

**Leaf-Litter Brood Chambers in *Dichotomius* (*Luederwaldtinia*)
Carbonarius (Mannerheim, 1829) (Coleoptera: Scarabaeidae): A
Novel Behavior for Dung Beetles**

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Source: The Coleopterists Bulletin, 67(3):388-396. 2013.

Published By: The Coleopterists Society

DOI: <http://dx.doi.org/10.1649/0010-065X-67.3.388>

URL: <http://www.bioone.org/doi/full/10.1649/0010-065X-67.3.388>

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**LEAF-LITTER BROOD CHAMBERS IN *DICHOTOMIUS (LUEDERWALDTINIA)*
CARBONARIUS (MANNERHEIM, 1829) (COLEOPTERA: SCARABAEIDAE):
A NOVEL BEHAVIOR FOR DUNG BEETLES**

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ABSTRACT

Dichotomius (Luederwaldtinia) carbonarius (Mannerheim, 1829) provisions its brood chambers entirely with comminuted leaf litter, mostly of *fumo bravo* (*Solanum granuloso-leprosum* Dunal), and covers them with a thin layer of entire or large fragments of leaves. This is the first recorded case of brood chambers provisioned exclusively with leaf litter. The brood chamber is composed of a main spherical chamber and a cylindrical protuberance in the proximal pole. The egg chamber is located at the distal pole. These brood chambers show, to some extent, intermediate features between brood masses and brood balls. The pupation chamber is constructed without any pellet arrangement and differs from others described from South America and also from those preserved inside Patagonian fossil brood balls, suggesting that this branch of *Dichotomius* Hope including *Luederwaldtinia* Martínez could be a separate lineage.

Key Words: Dichotomini, nesting behavior, ball-shaped provisions, plant detritus

The ecological success of Scarabaeidae is attributed to their behavioral diversification as an adaptation to occupy different niches and to avoid as much as possible interspecific competition for food and breeding sites (Scholtz *et al.* 2009). The hypothetical ancestral feeding habit is detritivory (Cambefort 1991; Scholtz and Chown 1995), whereas coprophagy is the most extended one, and necrophagy, saprophagy, and frugivory are also common but less extended (Halffter and Matthews 1966; Halffter and Edmonds 1982; Hanski and Cambefort 1991; Scholtz *et al.* 2009). In contrast, there are only a very few species of dung beetles provisioning nests with plant material, among which are species in the genera *Paraphytus* Harold (rotten wood), *Coptorhina* (Hope) (mushrooms), *Attavicinus* Philips and Bell (ant nest debris), *Pachysoma* Macleay (vegetable detritus and dry dung), and *Cephalodesmius* Westwood (decomposed leaf pieces, flowers, seeds, and fruits) (Halffter and Matthews 1966; Monteith and Storey 1981; Scholtz *et al.* 2004; Davis *et al.* 2008; Frolov *et al.* 2008; Philips and Bell 2008, 2009; Halffter and Halffter 2009; Holter *et al.* 2009).

Herein is presented the first recorded case of a dung beetle, *Dichotomius (Luederwaldtinia) carbonarius* (Mannerheim, 1829), providing its

brood chambers with a filling of small, comminuted, dry leaf pieces and an outer layer of more entire leaves. This newly reported behavior results in isolated brood chambers (*sensu* Sánchez and Genise 2008), which can be seen either as ball-like brood masses or as mass-like brood balls, in any case bearing the egg chamber at the distal pole.

MATERIAL AND METHODS

Brood chambers and four adults (three males and one female) of *D. carbonarius* were collected during December 2012 at the Karadya Bioreserve, which is located in northeastern Misiones province, 20 km south of Andresito (S25°52'14", W53°58'10"), Argentina. The warm subtropical climate of northern Misiones is not seasonal, with monthly precipitation ranging on average from 110 mm to 209 mm (period 1981–1990) (Servicio Meteorológico Nacional 2012).

