WHY AND WHERE COPROPHAGOUS BEETLES (COLEOPTERA: SCARABAEINAE) EAT SEEDS, FRUITS OR VEGETABLE DETRITUS

Gonzalo Halffter & Violeta Halffter

Instituto de Ecología, A.C. Km. 2.5 Carr. Antigua a Coatepec No. 351. Congr. El Haya, 91070, Xalapa, Mexico
gonzalo.halffter@inecol.edu.mx

Abstract: The objective of this paper is to present a comprehensive review of all published and unpublished (more than 50% of the information provided) data that we have been able to gather on the deviation from coprophagy in a typical coprophagous group of insects, the subfamily Scarabaeinae. Studied deviations from coprophagy include the consumption of seeds, fruits and even flowers, as well as of vegetable detritus and debris from Attini ants' nests.

We separately analyzed those cases in which adults were found in these sources of food, and those in which nidification —larvae feeding— takes place using these foods. The reason for this is that we consider that the change from coprophagy to frugivory or saprophagy (and for the same reasons to necrophagy or mycetophagy) does not represent a significant change for the adult Scarabaeinae. Their mouthparts, intestine, and feeding behavior are adapted to feeding on doughy food. From this food, microorganisms, juices and cellular leftovers go through the mouthparts (microphagic feeding). This happens for excrements, but also for fruits and fermented detritus. On the other hand, the change is more drastic for the larvae. There are ten times fewer known cases of use of alternative food sources for nidification than for adult feeding. However, a series of microbial fermentation processes in a secondary rumen enable some species to nidify using seeds and fruit pulp, as well as vegetable remains.

The consumption of seeds and fruits occurs with different frequencies throughout different biogeographical regions. In the Neotropics this phenomenon is at least ten times more frequent than in the Ethiopic and Oriental Regions. Furthermore, most cases take place in humid forest localities. We propose that the shift from coprophagy to alternative feeding habits was an adaptation to the massive extinction of medium and large size mammals —the main excrement sources— in this region, which started approximately 10,000 years ago. This adaptation was responsible not only for the survival of the Scarabaeinae in the region, but also for the significant richness that they exhibit.

In the arid northwest of Argentina and in the desert of southwest Africa, phylogenetically unrelated beetles use vegetable detritus, relocating and storing it in underground galleries, below the soil humidity level. This fermented detritus is used as the source of food for adults and larvae. The Australian genus *Cephalodesmius* relocates its food in the same way, but exhibits a higher degree of complexity.

In all cases in which nidification was studied in depth, there is a secondary rumen in which the food stored by both parents or by the mother suffers a first microbial fermentation. In *Cephalodesmius*, this rumen is present throughout the whole, prolonged nidification process, and is the base of a complex subsocial behavior.
Key words: Coleoptera, Scarabaeinae, frugivory, Attini ants' detritus, vegetable detritus, saprophagy.

Por qué y dónde los escarabajos coprófagos (Coleoptera: Scarabaeinae) comen frutas, semillas o detritos vegetales
Resumen: Con este trabajo pretendemos una revisión exhaustiva de todo lo publicado e inédito (más del 50% de la información total) que hemos podido reunir sobre una serie de desviaciones de la coprofagia en un grupo de insectos que es típicamente consumidor de excrementos, la subfamilia Scarabaeinae. Las desviaciones de la alimentación coprófaga estudiadas, comprenden el consumo de frutas, semillas e incluso flores, así como el de detritus vegetales y del debrís que se acumula en los hormigueros de hormigas Attini.

Se analizan por separados los casos de adultos encontrados en los alimentos señalados y los de nidificación (alimentación de las larvas). Lo anterior porque consideramos que el paso de coprofagia a frugivoría o saprofagia (y por las mismas razones a necrofagia y micetofagia) no representa para el Scarabaeinae adulto un cambio funcional importante. Sus piezas bucales, su intestino y su comportamiento alimentario están adaptados para el consumo de un alimento pastoso, del cual las piezas bucales dejan pasar microorganismos, jugos y restos celulares (alimentación microfágica). Esto ocurre con el excremento, pero igualmente con frutas y detritus en fermentación. Para las larvas el cambio es más drástico (se conocen diez veces menos casos de uso de los alimentos señalados para la nidificación, en comparación con los adultos). Sin embargo, una serie de procesos de fermentación microbiana en rúmenes externos hacen posible que algunas especies nidifiquen con pulpa y semillas de frutas, así como con restos vegetales.

