locality. In addition, a tunnel with an adult was located near the nesting chamber in the soil. The other brood ball contained a non-emerged female. Five nests were studied near Anillaco, adjacent a road at La Quebrada (28°48′8.25″ S, 66°58′21.31″ W) in an environment with more trees and few cows. No brood balls were found in these nests. Three nests of *S. imperator*, containing no balls, were studied at Vera Cruz (28°44′47.77″ S, 66°56′44.96″ W). The latter locality had environmental conditions similar to La Quebrada.

All brood balls collected were carried to the laboratory, where longitudinal sections, along the long axis, were made to describe the internal structure. One half of each ball was used to make thin sections to analyze micromorphology. Thin sections were prepared with undisturbed, vacuumed samples impregnated with stained polyester resin (Murphy 1986), and were observed under a Nikon HFX-DX Optiphot-pol petrographic microscope. The micromorphological features were observed in transmitted plain light, whereas the iso- and anisotropism and the birefringence fabrics of the fine material were observed in polarized light. The terminology and micromorphological descriptions follow the nomenclature previously utilized by Sánchez and Genise (2008) and Sánchez *et al.* (2010a). The brood balls had two different measurable axes because they were not completely spherical. Descriptions of structure are based on the most complete brood balls. Fragmentary specimens were used to complete the descriptions. Pupation chambers of the two species were described in detail by Sánchez *et al.* (2010a).

Results

Nest Structure. The 18 studied nests of *S. menelas* were found beneath nine dung pads, five of cow dung (1–3 nests per pad) and four of horse dung (1–4 nests per pad). Most of the nests were composed of tunnels showing three general morphologies (Fig. 1A–C). The first of these comprised curved tunnels composed of two sections and partly filled with dung (n = 7) (Fig. 1A). The first section, on average 7.5 cm long (n = 3), vertical and straight, had an open entrance, on average 1.3 cm in diameter (n = 3), whereas the second section was shorter, on average 5 cm long (n = 3), also straight, and at 45° with the vertical axis. This type of tunnel was on average 15 cm deep, and typically had an adult located in or on the provisioned dung. The second tunnel morphological type was straight and almost vertical (n = 4) (Fig. 1B), with a 1.5 cm diameter entrance (n = 2), on average 15 cm long (n = 3), which widens at the end to 2.5 cm. These tunnels were entirely filled with dung, leaving a chamber 3–4 cm long where an active female was located (n = 3). The third tunnel morphological type was a forked tunnel composed of two branches, each one similar to the second tunnel type (n = 3) (Fig. 1C). One third of each branch was occupied by a meniscate provision of dung. In two of the three cases were found a female lying on top of the provision of one branch. Two nesting chambers (Fig. 1D, E) were found in these nests, one of which was spheroidal, 3.5 cm long and 2.8 cm high, and located 2–3 cm from the surface (Fig. 1D). The brood ball was located with the plug parallel to the soil surface. This chamber was laterally connected to a horizontal, empty, short, and angled tunnel. The other chamber, located 29 cm from the soil surface, was spherical (4 cm in diameter), closed, and the brood ball was located with the plug perpendicular to the soil surface, slightly inclined from the vertical axis (Fig. 1E).

The six best preserved nests of *S. imperator*, studied at Chuquis, were found beneath cow dung pads. Four of them were composed only of tunnels, either single or interconnected (Fig. 1F, G), empty or partially filled with dung, while the remaining two, with single tunnels, also had the nesting chamber. The most complex nests, described herein in detail, were composed of interconnected tunnels or contain a nesting chamber. One of them was T-shaped, horizontal, and 3–5 cm deep (Fig. 1F). The short branches were straight, 2.5 cm wide and 26 cm long, with the central part bent downwards, where they were connected to the long branch, which was sinuous, 2.7 cm wide and 56 cm long, and ended 20 cm below the surface. The distal, deeper part of this tunnel was filled with 10 cm of dung. A third tunnel, 3 cm wide and 28 cm long, was located at the same depth and 5 cm from the long branch of the T-shaped tunnel, parallel to it and showing no connection. This tunnel had remains of dung at the bottom

