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Nest and Brood Chamber Structure of Two South American Dung Beetles: *Gromphas lacordairei* Brullé and *Ontherus sulcator* (Fabricius) (Coleoptera: Scarabaeidae: Scarabaeinae)

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Abstract

Thirty-three nests of *Gromphas lacordairei* Brullé and *Ontherus sulcator* (Fabricius) were studied at Navarro, Buenos Aires, Argentina. Nests examined in the field and micromorphological studies of brood chambers demonstrate for the first time that *G. lacordairei* shows delayed provisioning, constructs nests with storage burrows, and makes brood masses with a discrete external wall of soil. These characters place *G. lacordairei* in Pattern II nesting behavior. *Ontherus sulcator* constructs either brood balls beneath dung pads by direct provisioning or only feeding burrows. The orientation and structure of the egg chamber is different from those of *Ontherus mexicanus* Harold.

Dung beetles are well known for their complex nesting behavior and for their importance in recycling vertebrate dung (Fincher *et al.* 1970; Waterhouse 1974; Hughes 1975; Halffter and Edmonds 1982 and references therein). Three types of nests based on their relative location to dung were recognized originally by Bornemissza (1969, 1976): endocoprid nests when they are constructed within the food source; paracoprid nests beneath the food source; and telecoprid nests, when a piece of dung is carried some distance away from the dung. Later, Halffter and Matthews (1966); Halffter (1977); and Halffter and Edmonds (1982) refined this classification using more characters such as brood chamber structure and nest architecture, recognizing seven patterns of nesting behavior and proposing a general framework for their evolution.

Judulien (1899); Fabre (1899); Halffter and Matthews (1966); Halffter and Edmonds (1982); and Cabrera-Walsh and Gandolfo (1996) recorded different ethological aspects of the two species studied here, *Gromphas lacordairei* Brullé and *Ontherus sulcator* (Fabricius). According to those records, *G. lacordairei* would belong to Pattern I, whereas *O. sulcator* to Pattern II. However, those contributions lack detailed descriptions of brood masses and balls and nest structures, or indicate differences with observations presented here, and micromorphological studies are lacking. It is the purpose of this contribution to provide detailed macro- and micromorphological descriptions of the brood chambers for comparisons with similar fossil brood chambers currently under study (Sánchez *et al.* 2005).

Materials and Methods

Nests of *G. lacordairei* and *O. sulcator* were studied from January to March 2006, when adult dung beetles were active. Observations were made at Navarro (Buenos Aires province, Argentina) (39°00′S–69°30′W), in an establishment with abundant cows and horses. The relative abundance of both beetle species in the study area was distinct: *G. lacordairei* was most abundant around the margin of a pond, in a lower and moister environment, whereas *O. sulcator* was more prevalent in a higher field near the pond. In addition, in a third field of the same establishment, 300 m from the pond, *Sulcophanaeus menelas* (Laporte) was the most dominant dung beetle species. The species studied here construct paracoprid nests (Halffter and Matthews 1966; Halffter and Edmonds 1982) and they accept different kinds of dung, such as cattle, horse, pig, sheep, goat, llama, dog, and human feces (Cabrera-Walsh and Gandolfo 1996). The dung pads recently worked by beetles were recognized by the presence of removed soil on them and in some cases around them, and by the fresh, moist, internal condition in combination with a dry external appearance. About half of the approximately 60 excavated dung pads had nests beneath them. The soil beneath the selected dung pads was excavated up to 25.0–30.0 cm deep and about 40.0–60.0 cm around, depending on the dung size, to obtain an isolated soil portion. The removed sample was then cut in thin layers to study the nest structure and to recover the brood chambers and adults. The material was deposited in the ichnological collection of the Museo Argentino de Ciencias Naturales (Buenos Aires), where Cabrera-Walsh and Gandolfo (1996) deposited similar material. For all descriptions made here, we use the nest, brood mass, and brood ball nomenclature proposed by Halffter and Matthews (1966) and Halffter and Edmonds (1982). We introduce the term brood chamber to encompass both brood masses and balls, which should not be confused with nesting chamber that is the excavated chamber surrounding the brood ball. We also introduce the term storage burrow when a burrow provisioned with dung was observed but no adult feeding could be inferred; dung stored in this way may be destined indistinctly for use as larval provision or adult feeding. In the case of *G. lacordairei*, six nests were examined and measured *in situ*, containing three brood masses that were recovered and taken to the laboratory for further study. Twenty-seven nests of *O. sulcator* were observed and measured *in situ*, and brood balls removed and taken to the laboratory. The most complete nests were used for the detailed descriptions presented here, whereas the remaining nests were used to complete morphological details and for measurements.