El consumo de frutas y semillas ocurre con muy diferente frecuencia en las distintas regiones biogeográficas. En el Neotrópico se encuentran por lo menos 10 veces más casos que en las regiones que siguen: Oriental y Etiópica. Por otra parte, la mayor cantidad de ejemplos corresponden a localidades con selvas húmedas. Proponemos que la mucho mayor frecuencia en las selvas del Neotrópico es una respuesta adaptativa a la extinción masiva en esta región de mamíferos de tallas media y grande (las fuentes principales de excremento) iniciada hace aproximadamente 10000 años, y que determina que las selvas neotropicales sean comparativamente mucho más pobres en mamíferos de esas tallas. Proponemos que los Scarabaeinae han podido sobrevivir (con una riqueza importante de especies) a este fenómeno, por la adaptación de muchas especies -en forma parcial o total- al consumo de pequeños cadáveres y frutos en descomposición.

En el noroeste árido de Argentina y en el desierto del sudoeste de África se presenta en escarabajos no filogenéticamente relacionados, el acúmulo de detritus vegetales en galerías subterráneas debajo del nivel de humedad del suelo. Estos detritus, fermentados, son usados para la alimentación de los adultos y de las larvas. La misma relocalización, pero con un alto grado de complejidad, es empleada por el género australiano *Cephalodesmius*.

En todos los casos en que la nidificación se ha podido estudiar en detalle, se ha encontrado un rumen externo en el que el alimento acumulado por los padres, o por la madre, sufre una primera fermentación microbiana. En *Cephalodesmius* la presencia de este rumen que es permanente durante todo el prolongado proceso de nidificación, es la base de un complejo comportamiento subsocial.
Palabras clave: Scarabaeinae, frugivoría, saprofagia, detritus de hormigas Attini, detritus vegetales.

Introduction

The subfamily Scarabaeinae is the most important group of coprophagous beetles in the intertropical and warm-temperate zones of the world. In adults, their anatomy, i.e., mouthparts, forelegs tibia and digestive tube, is clearly adapted to manipulate and use mammal's excrements, especially those of herbivores and omnivores. Their feeding and nidification behavior comprise a series of diverse responses to find an originally concentrated food source, in order to avoid extreme competition in the nesting site (see Halffter & Edmonds, 1982). Despite this general adaptation to coprophagy, some species show adaptations to feed—and to a lesser extent to nidify and feed their larvae—on some other types of food such as fruits, small corpses, decomposing fungi, debris from Attini ants nests, and even some extraordinary specializations such as feeding on Diplopoda or abdomens of female *Atta* during their nuptial flight.

There is an important functional difference between adults and larvae in the change from being coprophagous to become frugivorous, necrophagous or mycetophagous. In the adult, the mouthparts are extraordinarily well adapted to ingest doughy food, rich in microorganisms. The incisive part of the mandibulae is membranous; the molar part (non symmetrical from right to left) form a grinding mortar; both lacinia and galea of the maxillae are membranous and with abundant setae, just as in the labrum-epipharinx (for a description and figures of the mouthparts, see Miller, 1961; Halffter, 1961; Halffter & Matthews, 1966, 1971; Hata & Edmonds, 1983; López-Guerrero, 2007) (Figs. 1, and 3 to 11). Very similar mouthparts are found in another group of Scarabaeoidea: Aphodiini, exclusively coprophagous. In the Scarabaeinae the digestive tube is also adapted to the coprophagy (microphagy). Very long and spiral like (Umeya, 1960; Miller, 1961; Halffter & Matthews, 1966, 1971), it is perfectly adapted to digest a doughy food with juices and microorganisms, previously selected by the mouthparts (Fig. 13).