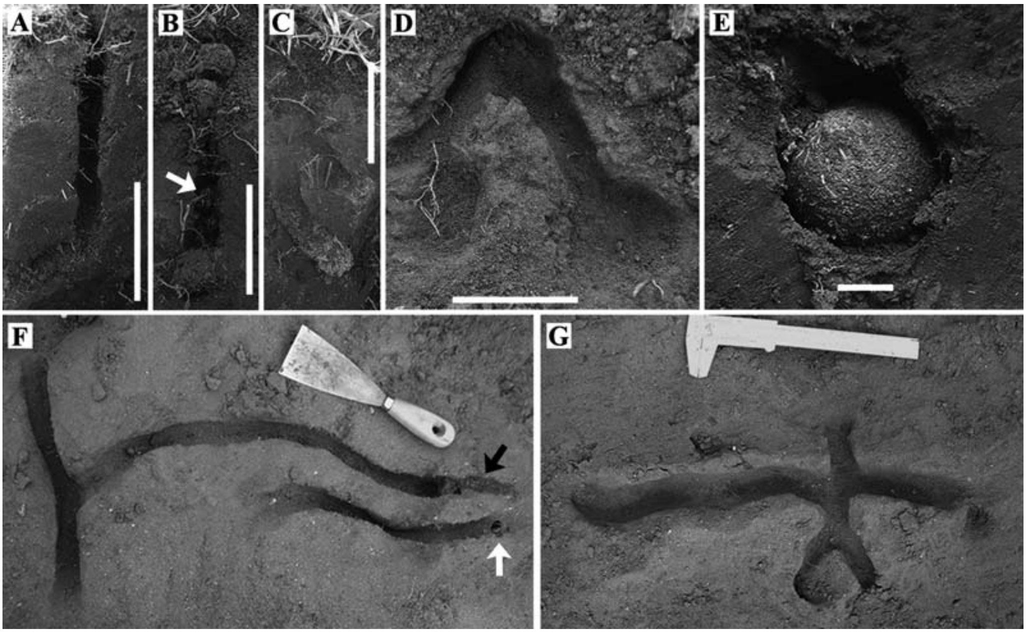

Fig. 1. Nests of *Sulcophanaeus menelas* and *Sulcophanaeus imperator*. A–C) Three morphologies of *S. menelas* nests: L-shaped tunnel partially filled with dung (A), straight and almost vertical tunnel containing a female (white arrow) (B), forked tunnel composed of two inclined branches provisioned with meniscate dung (C) (scale bars = 5 cm), D–E) Nesting chambers of *S. menelas*: shallow chamber laterally connected to a horizontal, angled tunnel (scale bar = 5 cm) (D) and deeper, closed chamber containing a brood ball located with the plug slightly inclined from the vertical axis (scale bar = 1 cm) (E), F–G) Branched nests of *S. imperator* composed of horizontal and shallow tunnels: T-shaped tunnel showing dung (black arrow) provisioned in the long branch and a female (white arrow) in a third parallel burrow (spatula = 25 cm) (F) and four interconnected tunnels, one of them Y-shaped (calipers = 21 cm) (G).

and a short branching tunnel also with dung and a female (Fig. 1F).