The brood masses of *G. lacordairei* were cut in longitudinal and transversal sections to observe their internal structure. Two brood masses contained eggs that failed to hatch in the laboratory; the third contained a larva that also failed to develop. One brood mass and another already deposited in the Museum were used for obtaining thin sections for micromorphological studies. Nine brood balls of *O. sulcator* containing larvae were used to follow larval development. The objective of this procedure was to check possible modifications of the brood ball by the larvae as reported for other species of dung beetles (Joseph 1929; Klemperer 1978; Barattini and Sáenz 1953). Each brood ball was cut, photographed, and then located in a container with moist soil or sand and packed with humid tissue paper. Once a week the balls were opened, and the state of the chamber and larvae checked. This procedure was maintained until adult emergence. For micromorphological studies, three brood balls were selected, one of which contained an egg and the other two larvae. In the remaining collected specimens, the larvae were removed and the brood balls were incorporated in the collection in dry condition to preserve the external appearance and shape.

Thin sections studied were observed under 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 in polarized light. The thin sections were prepared with undisturbed, vacuumed samples impregnated with stained polyester resin (Murphy 1986). The terminology used in micromorphological descriptions follows the nomenclature of soil micromorphology proposed by Bullock *et al.* (1985).

Results

Gromphas lacordairei Brullé

Nest structure (Fig. 1A). The six studied nests were found beneath four dung pads: one with three nests, and the others with one each. These nests showed three different stages of construction. The first distinguishable stage was in nests composed only of an inclined storage burrow connected with the soil surface and completely filled with meniscate dung (Fig. 2A). In some cases an adult was resting on the stored dung. In a more advanced stage, studied nests showed vertical nesting burrows with dung deposited up to a few centimeters from the bottom (Fig. 2B). The nesting burrow was connected to the storage burrow. The third stage showed a complete brood mass at the bottom of the nesting burrow, the storage burrow still open and filled partly with dung, and the adult inside it (Figs. 2C, D). The three nests beneath the single dung pad exhibited in two cases the intermediate stage and in the remaining one, the third stage.

In the complete nests, the nesting burrow, where the adult constructed the brood mass, was straight and vertical, 5.0–8.0 cm in length and 1.7–2.0 cm in diameter (n = 3). It could be traced up to the soil surface despite being filled with dung and loose soil after the brood mass construction (Figs. 2C, D). The storage burrow, which was 10 cm in length, 1.3–1.5 cm in diameter, and inclined up to 45° from the vertical, was connected with the nesting burrow 5.0–6.0 cm from the soil surface (n = 2). The wall of both burrows had no distinctive characters. In the storage burrow the dung was stored in concave upward menisci (Fig. 2A).

Brood mass structure. The brood masses were subcylindrical structures constructed at the bottom of the nesting burrows (Fig. 2C). The measured brood masses ranged from 3.0 to 3.7 cm in length and from 1.5 to 2.0 cm in diameter (n = 2). These masses had a discrete wall that was impossible to distinguish in the field. It could be hardly distinguished in the drier material deposited in the collection by a fissure that partially separated the mass from the surrounding soil (Fig. 2G) and in thin sections (Fig. 4B). The brood mass had a small pore on the top that connected the egg chamber with the burrow, which showed a plug of dung and loose soil material. Fibers of the dung plug penetrated into the egg chamber pore. The provision was composed of dung mostly deposited in concave upward menisci. The egg chamber, located at the top of the mass, was spherical, 1.0–1.1 cm in diameter (n = 3) and separated from the dung by a thin wall. This