In adults the change to necrophagy, frugivory, or mycetophagy is not radical, because from the carrion, fruit, or decaying fungi they can only ingest the thick paste containing juices and microorganisms. This explains why it is so frequent to find adults of the same species (especially in the humid tropical forests of America) feeding on dung, carrion, and decomposing fruits.

The structure of the mouthpieces and digestive tube in the larvae are completely different (see Goidanich & Malan, 1962, 1964; Halffter & Matthews, 1966, 1971). The mouthparts are well sclerified, hard, and sharp, like in many other Scarabaeoidea (Fig. 2). The digestive tube has an important fermentation camera and is shorter than that of adults (Fig. 12). The mouthparts and digestive tube are adapted to a much drier and fibrous material, with a high percentage of vegetable fiber, like that found in dung.

Except for very few cases (*Trichillum* and closely related genera [López-Alarcón *et al.*, 2009]), larvae eat the material that the female (with various degrees of cooperation from the male) has saved for them, in the form of brood ball or "sausage" (brood mass). Even though this material is selected by the parents in the preparation of the nest, it contains fibers to a greater or lesser degree. In many species, this material goes through a fermentation process in the form of a "cake" prepared by the parents before its transformation into brood-balls (the most remarkable case is described in *Copris*, Huerta *et al.*, 1980; Halffter, 2000), or brood masses. However, the most notable fermentation is done by the microorganisms found in the larvae's own excrement, which is deposited over and over again on the material collected by the parents (Halffter, 1991b). In the case of nidification, the change to frugivory or other feeding alternatives is more complicated than for adults. First, the parents have to manipulate the new type of food and store de brood ball or mass. Moreover, the fermentation processes in the stored food and in the corresponding camera of the larval intestine are very different. All these differences may be reason why there are many reported cases of adult frugivory by very few on larvae.

In this work we aim to make a comparison of frugivory in adults and larvae. To accomplish this, we present a review of the vast literature on the subject, plus we offer new data of adults found in fruits, and all the known and new cases of nidification in fruits, seeds and vegetable remains. Notwithstanding the numerous citations, there are few taxonomic groups involved, and almost without exception, they correspond to tropical forests, especially in America and Southeast Asia. Finally, we compare the feeding process in adults and larvae, as well as their geographic and ecological distribution.

Frugivory and saprophagy in adults

The first work entirely dedicated to frugivory in Scarabaeinae is that of Pereira & Halffter (1961), and it deals exclusively with the Neotropics. Halffter & Matthews (1966) presented a synthesis and a discussion of the known cases from around the world in which there are shifts from coprophagy to some other form of feeding, including frugivory. From 12 bibliographic sources and original data, Gill (1991) presented a Table with 34 Scarabaeinae species, where adults had been collected from fallen fruits in tropical America. All these works constitute the precedents of this study.

In this section we group previously published or new data of adult Scarabaeinae attracted by fruits, according to their biogeographic region, and related by species. In each case, we present the beetle species, the fruit in which it was found, the geographic location, and the source.

Neotropical region

Canthon angularis Harold; found in fruits of the *Butia* palm; Brazil. Pereira & Martínez, 1956.

Canthon conformis Harold; found in fruits of the *Butia* palm; Brazil. Pereira & Martínez, 1956.

Canthon fortemarginatus Balthasar; found in fruits of *Annona crassiflora* (Annonaceae); Brazil. Fernando Vaz de Mello (personal communication).

Canthon imitator Brown; a clearly coprophagous species. In the arid center of Mexico, Miguel Angel Morón (personal communication) found two specimens reaping a piece of decaying pulp from the *Opuntia* fruit (Cactaceae). Although several fallen fruits dispersed on the ground were checked, no further specimens were found.

Canthon indigaceus chevrolati Harold; this clearly coprophagous species can respond to an exceptional offer of vegetable resources. Thus, Morón *et al.* (1988) cite some individuals rolling pieces of *Opuntia* cladodes (Cactaceae) and *Opuntia* fruit peels, Mexico.