The other complex nest of *S. imperator* was composed of four horizontal and shallow tunnels (Fig. 1G). The main, long tunnel was relatively straight, 2.5–3.0 cm wide and 36 cm long, containing a female located inside 20 cm of dung arranged in several menisci 1 cm wide. At the opposite end, the tunnel also contained 3 cm of dung. Closer to this end, at 2/3 of its total length, this tunnel had two short, opposite, perpendicular tunnels. One of them was straight, 7 cm long, mostly filled with dung except for the bottom, where a male was located. The opposite tunnel was branched. The shorter branch, 8 cm long, had the entrance blocked by dry and shredded dung, whereas the longer branch, 12 cm long, was empty. These three tunnels were inclined downwards. The nest containing a brood ball was composed of a two-section tunnel. The first section, open to the soil surface, was vertical and 12 cm deep. The second section, 24 cm long and horizontal, ended laterally in the upper half of a spherical nesting chamber 9 cm in diameter. It contained a pear-shaped brood ball with the protuberance slightly inclined, oriented towards the soil surface. Beneath the chamber floor, 4 cm deeper and without connection to it, was found a short, inclined tunnel, partially filled with dung and containing a male. The remaining eight simpler nests, from all three localities, were composed of a single shallow, curved, slightly inclined tunnel, and usually contained an adult or a couple on or inside the provisioned dung.

Brood Ball Structure. Brood balls of *S. menelas* (n = 3) were drop-shaped (Fig. 2A) with a conical upper pole composed of interbraided dung fibers partially covered by soil material. Internally, this cone had a relatively cylindrical conduit, plugged with longitudinally oriented dung fibers, which connects the egg chamber with the exterior (Fig. 2B, C, G). The length of these balls ranged from 2.4 to 3.5 cm (n = 5), whereas the equatorial diameter ranged from 2.5 to 3.2 cm (n = 3). The wall thickness ranged from 2 to 4 mm (n = 2). The egg chamber was spherical, 3–6 mm in diameter, and located at the top of the dung provisions (n = 2). In the fresh brood ball, the egg chamber was lined with a material that appeared moist (Fig. 2C, G). A pale yellow