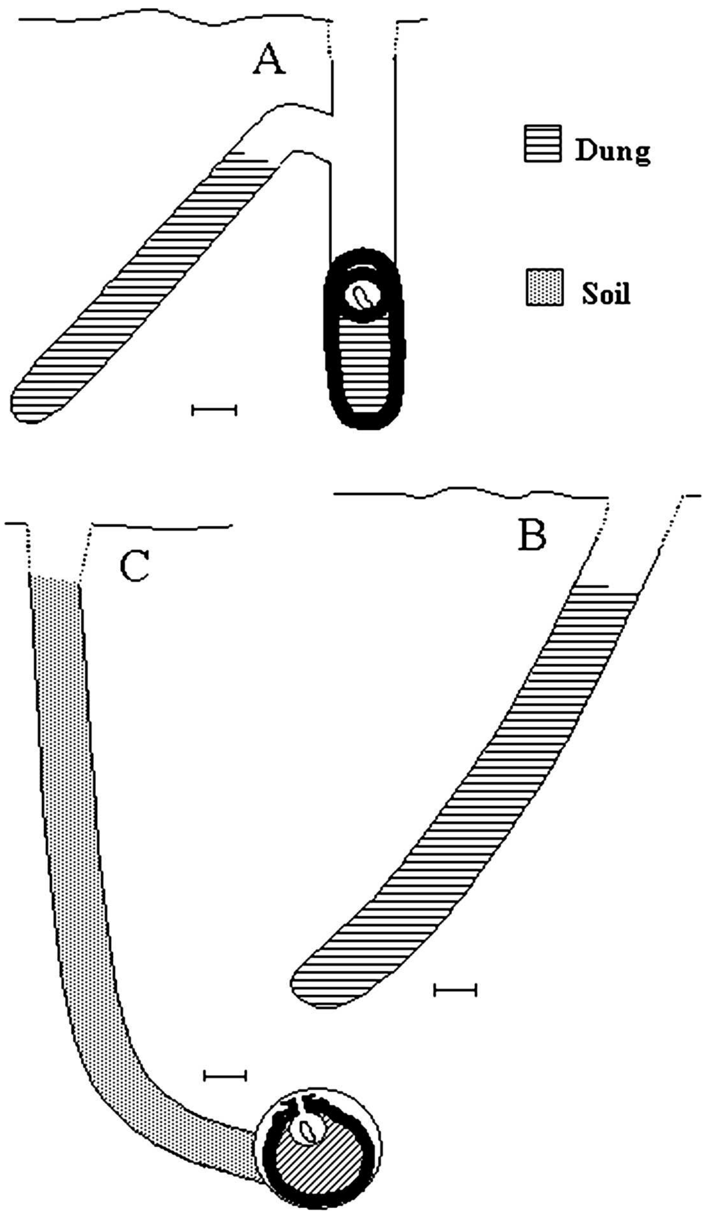

Fig. 1. Schematic drawings of nests. **A**. *Gromphas lacordairei*, nesting burrow containing the brood mass and connected storage burrow. Two types of nests by *Ontherus sulcator*: (**B**) Nest composed of a single storage burrow connected with the soil surface and completely filled with meniscate dung, (**C**) Nest composed of a nesting burrow filled with soil material and connected with one nesting chamber and the brood ball. Scale: 1 cm.

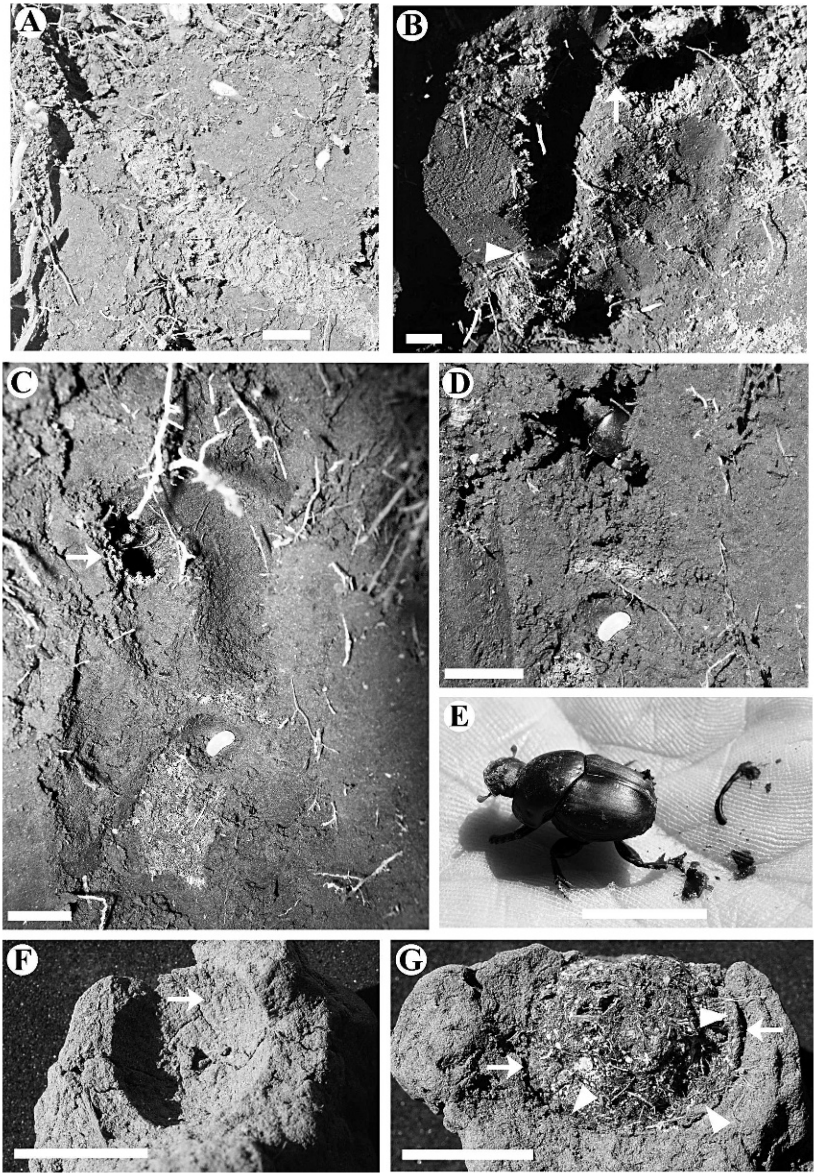

Fig. 2. Nest and brood mass of *Gromphas lacordairei*. **A**. Storage burrow in longitudinal section. **B**. Second stage of nest construction showing a few centimeters of dung deposited on the bottom of a vertical nesting burrow, with the adult on it (white triangle) and with the storage burrow connection (white arrow). **C**. Complete brood mass at the bottom of the nesting burrow and the storage burrow still open and filled partly with dung (white arrow). **D**. Distal view of brood mass showing the adult on the nesting burrow. **E**. Adult and its feces. **F**. Internal view of egg chamber wall showing thin, shallow, curved, and concentric grooves (arrow). **G**. Brood mass wall (white triangles) partly separated from the surrounding soil by a fissure (white arrows). Scales: 1 cm.