All material studied was found in an anthropogenic glade of the rainforest surrounding a house, particularly inside a kennel (approximately 8 × 5 m) (Fig. 1A). Around and inside the kennel, there were scattered trees of *fumo bravo* (*Solanum granuloso-leprosum* Dunal, Solanaceae) and *rabo duro* (*Lonchocarpus leucanthus* Burk, Fabaceae). In the kennel, three trees of *fumo bravo* provided



Fig. 1. A) General aspect of the kennel where brood chambers of *Dichotomius carbonarius* were collected; the soil is covered by leaf litter and short grasses and the tree trunks are *fumo bravo*, B) Leaf of *fumo bravo* on the soil and fragmented in subrectangular pieces, scale bar = 2 cm, C) Brood chamber of *D. carbonarius* showing contact with soil, scale bar = 2 cm, D) Adult *D. carbonarius* buried in the soil about 7 cm from the surface, scale bar = 1 cm.

the leaves that covered the soil surface, leaving at some places a 5-cm thick layer of litter. Its fallen leaves disintegrate along the ribs on the soil, separating into sub-rectangular small fragments (Fig. 1B). This autochthonous tree is frequently found as a colonizer of *capueras* (patches of degraded forest) in Misiones. It is abundant in tropical and subtropical areas of America and can reach 8 m in height, with trunks up to 30 cm in diameter. There were also short grasses (Poaceae) and sedges (Cyperaceae) in the kennel.

All brood chambers collected ($n = 9$) were carried to the laboratory, where longitudinal sections were made to view the internal structure, take measurements, and check the state of larval development. In three cases, a month after hatching, the larvae reached the third instar. Fifteen days later, the third instars began the construction of the pupation chambers. In April, they remained as larvae in the laboratory.

The four collected adults were maintained in a cylindrical, 20-L plastic container, with the original soil and 3 cm of *fumo bravo* leaf litter on the surface. At least once a day, the container was sprayed with water to maintain moisture. The activity of the adults was followed, video recorded, and photographed during 45 days, until all of them died in the same week. The soil in the container was examined for possible traces of activity. Adults were preserved in 100% ethanol. Brood chambers, along with dung beetles, were deposited in the Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina).

RESULTS

The nine brood chambers, and their producers, were found in an area of about 4 m² of the kennel, 7–10 cm deep, beneath a layer of leaf litter. The brood chambers showed no free space (no nesting chamber, *sensu* Sánchez and Genise 2008) between them and the surrounding soil (Fig. 1C). They were inclined about 45° with respect to the soil surface. Dung beetles were found isolated in the soil at the same depth as the brood chambers, but not directly associated with them (Fig. 1D). Burrows or other structures were not observed. In only one case, a brood chamber at a depth of 7 cm had its upper part connected to a short, curved tunnel, 1.7 cm wide, filled with loose soil, which ended at the soil surface.

Brood Chamber. Complete brood chamber specimens are composed of two connected structures: a main spherical structure and a cylindrical protuberance. The main structure is 3.0 cm in mean diameter ($n = 8$). This structure is covered by a thin, 1-mm thick layer of large pieces of leaves of *fumo bravo* (Fig. 2A–F), grasses and/or

sedges (Fig. 2A, D–E), and also entire small leaves of *L. leucanthus* (Fig. 2B). Internally, it is composed of concave, downward meniscate packets of small, comminuted pieces of *fumo bravo* litter (Fig. 3A). In some cases, the provision is more compact outwards, showing a distinct layer 2–4 mm thick. The only recognizable content of the provision is leaf litter. In two cases, large pieces of grass leaves were also included, probably detached from the external lining (Fig. 2F). The abundant star-shaped trichomes suggest that the provision is mostly composed of *fumo bravo* leaves (Fig. 3B–E). The spherical chamber, 0.75 cm in diameter ($n = 4$), is located at the distal pole, opposite the cylindrical protuberance, and shows no lining (Fig. 3A). Eggs are translucent pinkish yellow, stout, and lay parallel to the distal pole (Fig. 3A). In some cases, the pharate larva was visible inside the egg (Fig. 3B).

The short, cylindrical protuberance is about 1.5 cm long and 1.5 cm in diameter ($n = 5$) (Fig. 2). This structure, fully connected with the main chamber, is internally composed of 2–3 thick, meniscate packets of compact *fumo bravo* litter. In most cases, it remained attached to an irregular soil cover (Fig. 2A–C, E, F). It may have no external layer (Figs. 1C, 2B–C) or an external layer of leaves as the main chamber (Fig. 2D). Usually, collected brood chambers suffered a natural split, separating the spherical and cylindrical structures (Fig. 2E–F). When split, the contact area of both structures shows no layer of entire or large fragments of leaves, but only comminuted litter (Fig. 2F).