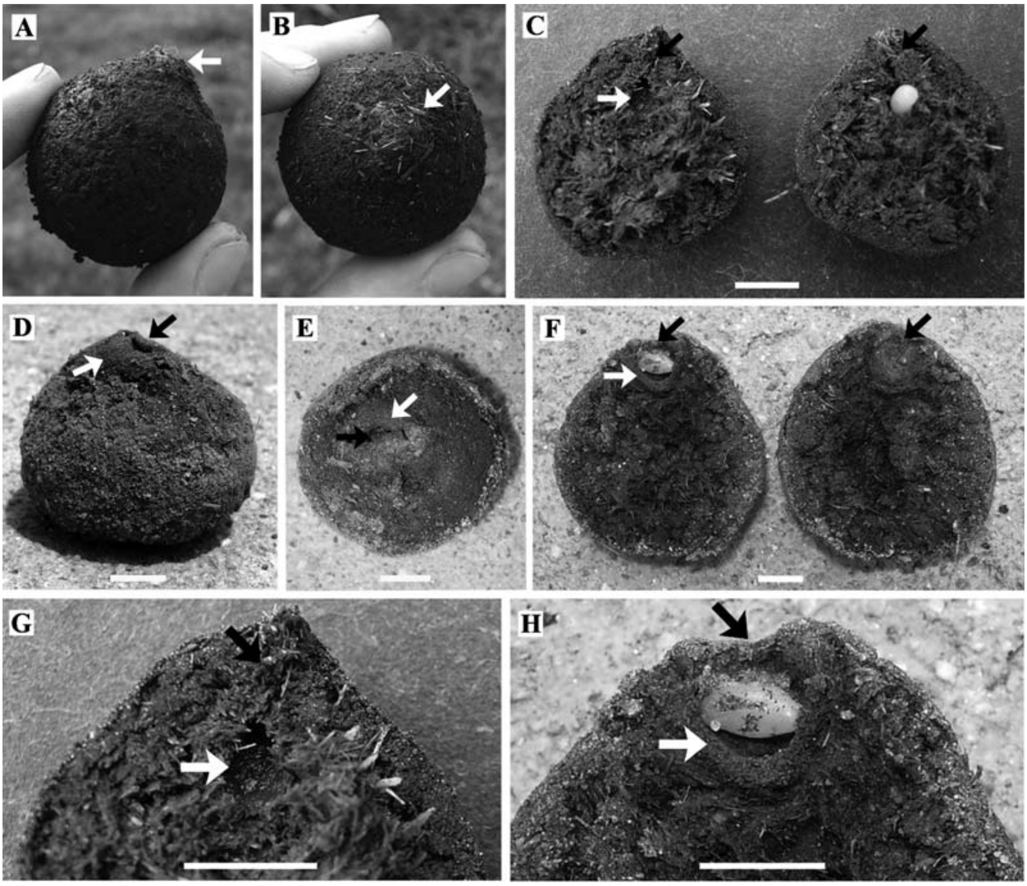

Fig. 2. Brood balls of *Sulcophanaeus menelas* and *Sulcophanaeus imperator*. A–C) Drop-shaped brood ball of *S. menelas* showing an upper cone composed of dung fibers partially covered by soil material (A–B, white arrows) and cross-section showing the conduit plugged with dung fibers (black arrows), the egg chamber (left, white arrow), and an egg (right) (C), D–F) Pear-shaped brood ball of *S. imperator* showing a distinct upper protuberance (D, E, white arrows) with a central open pore (D–F, black arrows) and cross-section showing the egg chamber (white arrow) with an egg and the upper pore (black arrow) (F), G) Egg chamber of *S. menelas* showing the presence of a moist, thin lining (white arrow) and the conduit plugged with parallel dung fibers (black arrow), H) Egg and egg chamber of *S. imperator* showing the presence of a thick wall mostly composed of soil material (white arrow) and an upper pore (black arrow). Scale bars = 1 cm.

egg, 6 mm long and 2–3 mm wide (n = 1), vertically orientated, occupied almost the entire chamber (Fig. 2C). The brood ball provision, which apparently showed no particular arrangement, was mostly composed of dung fibers with a minor content of scattered soil material (Fig. 2C).

Brood balls of *S. imperator* (n = 2) were pear-shaped (Fig. 2D), with a distinct upper protuberance of soil material, with a central open pore connected to the egg chamber (Fig. 2E, F, H). The egg, in its chamber, could be seen through this pore from the outside. The length of these balls ranged from 2.9 to 4.5 cm (n = 2), whereas the equatorial diameter ranged from 2.9 to 4.9 cm (n = 2). The wall thickness differed along the brood ball. Minimum values at the lower pole ranged from 1 to 2 mm (n = 2), whereas the maximum values near the egg chamber ranged from 2.7 mm to 4.5 mm (n = 2). At the upper pole of the brood ball was a protuberance (Fig. 2D, E) 15.4 mm wide at the base, 11.3 mm at the top, and 5.2 mm high (n = 2). The aeration pore was 4.4 mm in diameter (n = 2). The egg chamber was spherical, 1 cm in diameter (n = 1), with a discrete wall 1.5 mm thick, similar to the external wall (Fig. 2F, H). The egg chamber was partly located in the protuberance with its lower half in the provisioned dung (Fig. 2H). A pale yellow egg, 9 mm long and 3.5 mm wide (n = 1) was horizontally oriented inside the chamber. The brood ball provision, which apparently showed no particular arrangement, was mostly composed of dung fibers and devoid of soil matter (Fig. 2F).