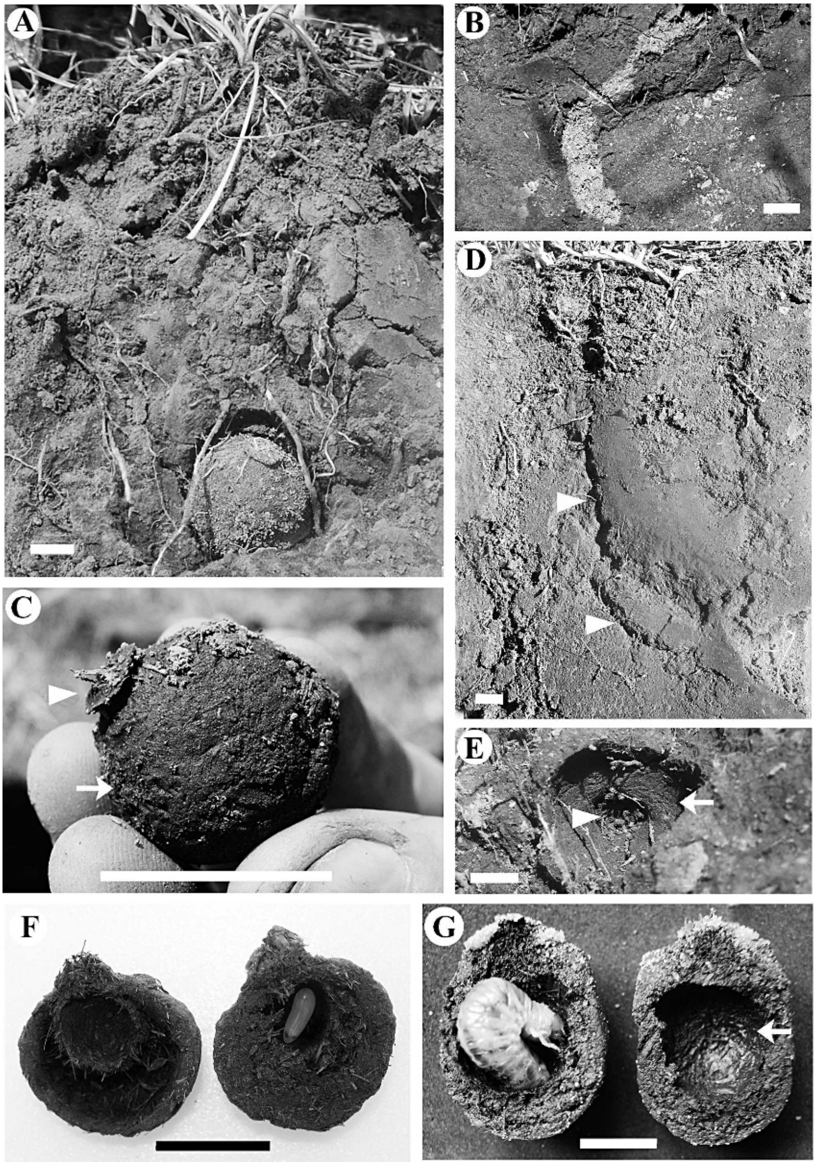

Fig. 3. Nest and brood ball of *Ontherus sulcator*. **A**. Nest containing a complete brood ball. **B**. Nest composed of a single storage burrow completely filled with meniscate dung. **C**. Brood ball showing an upper cylindrical protuberance (white triangle) surrounded by a flat annular surface; the external wall surface shows shallow, irregularly distributed pits (white arrow). **D**. Nesting burrow completely filled with soil (white triangles) connected to the nesting chamber. **E**. Internal view of the nesting chamber wall showing thin, shallow, inclined, and curved grooves (white arrow); and a rounded pit which connects this chamber to the nesting burrow (white triangle). **F**. Longitudinal section of the brood ball showing the

wall shows internally thin, shallow, curved, and concentric grooves (Fig. 2F). In two studied cases, a large pale-yellow egg (5.0–5.5 mm long, 3 mm diameter) was laid on a small base (Figs. 2C, D).