Pupation Chamber. The larva feeds on the provisions, enlarging the space around it (Fig. 4A–B). In some cases, it also feeds on the external layer of leaves. As a result, pupation chambers may have remains of this external layer (Fig. 4C) or show no remains (Fig. 4D). The pupation chamber is subspherical, 2.9 cm high and 2.6 cm in equatorial diameter ($n = 3$). The wall, 3 mm thick, is composed of subrounded to subrectangular fecal pellets, which show no particular arrangement. These pellets give to the structure an external botryoidal appearance (Fig. 4C–D).

Adult Behavior. Adults in the container exhibited periods of activity on the soil surface from dusk to dawn. Also, they showed activity for a few minutes after surface spraying with water during the day. Their main behavior included feeding on leaf material on the soil surface, interspersed with inactivity. They also excavated several entrances in the *fumo bravo* leaf litter, circular in cross-section, which were connected to empty spaces between the litter and the soil. Adults spent their inactive periods inside these spaces. When the container was open and the leaf litter removed, there were also at least eight vertical

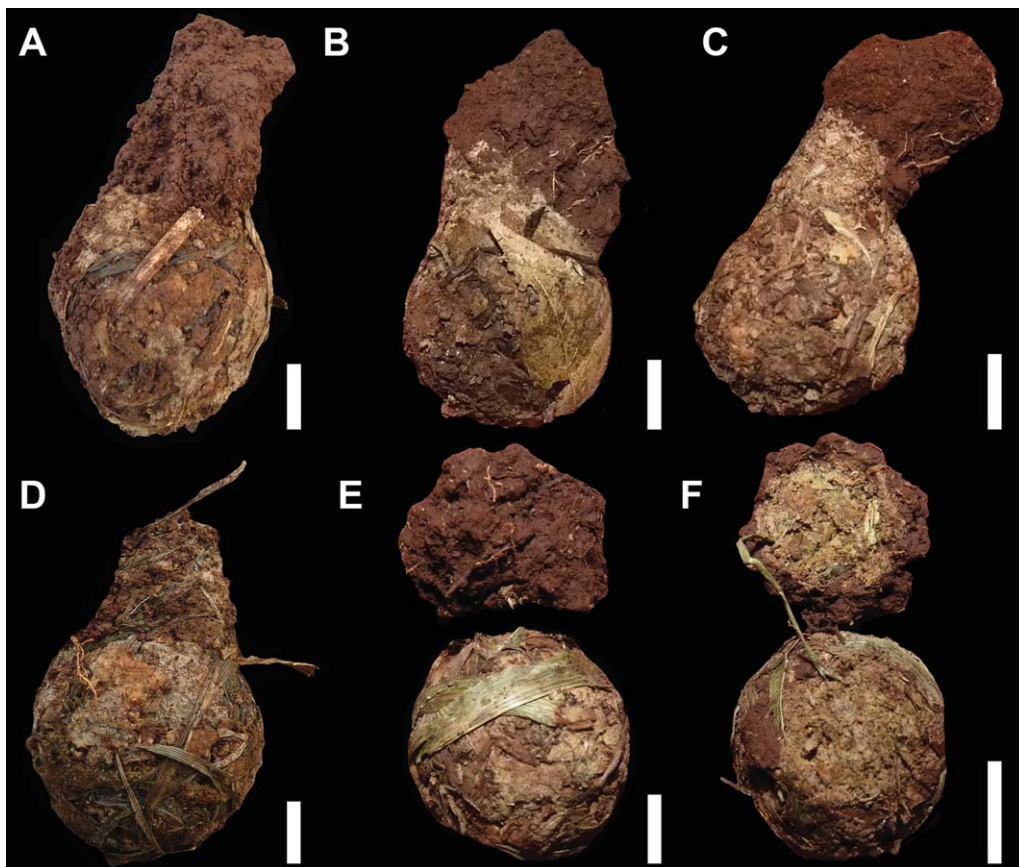


Fig. 2. Brood chambers of *Dichotomius carbonarius*. A) Leaf layer composed of monocot leaves and soil covering the protuberance, B) With entire leaf of *rabo duro* in the external layer, C) External leaf layer mostly missing, D) Protuberance covered by a layer of grasses, E and F) Same chamber showing split between protuberance and spherical structure; note the absence of a leaf layer in the contact zone of the two parts and the grass leaf included in provisions connecting both parts. Scale bar = 1 cm.

burrows excavated in the soil, four of them filled with 2–5 cm of *fumo bravo* leaf litter.