Fig. 1. Mouthpieces from an adult Scarabaeinae. From Halffter & Edmonds, 1982.
Fig. 2. Mouthpieces from a Scarabaeinae larva. From Halffter & Edmonds, 1982.
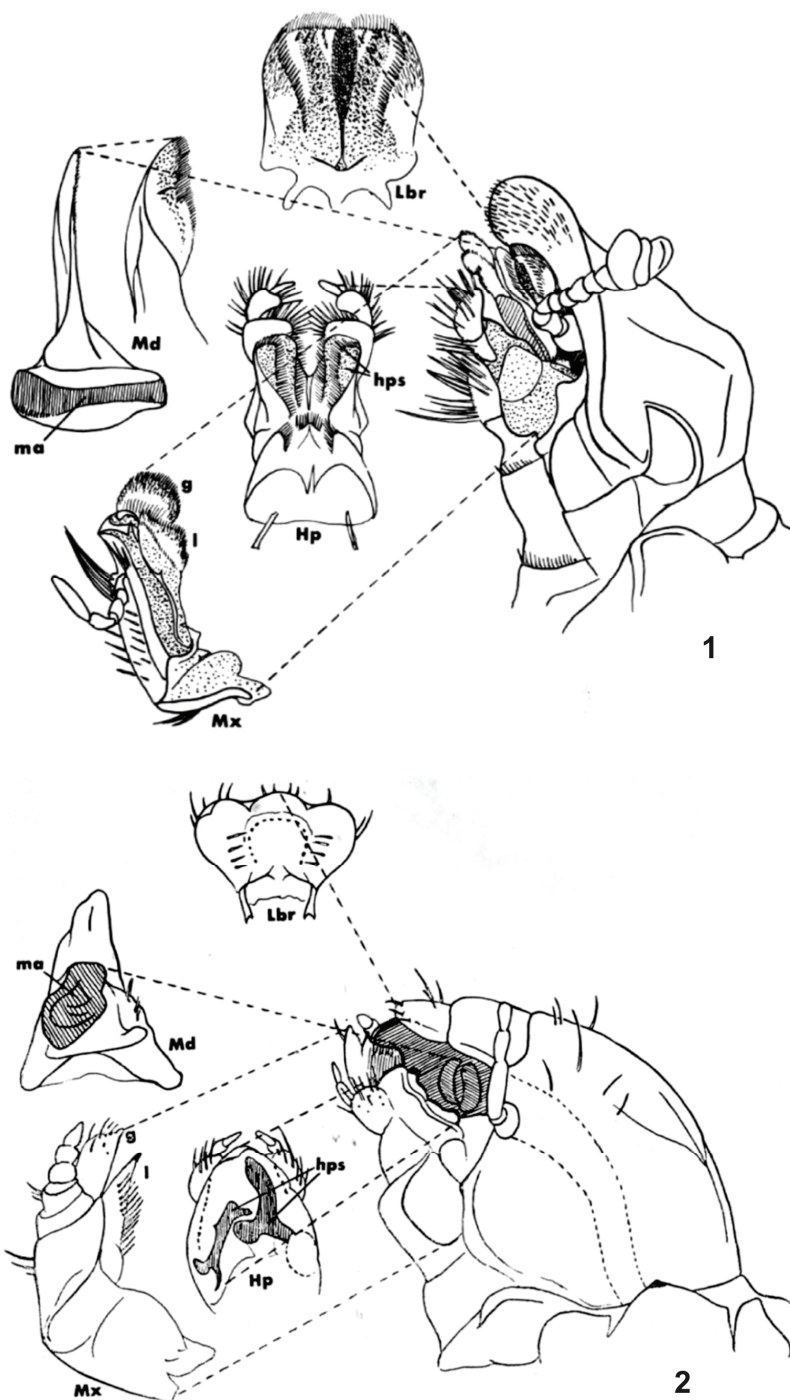
Canthon latipes Blanchard; found in fruits of the *Butia* palm; Brazil. Pereira & Martínez, 1956.