Brood mass micromorphology. The wall was 4.25–4.75 mm thick (n = 1) and had a microstructure mostly massive with 5.0–7.0% porosity. The coarse fraction was composed of fine sand–silt size grains. This fraction represented 50.0% of the total volume and was composed of quartz, K-feldspar, plagioclase, mica, lithic fragments, volcanic glass shards, and heavy minerals (epidote, pyroxene, amphibole). The fine fraction was composed of clay size-grain, pale brown material, which was darker near the fill because of the high content of organic matter (Fig. 4A). Externally, the wall had a thin layer of clay size material with high organic matter content, 10.0–20.0 µm thick, which delineated the boundary between the wall and the soil matrix (Fig. 4B). The fill was composed of elongated, about 2.0 mm long, birefringent dung fibers. The fibers closer to the wall were orientated parallel to it, composing a layer 0.75–1.0 mm thick, whereas towards the center of the mass, fibers lacked any orientation (Fig. 4A) or in some cases the meniscate arrangement could be recognized.

The wall of the egg chamber was 3.2–6.6 mm thick and had a microstructure mostly massive with 5.0% porosity (Fig. 4C). The coarse fraction (45.0%) was characterized by fine sand-coarse silt size-grain (moderate sorting) and composed of quartz, K-feldspar, plagioclase, volcanic glass shards, mica (in order of importance), and very scarce pyroxene. The fine fraction was represented by a high content of clay size-grain, pale, dark brown organic matter.

***Ontherus sulcator* (Fabricius)**

Nest structure (Figs. 1B, C). The thirty studied nests were found beneath sixteen dung pads: in seven cases a single storage burrow per dung pad was found; in three cases a single nesting chamber; in five cases more than one (up to eight) nesting chambers; and in one case three storage burrows were found belonging to *O. sulcator*, *G. lacordairei*, and *S. menelas*. Two types of burrows, considered here as nests in a broad sense, were distinguishable beneath the dung pads, which only in one case occurred together beneath a single dung pad. The first type consisted of a single storage burrow connected with the soil surface and completely filled with meniscate dung (Fig. 3B), in some cases with an adult laying on it. The other type was the nesting burrow, which was connected to the nesting chamber containing a complete brood ball inside (Figs. 3A, D). In the latter case adults or remains of storage burrows were not present, and nesting burrows were filled with soil material that in most cases was indistinguishable from the surrounding soil. Only in one case could the fill of a nesting burrow be scarcely distinguished (Fig. 3D).

The storage burrow may be completely straight and vertical, mostly horizontal with some vertical segments, or oblique with one or more bends (Fig. 3B). This tunnel, which may reach a depth of 10.0–20.0 cm, was 1.5–2.5 cm in diameter and up to 15.0 cm long (n = 6). Usually, when the tunnel was long, it was oblique and deeper. The storage burrow was filled with dung deposited in menisci. The wall of

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layer of dark brown material internally coating the egg chamber (left), and the meniscated dung provision (right). **G**. Longitudinal section of the brood ball showing the larva (left) and the dark layer covering the provisions internally (right, white arrow). Scales: 1 cm.