DISCUSSION

The possible sequence in the construction of brood chambers, inferred from their structure, is: 1) a vertical to slightly inclined burrow is excavated (Fig. 5A); 2) the distal extreme is enlarged to form a spherical cavity (Fig. 5B); 3) the cavity is lined with entire or large fragments of leaves (Fig. 5C); 4) at the distal pole, leaf litter is deposited, leaving a hemispherical space where one egg is laid (Fig. 5D); 5) the egg chamber is closed with more layers of litter, forming its spherical shape; 6) more meniscate packets are added until the complete cavity is filled (Fig. 5E); 7) on the proximal pole, the adjacent part of the burrow is

blocked with thick, perpendicular litter layers, forming the cylindrical protuberance; and 8) the remaining burrow is filled with soil (Fig. 5F). The resulting structure, which can be broadly defined as a brood chamber (Sánchez and Genise 2008), combines features of brood masses and brood balls. According to Halffter and Edmonds (1982), a brood mass consists of a quantity of provision, receiving an egg, which has been packed into the blind end of a tunnel or tunnel branch, or into a dilation of a tunnel. The shape is determined by the original cavity. It can be cylindrical (*i.e.*, ‘sausage’) to oval or spheroid. On the other hand, a brood ball is a quantity of provision, receiving an egg, which has been molded by a parent into a spheroid onto the outer surface of which a soil layer may be added. The finished brood ball lies in a cavity partially

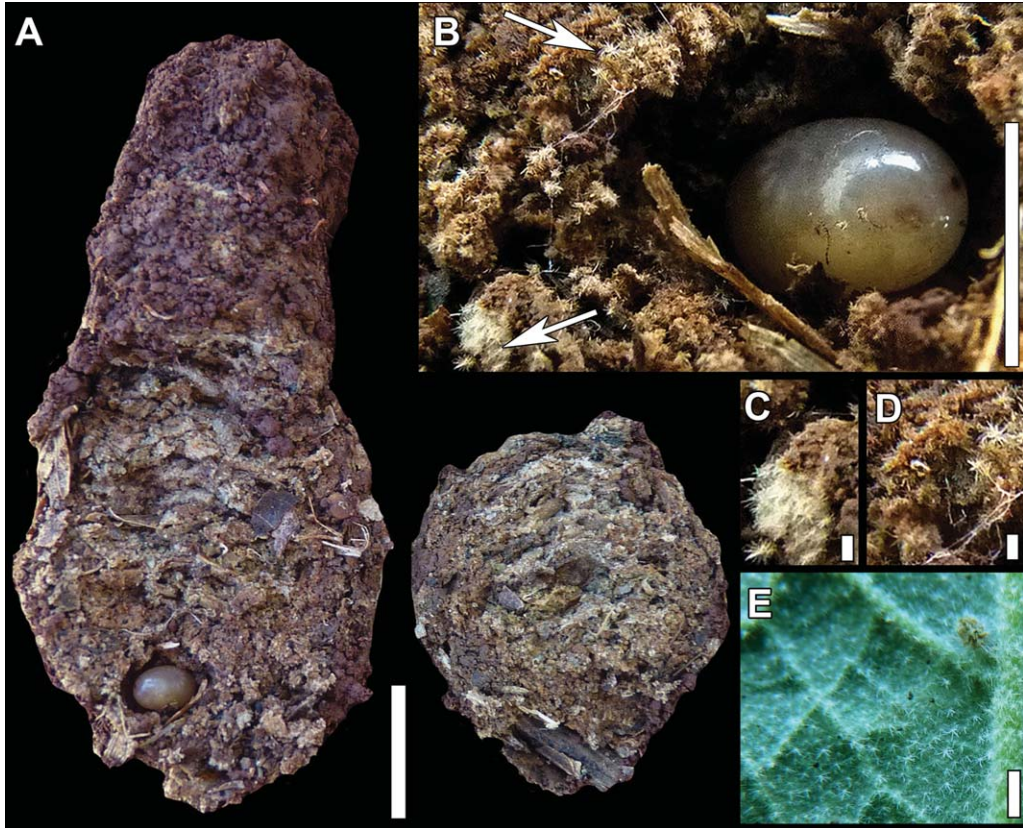


Fig. 3. A) Longitudinal section of a brood chamber of *Dichotomius carbonarius*, showing the egg chamber and some meniscate packets concavely downwards, scale bar = 1 cm, B) Egg with pharate larva inside and provisions with abundant trichomes (arrows), scale bar = 0.5 cm, C–D) Magnified trichomes, scale bar = 0.25 mm, E) Trichomes on a leaf of *fumo bravo*, scale bar = 1 mm.

surrounded by an air layer (nesting chamber *sensu* Sánchez and Genise 2008).