Canthon lituratus Germar; found in fruits of the *Butia* palm; Brazil. Pereira & Martínez, 1956.

Canthon moniliatus Bates; found in decomposing fruits of *Entada* (Leguminosaceae), as well as in other fruits; Costa Rica, Panama. Howden & Young, 1981; Solís & Kohlmann, 2002; Escobar *et al.*, 2008.

Canthon muticus Harold; found in fruits of the *Butia* palm; Brazil. Pereira & Martínez, 1956.

Canthon virens (Mannerheim) found in fruits of pequí (*Cariocas brasiliense*, Cariocaceae); Brazil. Fernando Vaz de Mello (personal communication).

Canthon virens scrutator Balthasar (cited as *C. scrutator* Balthasar); found in fruits of the *Butia* palm; Brazil. Pereira & Martínez, 1956.

Canthon (*Glaphyrocanthon*) *leechi* Martínez, Halffter & Halffter; found in figs and other rotten fruits; Mexico. Lucrecia Arellano (personal communication).

Canthon (*Glaphyrocanthon*) *zuninoi* Rivera & Halffter; in decaying mangoes; Mexico. Lucrecia Arellano (personal communication).

Canthonella silphoides (Harold); found in traps baited with fermented bananas. However, they were more common in traps baited with excrement, and to a lesser degree in those baited with carrion; Brazil. Julio Louzada (*in litt.* 25/II/2009).

Deltochilum brasiliense Laporte; copro-necrophagous species; very few individuals collected in traps baited with fermented bananas; Brazil. Julio Louzada (*in litt.* 25/II/2009).

Deltochilum furcatum Laporte; copro-necrophagous species collected relatively frequently in traps bated with fermented bananas; Brazil. Julio Louzada (*in litt.* 25/II/ 2009).

Deltochilum pseudoparile Paulian; occasionally found in fruits of *Stemmademia donellsmithi* (Apocynaceae); Mexico. Alfonso Díaz (personal communication). See the Nidification section.

Eurysternus cyanescens Balthasar; although more commonly found in traps baited with carrion or excrement, also collected in those baited with fermented bananas; Brazil. Julio Louzada (*in litt.* 25/II/2009).

Eurysternus hirtellus Dalman; collected with similar frecuency in traps baited with fermented bananas, carrion or excrement; Brazil. Julio Louzada (*in litt.* 25/II/2009).

Eurysternus plebejus Harold; found relatively abundant in fallen fruits and flowers (eating the petals) of *Gustavia* (Lecythidaceae), although it is also attracted by excrement and carrion; Costa Rica, Panama and Colombia. Howden & Young, 1981; Noriega & Calle, 2008; Escobar *et al.*, 2008.

Ateuchus candezei Harold; found in palm fruits; Costa Rica, Panama. Howden & Young, 1981; Escobar *et al.*, 2008.

Ateuchus illaesum Harold; found in rotten fruits; West Indies, Mexico. Arrow, 1903; Halffter & Halffter (original information).

Ateuchus squalidus (Fabricius); found under guriri fruits (*Allagoptera arenaria*, Araceae); Brazil. Fernando Vaz de Mello (personal communication).

Canthidium ardens Bates; found in palm fruits; Costa Rica, Panama. Howden & Young, 1981; Escobar *et al.*, 2008.

Canthidium aterrimum Harold; attracted to traps baited with fermented bananas, although it's more commonly attracted to those with carrion and mainly to those with excrement; Brazil. Julio Louzada (*in litt.* 25/II/2009).

Canthidium barbacenicum Preudh.; found in mature coconuts of the *Butia* palm; Brazil. Pereira & Halffter, 1961.

Canthidium cupreum Blanchard; found in freshly cut palm heart; Bolivia. Pereira & Halffter, 1961.