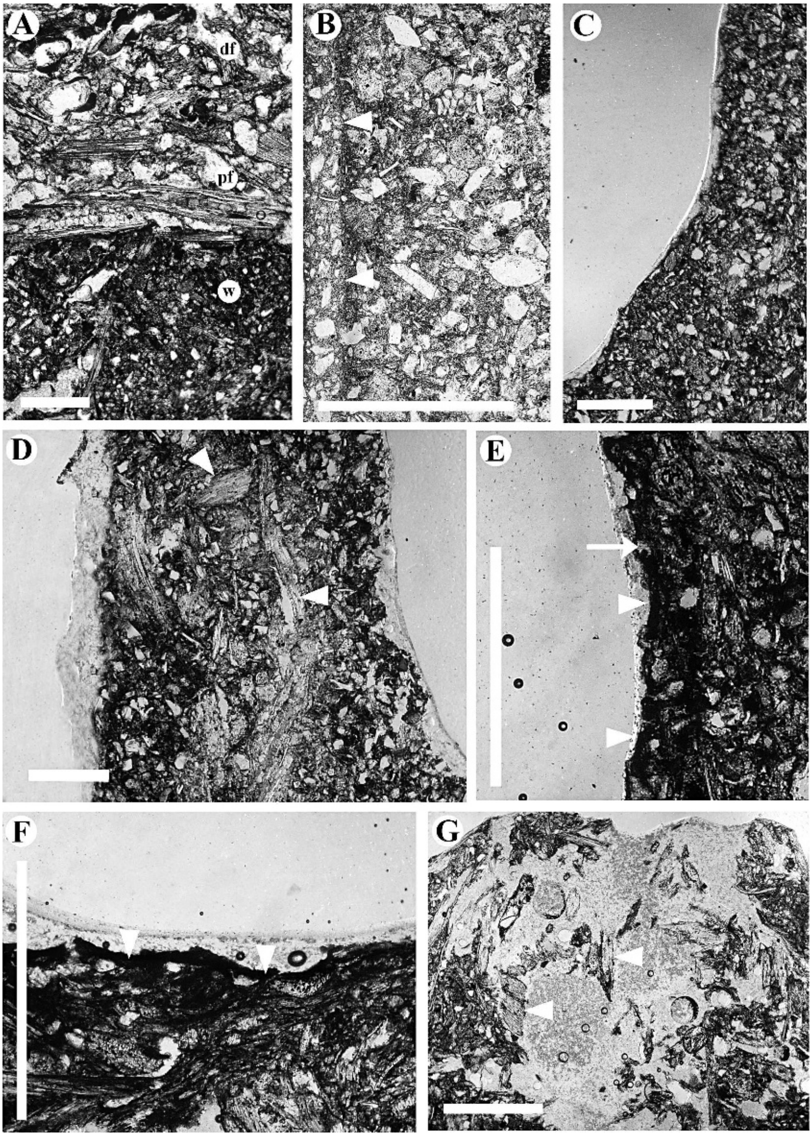

Fig. 4. Brood chamber micromorphology. *Gromphas lacordairei*: **A**. Wall (w), fibers parallel to the wall (pf) and more internal fibers showing no arrangement (df) in a brood mass. Scale: 500 μm. **B**. Thin layer of clay size material with high organic matter content that delineates the boundary between the wall and the soil matrix (white triangles). Scale: 500 μm. **C**. Egg chamber wall. Scale: 500 μm. *Ontherus sulcator*: **D**. Brood ball wall composed by soil and dung fibers (white triangles). Scale: 500 μm. **E**. Egg chamber wall mainly composed of organic material (white triangles) with dispersed minerals (white arrow). Scale: 1,000 μm. **F**. Larval cavity covered with an organic lining (triangles) without dung fibers and minerals. Scale: 1,000 μm. **G**. Cylindrical protuberance showing the aeration plug with remains of dung fibers (triangles) (most removed when sectioned). Scale: 500 μm.

this burrow had no distinctive characters. In two cases the nesting chambers found beneath a single dung pad were separated from each other by a few centimeters. One of these groups had three nesting chambers at the same depth and separated by 2.0–3.0 cm. The other had two nesting chambers at the same depth and separated by 1.5 cm. Beneath the remaining dung pads, the nests were separated by 5.0–13.0 cm.

All nesting chambers were located at a depth ranging from 9.5 to 19.0 cm (n = 22). The chamber was spherical, 2.8–3.6 cm in height and 2.3–3.7 cm in diameter (n = 17). Between the nesting chamber and the brood ball was a free space of 3.0–4.0 mm (n = 14). The wall of the nesting chamber showed thin, shallow, inclined, and curved grooves (Fig. 3E). The complete nesting chambers were closed with soil material. In some of them was found a rounded pit on the wall, 1.0 cm in diameter, in a lateral and superior position. This pit was probably the original communication with the nesting burrow (Fig. 3E).

Brood ball structure. Brood balls were spherical, 1.5–2.7 cm in diameter (n = 14), and composed of an external, 1.2–2.6 mm thick wall and an internal fill of dung (n = 13) (Fig. 3F). Externally, the wall surface showed irregularly distributed, shallow pits probably made by the adult as it molded the brood ball (Fig. 3C). On the upper part of the ball, separated from the dung by a wall, was located the egg chamber (Fig. 3C). The dung deposited around the base of the egg chamber wall had fibers parallel to it. The egg chamber was open to the exterior in the upper pole. Externally, the brood ball wall showed at this point a cylindrical protuberance 6.0–10.0 mm in diameter and 3.0 mm high, finished in a prominent rim (Figs. 3A, C, D). Surrounding this structure the chamber wall was a flat annular surface. Within the protuberance were loose, horizontal and vertical dung fibers creating an aeration plug (*sensu* Halffter and Edmonds 1982), which connected the interior of the egg chamber with the nesting chamber (Figs. 3C, F and 4G). A thin layer of dark brown material internally lined the egg chamber (Figs. 3F and 4E). A large, pale yellow egg (5.0–6.0 mm long, 2.0 mm diameter, n = 2) was laid vertically into the egg chamber (Fig. 3F). The balls cut in the laboratory to observe larval development had a thin, brown layer covering the provisions surrounding the larvae (Figs. 3G and 4F). This layer was absent when the balls were opened for the first time.