Brood Ball Micromorphology. The wall of brood balls made by *S. menelas* was mostly composed of soil material and scarce birefringent dung fibers (Fig. 3A). Its microstructure was mostly massive, with 10% porosity. The coarse fraction represented 45–50% of the wall, and was composed of mineral grains from silt to fine sand-sized quartz, plagioclase, K-feldspar, lithic fragments, scarce volcanic glass shards, and dung fibers. The fine fraction was composed of amorphous organic matter, brown to dark brown, and clay patches. Between the wall and the infilling, there was an intermediate zone with 15% porosity that was composed of elongated (200 μm - 1 mm), birefringent dung fibers, which were orientated parallel to the wall, and subordinated minerals (Fig. 3A). Mineral fraction of this zone was similar in composition and grain size to the wall. The more central part of the provision was mostly composed of dung fibers (90%) with 10% amorphous, brown, organic matter and scarce isolated mineral grains. Most of the amorphous organic matter was covering dung fibers. The central part of the provision was roughly disposed in concave, upward, crescent-shaped, layers, which can be distinguished by sets of long, parallel dung fibers. The uppermost darker layer, 400–600 μm thick, had only short, parallel dung fibers. The concavity of this layer resulted in an almost spherical

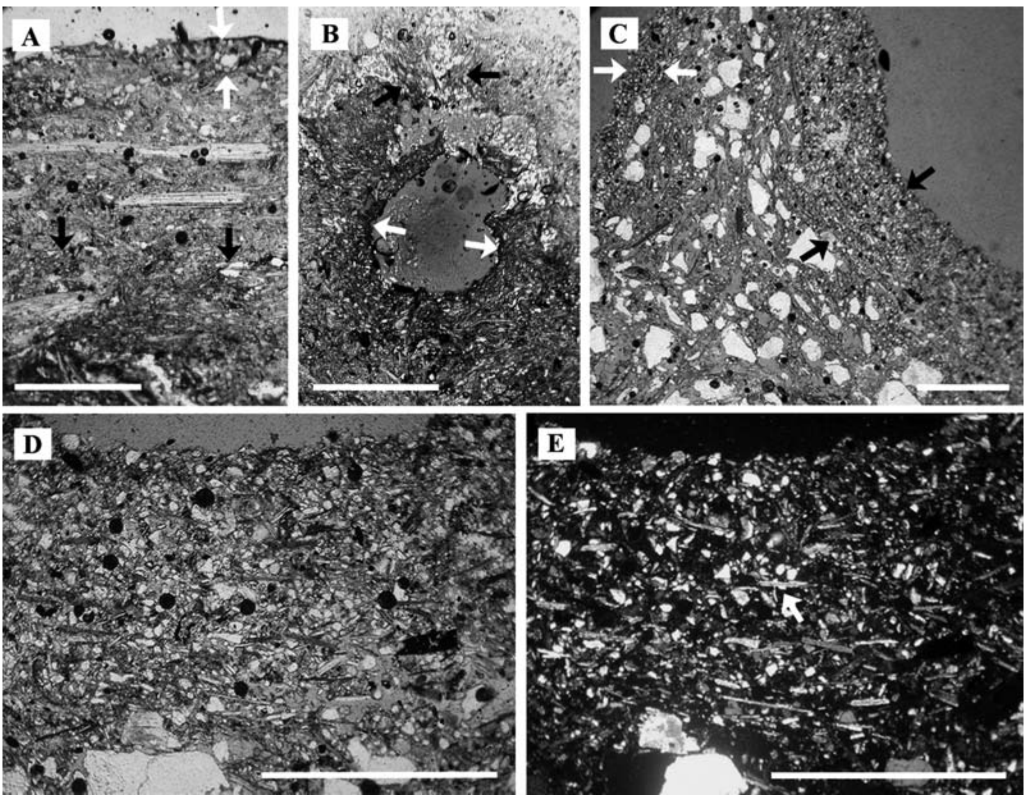

Fig. 3. Micromorphology of brood balls made by *Sulcophanaeus menelas* and *Sulcophanaeus imperator*. A) Brood ball of *S. menelas* showing the wall (between white arrows) mostly composed of soil material and scarce dung fibers, the intermediate zone composed of elongated dung fibers, which are oriented parallel to the wall, and subordinated minerals, and the central part of the provision (black arrows) (scale bar = 1 mm), B) Spherical egg chamber in the brood ball of *S. menelas* lined by brown, amorphous organic matter (white arrows); the egg chamber roof shows an aeration conduit filled with longitudinal dung fibers (black arrows) (scale bar = 2.5 mm), C) Protuberance on the brrod ball of *S. imperator* showing similarity between external wall (white arrows) and the egg chamber wall (black arrows); note the coarse grains included in the provisioned dung between both walls (scale bar = 1.5 mm), D–E) Detail of the egg chamber wall of *S. imperator* showing parallel alignments of elongated mica grains (D taken with parallel light, E taken with polarized light) (scale bars = 1.5 mm).

egg chamber, which had a lining of brown, amorphous organic matter (Fig. 3B). The lining material was impregnated dung fibers and in some parts formed discrete patches. The egg chamber roof had an aeration conduit filled with dung fibers that were longitudinally orientated (Fig. 3B).