Canthidium decoratum Perty; found in fruits of the *Butia* palm and burying piqui fruits (*Cariocas brasiliense*, Cariocaceae); Brazil. Pereira & Halffter, 1961; Fernando Vaz de Mello (personal communication).

Canthidium elegantulum Balthasar; found in *Ficus* fruits; Panama. Howden & Young, 1981.

Canthidium laetum Harold; found eating and burying legume seeds; locally is a true specialist of them (more information in the Nidification section); also found in fallen fruits of *Poulsenia armata* (Moraceae); Mexico, Costa Rica. Kohlmann & Solís, 2004; Halffter & Halffter, original information.

Canthidium marseuli Harold; found burying piqui fruits (*Cariocas brasiliense*, Cariocaceae); Brazil. Fernando Vaz de Mello (personal communication).

Canthidium nobilis Harold; found in fruits of the *Butia* palm; Brazil. Pereira & Halffter, 1961.

Canthidium aff. *pinotoides* Balthasar; found in *Annona crassiflora* fruits (Annonaceae); Brazil. Fernando Vaz de Mello (personal communication).

Canthidium aff. *quadridens* Harold; found in cacao fruits (*Theobroma cacao*); Peru. Larsen *et al.*, 2005.

Canthidium splendidum Preudh.; found in fruits of the *Butia* palm; Brazil, Pereira & Halffter, 1961.

Canthidium tuberifrons Howden & Young; found in *Solancus* fruits; Panama. Gill, 1986.

Canthidium sulcatum Perry; attracted exclusively and abundantely to fermented banana traps (the other alternatives being carrion and excrement); Brazil. Julio Louzada (*in litt.* 25/II/2009).

Although Halffter & Matthews (1966: 35-36) cite references of *Bdelyrus* and other small Scarabaeinae found in decaying vegetable matter in different parts of the world, there is no certainty that they feed on humus, and there is the possibility that they feed on small excrement from rodents or snails. This could also be the case for the small species of *Canthidium* and *Cryptocanthon*, collected by sifting leaf litter in the forests of Mexico and Central America.

This is an interesting problem, because it has been proposed that humus feeding is the ancestral character in Scarabaeinae (see Discussion). Making reference to *Bdelyrus bromeliatilis* and to another non identified species found in decaying vegetable matter accumulated between the petioles of palm leaves in the Amazonia, Halffter & Matthews (1966) noted that "… the species of *Bdelyrus* mentioned above are more likely to be truly saprophagous that any other known Scarabaeinae".. This statement has been reiterated by later authors. But, what is the current state of knowledge concerning this matter? There are 25 known species of *Bdelyrus* (Cook, 1998, 2000; Vaz de Mello *et al.*, 2008) distributed in the humid forests of the Neotropics, from Mexico to the south of Brazil. According to Cook (1998), adults of these species have been found among detritus of terrestrial and arboreal bromeliads (see also Huijbregts, 1984), in traps baited with excrement and carrion, in soil detritus, and in *Heliconia* flowers (see also the references included on fruit capture). Those species for which we have exact references as to have been collected in bromeliads are: *B. geijskesi* Huijbregts and *B. bromeliatilis* Cook. We consider that there is enough evidence to prove the association between these two species and the detritus accumulated in the bromeliads. However, there are still another 23 collected species from ground leaf litter (a fact that by itself does not indicate anything about their feeding habits), from traps baited with excrement and carrion, from fruits or even from *Heliconia* flowers.