Brood chambers of *D. carbonarius* are intermediate between brood masses and brood balls. On the one hand, they are spherical with a cylindrical protuberance, and they have a distinct outer layer as in brood balls. The outer wall of brood balls of *Deltochilum gibbosum* (F.) is also made with entire leaves (Howden and Ritcher 1952). The lack of an external soil wall may be considered as replaced by a leaf layer. The selection of two different kinds of substrates, entire leaves for the wall and litter for provisions, to construct the chamber is more compatible with brood balls. The spherical part of the structure split completely and easily from the cylindrical part. During larval development, this cylindrical structure was never consumed by the larva and is not involved in the pupation chamber's construction. On the other hand, the lack of an external soil wall, nesting

chamber, and the egg chamber located at the distal end argue for ball-shaped brood masses. These particular brood chambers resemble incipient brood balls of *Neocanthidium martinezi* Edmonds and Halffter, which were considered as a link between the typical brood masses of Pattern I nesters and the lineage leading to Pattern II brood balls (Halffter and Edmonds 1982).

The ancestral state of detritus-feeding in Scarabaeinae (Scholtz *et al.* 2009) led to coprophagy when new ecological niches associated with large sized mammal radiation appeared (Genise 2004), probably during the Eocene. Derived from this new source of food, an exaptation of the mouthparts for the manipulation of dung arose (Halffter and Edmonds 1982). This novel ability resulted in the evolution of food relocation strategies and new behaviors that involved changes associated with the construction of brood masses or balls made