In one brood ball made by *S. imperator*, the wall was mostly composed of soil matter and dung fibers, which were more abundant toward the infilling (Fig. 3C). The microstructure was massive with approximately 5% porosity. The coarse fraction represented 80% of the wall, and was composed of mineral grains from silt to fine sand-sized mica (biotite and muscovite), quartz, plagioclase, and heavy minerals (*e.g*., pyroxene), plus scattered dung fibers. The fine fraction was composed of opaque clay material and amorphous organic matter. The provision was composed of elongated and birefringent dung fibers 120 μm long, amorphous organic matter (40%), and fragments of soil matter and isolated mineral grains (60%) (Fig. 3C). The fine fraction was composed of clay material that mostly covered the mineral grains. Dung fibers and grains of mica close to the egg chamber and brood ball walls showed parallel orientation, but no distinct layers were recognized (Fig. 3C). The egg chamber wall was 1.75 mm thick, with micromorphological characters similar to the brood ball wall (Fig. 3C–E). However, the coarse fraction had fewer dung fibers and the material was arranged in layers that were recognized due to parallel alignments of elongated mica grains (Fig. 3D, E). A second brood ball, containing an unemerged female inside a complete pupation chamber, had only remains of the egg chamber (Sánchez *et al.* 2010a). The egg chamber wall remains, similar to the previous specimen, were composed of soil material.

Discussion

Judulien (1899) was the first to study nests of *S. menelas*, which he described as vertical tunnels, sinuous, 15–50 cm deep, enlarged at the end where a spherical brood ball of 2.5–3 cm in diameter was constructed. At the upper pole, the brood ball has a hemispherical protuberance, 0.5 cm high and composed of dung fibers, which contains a small conical egg chamber.

More recently, Morelli *et al.* (1996) observed in the laboratory and field that the female of *S. menelas* constructs the brood ball at a terminal chamber of a main tunnel, which, in a more advanced stage, may be branched, containing 2 or 3 brood balls, or in other cases, several tunnels may converge to the same chamber, composing a network that may bear other brood balls. Frequently, horizontal tunnels arising from the chamber or the network are also observed. During brood ball construction, the female shapes a dung sphere and covers it with a layer of soil material. In one of the poles, she makes a depression in the soil layer, where she lays an egg. The upper part is covered with a lax mixture of soil and dung fibers, composing a conical egg chamber, resulting in a pear-shaped brood ball.

Cabrera Walsh and Gandolfo (1996) also studied the brood balls of *S. menelas* and *S. imperator*. According to them, the beetles dig a tunnel, where the dung is shaped into a ball. In contrast to the observations of Morelli *et al.* (1996), Cabrera Walsh and Gandolfo (1996) found that the egg chamber is first excavated in the dung ball, and later both the ball and this first depression are covered by a layer of "cement". After laying an egg inside this depression, the roof is completed with "cement", leaving a small hole at the center. Finally, the egg chamber is covered by a conical protuberance of dry dung fibers and "cement". Cabrera Walsh and Gandolfo (1996) defined the "cement" as "fine mud mixed with a creamy secretion, probably feces or chewed soil".