Brood ball micromorphology. In brood balls with an egg, the wall ranged from 1.2 to 2.0 mm in thickness (n = 4), and was composed of soil material and dung fibers. The relative abundance of both components differed: the external part of the wall was mostly composed of soil material, whereas internally there were more dung fibers. In some cases these dung fibers were orientated parallel to the fill (Fig. 4D). The wall microstructure was mostly massive with 10.0–15.0% porosity. The coarse fraction was composed of fine sand-silt size grains. This fraction, representing 70.0 % of the wall, was composed of quartz, K-feldspar, plagioclase, mica, and volcanic glass shards (in order of importance). Sparse dung fibers represented 40.0% of this fraction. Fibers were about 1.0 mm long and birefringent. The fine fraction had a high contain of organic matter, represented by clay size-grain, non-birefringent, dark brown material, which was darker toward the fill. The fill was composed of 70.0–75.0% dung fibers without orientation. Soil fragments represented the remaining 30.0–35.0% of the fill. The wall of the egg chamber was 250.0–500.0 μm thick and composed mainly of organic material, dark brown in color, with dispersed minerals (Fig. 4E). The aeration plug was characterized by the presence of horizontal and vertical dung fibers in the center of the cylindrical protuberance (Fig. 4G).

The walls of brood balls containing larvae were 1.7–2.6 mm thick (n = 8) and had a massive microstructure with 3.0% porosity (Fig. 4F). The coarse fraction, representing 40.0% of the total wall, was characterized by silt size-grain minerals, moderately sorted, such as quartz, K-feldspar, plagioclase and volcanic glass shards (in order of importance), scarce mica (biotite and muscovite) and some heavy minerals like pyroxene and epidote. The fine fraction had a high content of organic matter represented by clay size-grain, dark brown material. The fill was composed exclusively of 750.0 μm long, birefringent dung fibers, which were more orientated close to the lining. The remaining part of the fill was conformed by disperse minerals. Inside the fill, the larva was in a cavity covered with a dark brown to very dark brown organic lining 75.0–360.0 μm thick (Fig. 4F). This lining was different from the lining in the brood ball wall and in the fill because it lacked minerals and had only organic material without dung fibers.

Discussion

Judulien (1899); Fabre (1899); Halffter and Matthews (1966); Halffter and Edmonds (1982); and Cabrera-Walsh and Gandolfo (1996) have published on various aspects of the nesting behavior of species of the two genera treated here. However, some of the new data presented here contradicts earlier observations, and in other cases complements them. Particularly important are the data on the micromorphology of brood masses and balls: micromorphological data have not been used heretofore for comparative studies of dung beetle nesting behavior.

The nesting behavior and nest of *G. lacordairei* have been only incompletely understood until now. Fabre (1899) published observations included in correspondence to him by Judulien, although Judulien (1899) in his own contribution provided different data. Judulien (in Fabre 1899) believed that this species constructed branched nests, each one with a few cylindrical brood masses. Later, Halffter and Edmonds (1982) briefly mentioned that these nests were composed of a vertical gallery containing a cylindrical brood mass. The contribution by Cabrera-Walsh and Gandolfo (1996) included only a description of brood masses, which they obtained in rearing containers. Data presented here show for the first time that nests of *G. lacordairei* have storage burrows where the dung is warehoused before being used to construct brood masses. This delayed provisioning is not the rule in Pattern I nesters, which use direct provisioning (Halffter and Edmonds 1982). In addition, in two cases the storage burrows still contained dung and one adult remained in the nest after completing a first brood mass, suggesting that the construction of more than one brood mass cannot be ruled out (c.f., Fabre 1899; Judulien 1899; Halffter and Matthews 1966; Halffter and Edmonds 1982). Moreover, these previous studies mentioned nothing about the presence of a discrete wall covering the brood mass. Cabrera-Walsh and Gandolfo (1996) described the brood masses of *G. lacordairei* as an excavation at the bottom of a burrow, without describing any characters of the wall. However, when samples containing a brood mass with surrounding soil were dried in the laboratory, the masses showed a discrete wall separated from the soil by a fissure (Fig. 2G). Micromorphological data presented here confirms that brood masses have a discrete wall whose boundary can be distinguished from the soil by a thin layer of fine material with a high content of organic matter content (Fig. 4B). The wall is constructed without using dung fibers, but soil probably with fine organic material added (Fig. 4B).

In *G. lacordairei*, the brood mass has an egg chamber isolated from the dung by a wall (Judulien 1899; Fabre 1899; Halffter and Matthews 1966; Cabrera-Walsh and Gandolfo 1996). Former authors believed that this wall was made with "clay", but these descriptions were made with the naked eye, and as such are more likely to be interpreted as clay-size material. Cabrera-Walsh and Gandolfo (1996) considered that it was constructed with fine mud mixed with a creamy secretion, feces or chewed soil, which was defined as "cement". They stated that this "cement" does not have the same textural composition of the soil in which the nest is made, because it is composed only by fine particles. Thin sections show that this wall is composed of unsorted soil material with organic matter possibly added by the adult, considering that the wall has 55.0% organic matter, whereas the soil has only 30.0%. The organic matter may come from adult fecal material.