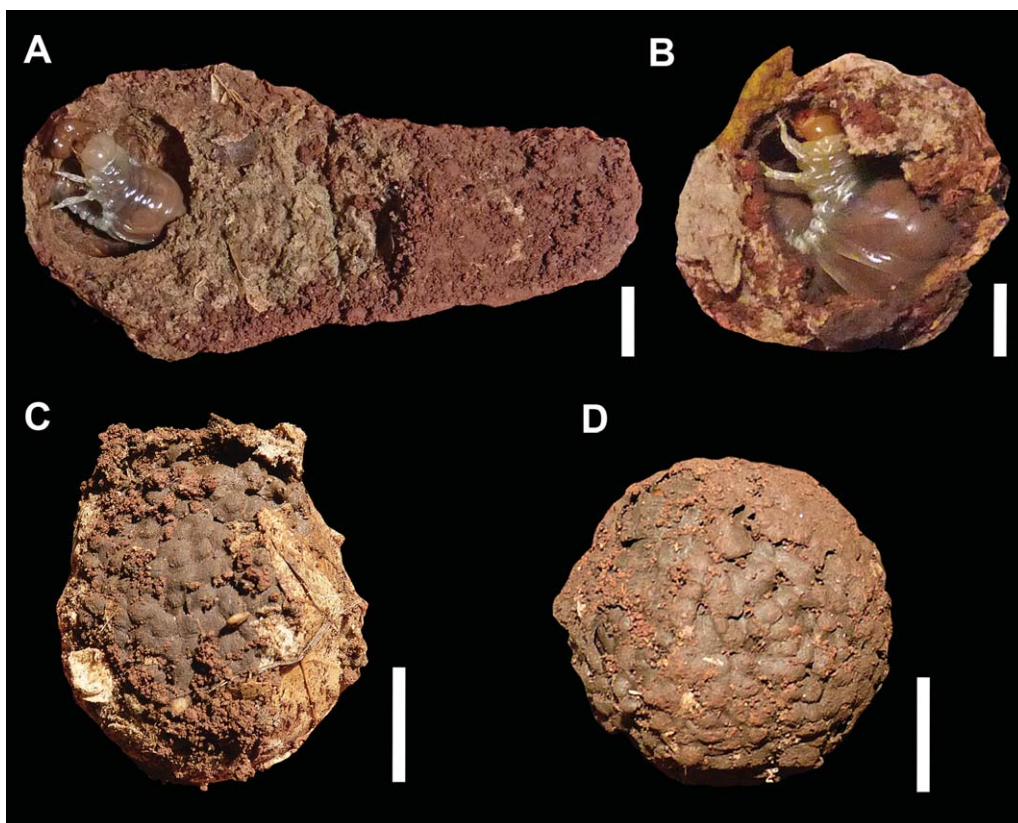


Fig. 4. A) Longitudinal section of a brood chamber of *Dichotomius carbonarius*, showing a two-week-old larva molding a fecal pellet with its mouthparts inside a cavity within provisions, scale bar = 0.5 cm, B) Five-week-old larva with large hump inside brood chamber, scale bar = 0.5 cm, C) Pupation chamber with remains of the leaf layer; note the lack of arrangement of pellets and the botryoidal aspect, scale bar = 1 cm, D) Other pupation chamber without remains of the leaf layer, scale bar = 1 cm.

with the new, softer resource (Halffter and Matthews 1966; Halffter and Edmonds 1982; Hanski and Cambefort 1991; Scholtz *et al.* 2009). As a consequence, the Scarabaeinae went through an evolutionary radiation from the Eocene onwards, related to the expansion of medium/large sized herbivores in grass-dominated open habitats (Genise 2004; Sánchez *et al.* 2010b). This event was so significant that in Patagonian paleosols, for instance, fossilized brood balls (*Coprinisphaera* Sauer) may be found in extremely high densities (Genise 2004; Laza 2006; Sánchez *et al.* 2010b). In the Neotropical region, the extinction of large mammals by the Pleistocene–Holocene resulted in a larger diversity of dung beetles in the rainforest and the acquisition of new feeding strategies, such as necrophagy, saprophagy, and frugivory (Halffter 1959; Halffter and Matthews 1966).

The reversal change to the ancestral feeding on detritus is somewhat common (Halffter and

Halffter 2009), whereas the use of plant detritus for nesting is extremely rare, with only a few cases recorded until now. The African species of *Pachysoma* McLeay feed on leaf detritus and dry fecal pellets, displaying a major modification related to food relocation. The larvae are free to move and feed inside provisioned burrows (Scholtz *et al.* 2004; Holter *et al.* 2009). *Attavicinus monstrosus* (Bates), which is associated with ant nests, makes provisions from plant detritus obtained from the waste of attine nests (Halffter and Matthews 1966; Philips and Bell 2008). Among ball-producers, there are also very few examples. In Africa, species of *Paraphytus* Harold feed and breed on well-rotted wood, fungi, and excrement from xylophagous insects, and species of *Coptorhina* Hope collect pieces of mushrooms which are provisioned in subterranean burrows to construct soil-covered brood balls (Davis *et al.* 2008; Frolov *et al.* 2008). The Australian *Cephalodesmus*