According to the observations in these three studies and data presented herein, the nesting behavior of *S. menelas* and *S. imperator* is Pattern II (Halffter and Edmonds 1982), which is characteristic of the Phanaeini. Our observations also show that nests containing adults contain no brood balls and vice versa, supporting the hypothesis that there is no parental care in species displaying Pattern II nesting behavior (Halffter and Edmonds 1982). Additionally, the nests described herein, composed either by single or interconnected tunnels, are similar to others described previously for both species (Judulien 1899; Morelli *et al.* 1996; Cabrera Walsh and Gandolfo 1996) and also for other species of Phaneini (Halffter and Edmonds 1982).

Judulien (1899) made a quite simple description and illustration of the brood ball of *S. menelas*, but it lacks important details such as the location of the egg chamber in relation to the provision chamber. In any case, his description agrees in general terms with that of later authors. In contrast, descriptions of the brood balls of *S. menelas* by Morelli *et al.* (1996), which lack detailed illustrations, and those of Cabrera Walsh and Gandolfo (1996) of the two species described herein differ in an important trait. Morelli *et al*. (1996) found that the floor of the egg chamber is a depression in the outer layer of soil, whereas Cabrera Walsh and Gandolfo (1996) found that it was excavated in the dung ball and then covered with cement (soil plus feces).

Our observations include macro- and micromorphological characters. The latter are critical to understand the building behavior and origin of the different structures of brood balls. The brood ball wall of the studied specimens of both species is composed of soil material mixed with dung fibers, the coarse fraction reaching up to 80%. This composition contrasts with that found by Morelli *et al.* (1996), who described it as made of soil material, and that of Cabrera Walsh and Gandolfo (1996), who described it as made with a cement composed only of fine soil material and feces. The provisions are crescent-shaped layers arranged concavely upwards in balls of *S. menelas*, but have no particular arrangement in those of *S. imperator*.

The most important differences found between brood balls of both species studied herein and also with observations made by previous authors (Judulien 1899; Morelli *et al.* 1996; Cabrera Walsh and Gandolfo 1996) are related to the location and structure of the egg chamber. In *S. menelas*, according to our observations, the brood ball is drop-shaped, showing a conical upper pole composed mostly of interbraided dung fibers, which internally contains a cylindrical conduit plugged with longitudinally oriented dung fibers. The egg chamber is defined by the concavity of the uppermost crescent-shaped layer of provisions and lined with amorphous organic matter, probably adult feces (Sánchez and Genise 2008). In *S. imperator*, the lower half of the egg chamber is located at the top of the provisions, whereas the upper half is inside a protuberance of soil material, which gives the ball a pear-shaped aspect. In addition, the egg chamber wall is made of the same soil material and dung fibers as the external wall, but arranged in layers. In the egg chamber roof, there is an aeration pore that connects it to the exterior. Previous observations suggested that larvae of *S. imperator* use soil material from the egg chamber wall to construct the roof of its pupation chamber (Sánchez *et al.* 2010a).

Differences between the brood balls of *S. menelas* and *S. imperator* may reflect behavioral plasticity or different geographical distributions. Behavioral plasticity would imply that the same species, either *S. menelas* or *S. imperator*, may construct indistinctly the two types of brood balls, possibly under different environmental conditions. The second alternative involves no behavioral plasticity, but a fixed behavioral pattern resulting from the different geographical distributions of the species. *Sulcophanaeus imperator* inhabits drier environments than *S. menelas* (Martínez 1959; Edmonds 2000). The hypothesis is that *S. imperator* would always construct thicker egg chamber walls and open aeration pores, which would be adaptations to drier environmental conditions.