Halffter and Matthews (1966) included *G. lacordairei* in their nesting Pattern II, variation 1, particularly because the egg was laid in a hollow chamber isolated from the dung provision, which was confirmed in later contributions and in this study. Halffter and Edmonds (1982), reconsidering the same evidence, included *G. lacordairei* in Pattern I because they regarded the nests to be more similar to those of Pattern I in spite of the egg chamber morphology. The presence of a wall in the brood mass, as demonstrated in our study, is a new character that suggests that *G. lacordairei* behavior can reasonably be associated with that of Pattern II nesters. In addition, the fact that the nests have storage burrows suggests that the provisioning is delayed as in Pattern II nesters. These two characters may be related to each other because the adult would need to store the dung away from the pad while constructing the wall for the brood mass. The potential inclusion of *Gromphas* in Pattern II nesters with phanaeines would be in accordance with the phylogeny recently proposed by Philips *et al* (2004).

Halffter and Edmonds (1982) were the first to describe the nesting behavior and brood ball of a species of *Ontherus*, *O. mexicanus* Harold. Its nests, according to these authors, are simple and composed of only one brood ball per nesting burrow as those described herein. No feeding or storage burrow was mentioned. Storage burrows are described here for *O. sulcator*. However, these were not found together with nesting burrows, suggesting that the function of these burrows is more likely for adult feeding than dung storage for provisioning of the ball. This behavior also suggests that the brood balls are constructed by direct provisioning as described for some Phanaeina included in Pattern II (Halffter and Edmonds 1982). Nesting burrows are filled with soil after the completion of the brood ball. In the absence of parental care, this behavior may prevent nests from the attack of predators or cleptoparasites.

Halffter and Edmonds (1982) described the brood ball wall of *O. mexicanus* as a thick layer of soil, whereas Cabrera-Walsh and Gandolfo (1996) mentioned the brood ball wall of *O. sulcator* as made with "cement". Micromorphological studies presented here show that the brood ball wall of *O. sulcator* is made with about 30.0% dung fibers and soil material slightly enriched with fine organic matter. The brood balls of *O. mexicanus* have a closed egg chamber in a lateral position facing the former entrance of the nesting chamber, and completely included in the brood ball wall. Halffter and Edmonds (1982) also noted that there was a "fibrous aeration plug" in the protuberance, which has no connection with the egg chamber. In the nests of *O. sulcator*, the egg chambers are located in a lateral and upper position, whereas the former entrances of the nesting chambers are in a lateral position as in *O. mexicanus*. Another difference between *O. sulcator* and *O. mexicanus* is that in the former, the egg chamber is not included in the brood ball wall, but rather is formed in the provision, as in

Catharsius. This character may be related to differences in humidity conditions of the study areas of both species (Halffter and Matthews 1966), although behavioral differences cannot be discarded as well. Cabrera-Walsh and Gandolfo (1996), who studied the brood balls of *O. sulcator* for the first time in Buenos Aires under the same local climate as that of Navarro, reported the egg chamber also as an excavation into the dung provision on the brood ball. These authors mentioned no lining or particular wall for it. Herein we document the presence of a thin layer of fine organic material, probably adult feces, which covers the interior of the egg chamber. This character, observed in thin sections, is very important because it was not mentioned until now either for this species or for *O. mexicanus* (Halffter and Edmonds 1982).

The protuberance from the brood ball of *O. sulcator* is also subject to different interpretations. According to Cabrera-Walsh and Gandolfo (1996), after laying the egg the adult completes the ball with dung, plastering it from the outside and producing the cylindrical protuberance. They described this structure like a "round and flat button" that blocks the nesting chamber entrance and as being the result of the nesting chamber and brood ball construction. They suggested that this flat button is constructed to prevent brood ball rotation inside the nesting chamber and that the location of this structure does not always coincide with that of the egg chamber. The field nests observed in our study show that the brood balls are never secured by any structure. The nesting chamber entrance is positioned laterally, whereas the protuberance of the brood ball is oriented upward and at an angle of 45°. Thus, the protuberance has no direct relationship with the nesting chamber entrance. In addition, we observed the protuberance was always connected to the egg chamber. The micromorphological studies demonstrate that the egg chamber is not completely closed and that this cylindrical protuberance has a direct connection with it because inside this protuberance, an accumulation of dung fibers creates an aeration pore (*sensu* Halffter and Edmonds 1982) that probably allows gas exchange between the interior of the egg chamber and the nesting chamber.

In summary, *G. lacordairei* builds nests with storage burrows that permit delayed provisioning and the brood masses have a discrete wall. These two features suggest that the nesting behavior of this species more closely conforms to Pattern II than Pattern I. *Ontherus sulcator* digs storage burrows probably used for feeding; brood balls are made via direct provisioning. The egg chamber is constructed in the brood ball provision and isolated by a thin lining of organic material from the dung. The brood ball is located with its egg chamber in lateral and upper positions, whereas the original entrance of the nesting chamber is in a lateral position. Micromorphological studies show that *G. lacordairei* constructs brood and egg chamber walls with unsorted soil material mixed with fine organic matter; and that *Ontherus sulcator* adds dung fibers for constructing the brood ball wall but makes the egg chamber wall with only fine organic material.

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