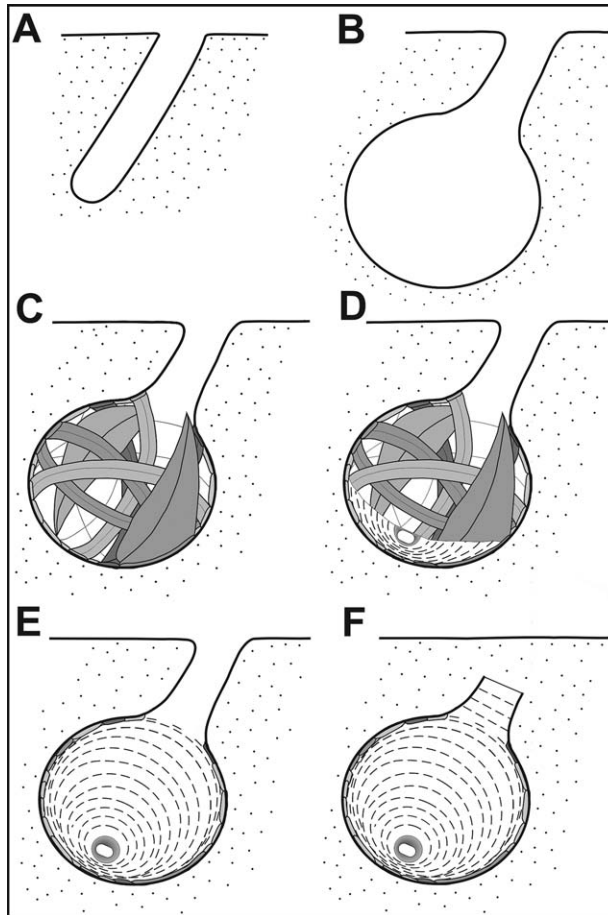


Fig. 5. Probable sequence of construction of brood chambers: A) Original inclined burrow, B) Distal extreme enlarged, forming a spherical cavity, C) Cavity lined with entire or large fragments of leaves, D) Leaf litter at the distal pole leaving a hemispherical space for the egg, E) Egg chamber closed and more meniscate packets added until cavity completely filled, F) Burrow adjacent to proximal pole blocked with thick, perpendicular litter layers forming cylindrical protuberance and remaining burrow filled with soil.

armiger Westwood, which exhibits a very complex nesting behavior, uses decomposed leaf pieces, small flowers, seeds, fruits, and its own feces to prepare macerated fungus-enriched provision balls. Adults of both sexes feed on these balls, whereas the females construct brood balls from them. Nests are composed of several brood balls and complex parental care is involved (Monteith and Storey 1981).

Regarding the feeding and nesting behavior within *Dichotomius* Hope, adults of several species mentioned in the exhaustive review by Halffter and Halffter (2009) are exceptions to coprophagy by being attracted to fermented fruits and seeds. *Dichotomius carbonarius* is referred to as copro-necrophagous because it has been very occasionally collected in traps baited with fer-

mented bananas. *Dichotomius carolinus* (L.) constructs two spherical brood masses in the blind end of a nesting burrow, which are composed of dung from which the adults removed previously all larger grass fragments (Halffter and Matthews 1966; Edmonds and Halffter 1972). *Dichotomius anaglypticus* (Mannerheim), *Dichotomius haroldi* (Waterhouse), *Dichotomius micans* (Luederwaldt), and *Dichotomius semiaeneus* (Germar) construct cylindrical brood masses of dung (Cabrera Walsh and Gandolfo 1996). Consequently, the morphology and the provisions of the brood masses of the other studied species included in the genus are not similar to that of *D. carbonarius*.

The behavior of *D. carbonarius* described herein records the first dung beetle brood chambers entirely made of leaf litter and covered

by a thin layer of small leaves. It is also the first recorded case of leaf-litter provisioning. *Dichotomius micans* also belongs to the subgenus *Luederwaldtinia*, suggesting that the behavior described herein might be an autoapomorphy for *D. carbonarius*. Adult feeding on *fumo bravo* leaves could indicate some morphological or physiological adaptations. Members of *Luederwaldtinia* also show exceptional phenotypic plasticity involving brachyptery in *Dichotomius* (*L.*) *vidaurrei* Nunes and Vaz-de-Mello and *Dichotomius* (*L.*) *mysticus* (Luederwaldt) (Nunes and Vaz-de-Mello 2013).

Finally, the pupation chamber constructed without any pellet arrangement differs from those helicoidal chambers composed of whorls of imbricated pellets described for *Sulcophanaeus* d'Olsoufieff (Phanaeini), *Malagoniella* Martínez (Canthonini), *Anomiopsoides* Blackwelder (Eucraniini), and even other *Dichotomiini* such as *Ontherus sulcator* (F.) (Sánchez *et al.* 2010a). Also, it is different from those of *Homocopris torulosus* (Burmeister) (Dinghi *et al.* 2012) and those preserved inside fossil brood balls (*Coprinisphaera*) from the Cenozoic of Patagonia (Laza 2006). This might suggest that this branch of *Dichotomius* including the species of *Luederwaldtinia* perhaps is a separate lineage.

ACKNOWLEDGMENTS

We thank Julián Baigorria (Karadya Bioserve, Misiones), Ernesto Krauczuk (Director de Biodiversidad de Misiones), Horacio and Nahuel Schenone, Javier Unizoni (CIAR, Misiones - Fundación Bosques Nativos Argentinos para la Biodiversidad), and Francisco "Paco" La Roche (Universidad de La Laguna, Tenerife). We thank Mufasa, Osvaldo, and Afrodita for allowing us to work inside their kennel. We also thank two anonymous reviewers. This research was supported by grants from Agencia Nacional de Promoción Científica y Tecnológica of Argentina, FONCYT-PICT 1972 (J. F. Genise) and FONCYT-PICT 2463 (M. V. Sánchez).

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(Received 25 April 2013; accepted 16 July 2013. Publication date 20 September 2013.)