Fixed behavioral traits may be useful tools for phylogenetic analysis. The phylogenetic relationships of *Sulcophanaeus* Olsoufieff are still controversial. Philips *et al.* (2004) showed that the group is probably an artificial construct, which is in concordance with Edmonds (2000). They concluded that the group should be divided into four or even five genera. The best result was obtained using implied weighting methodology, where *Sulcophanaeus* appears as two separate groups, one monophyletic composed of *Sulcophanaeus faunus* F. and *Sulcophanaeus carnifex* L. and another paraphyletic composed of *Sulcophanaeus velutinus* (Murray), *S. menelas*, *S. imperator*, *Oxysternon* Laporte and *Phanaeus* Macleay as follows (*S. velutinus* (*S. menelas* (*S. imperator* (*Oxysternon, Phanaeus*)))). The problem is still unresolved because the morphological characters used are controversial and, as a consequence, the clades are supported by controversial synapomorphies. Brood balls of *S. menelas* and *S. imperator* differ in important traits, such as general shape, provision arrangement, egg chamber wall and location, and plug/pore presence. These behavioral characters may be added to future analyses to achieve more robust results in a phylogeny of *Sulcophanaeus*.

Finally, the pear-shaped outline, egg chamber location, and presence of a pore in brood balls of *S. imperator* are characters also found in the fossil brood balls of the ichnospecies *Coprinisphaera kheprii* Laza. The record of this ichnospecies from the Middle Eocene to the Early Miocene Sarmiento Formation of Patagonia (Sánchez *et al.* 2010b) suggests that some Phanaeini would have already existed by that period in southern South America.

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References Cited

Cabrera Walsh, G., and G. Gandolfo. 1996. Nidification of thirteen common Argentine dung beetles (Scarabaeidae: Scarabaeinae). Annals of Entomological Society of America 89(4): 581–588.

Edmonds, W. D. 2000. Revision of the Neotropical dung beetle genus *Sulcophanaeus* (Coleoptera: Scarabaeidae: Scarabaeinae). Folia Heyrovskyana 6: 1–60.

Edmonds, W. D., and G. Halffter. 1978. Taxonomic review of immature dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). Systematic Entomology 3: 307–331.

Halffter, G., and W. D. Edmonds. 1982. The Nesting Behaviour of Dung Beetles (Scarabaeinae). An Ecological and Evolutive Approach. Editorial Galache, Instituto de Ecología, Mexico.

Judulien, F. 1899. Quelques notes sur plusieurs coprophages de Buenos Aires. Revista del Museo de la Plata (Argentina) 9: 371–380.

Martínez, A. 1959. Catálogo de los Scarabaeidae argentinos (Coleoptera). Revista del Museo Argentino de Ciencias Naturales, Ciencias Zoológicas, Tomo V, Vol. 1.

Morelli, E., González-Vainer, P., and C. Canziani. 1996. Nidificación, ciclo de vida y estadios preimaginales de *Sulcophanaeus menelas* (Laporte, 1840) (Coleoptera: Scarabaeidae). Elytron 10: 11–22.

Murphy, C. P. 1986. Thin Sections Preparation of Soils and Sediments. A. B. Academic Publishers, London, UK.

Philips, T. K., W. D. Edmonds, and C. H. Scholtz. 2004. A phylogenetic analysis of the New World tribe Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae): Hypotheses on relationships and origins. Insect Systematics and Evolution 35: 43–63.

Sánchez, M. V., and J. F. Genise. 2008. Nest and brood chamber structure of two South American dung beetles: *Gromphas lacordairei* Brullé and *Ontherus sulcator* (Fabricius) (Coleoptera: Scarabaeidae: Scarabaeinae). The Coleopterists Bulletin 62: 49–61.

Sánchez, M. V., J. M. Krause, M. G. González, P. A. Dinghi, and J. F. Genise. 2010a. The pupation chamber of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). The Coleopterists Bulletin 64(3): 277–284.

Sánchez, M. V., J. H. Laza, E. S. Bellosi, and J. F. Genise. 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.

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