➤ **Fig. 3-11.** Microphotographs of mouthpieces from adult Scarabaeinae. **Fig. 3.** Labrum-epipharinx (ventral view) in *Onthophagus hippopotamus* Harold; **Fig. 4.** Apical portion of the labrum-epipharinx in *Onthophagus punctatus* (ventral view); **Fig. 5.** Basal portion (ventral view) of the labrum-epipharinx in *O. punctatus*; **Fig. 6.** Left mandible (ventral view) in *Onthophagus incensus*; **Fig. 7.** Incisive portion (lateral view) of the right mandible of *Onthophagus moroni* Zunino and Halffter; **Fig. 8.** Molar area of the mandible (left concave, right convex) in *Canthon pilularis* (Linneo); **Fig. 9.** Molar area (lateral view) of the right madible in *Digithonthophagus gazella*; **Fig. 10.** Left maxilla (lateral view) in *O. punctatus*; **Fig. 11.** Detail of the lacinia (lateral view) in *O. punctatus*. Except Fig. 8, which belongs to Halffter & Edmonds, 1982, all images are original SEM microphotographs from Yrma López-Guerrero, Instituto de Ecología, A.C.
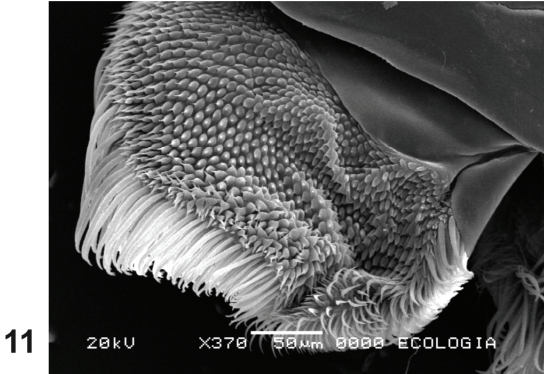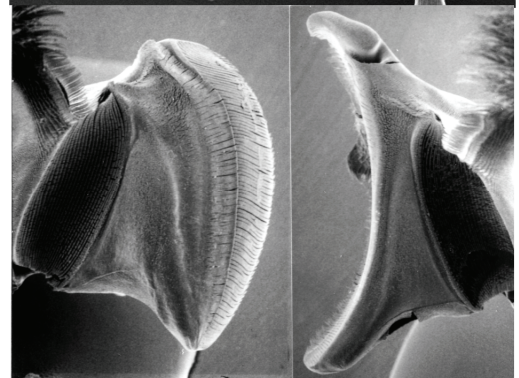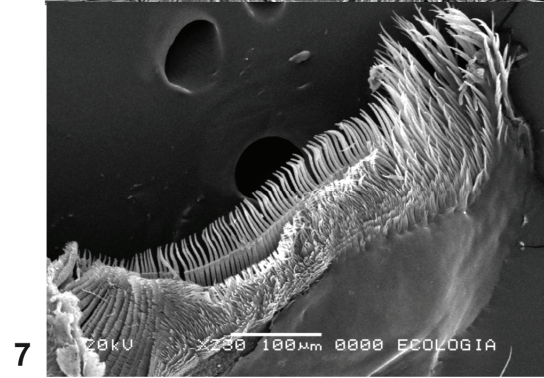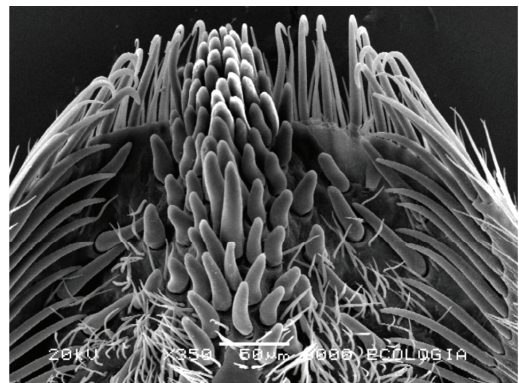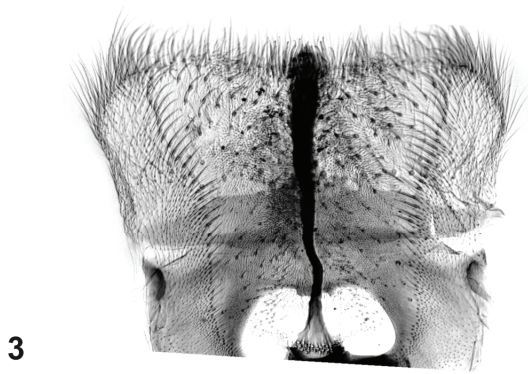
Bdelyrus bromeliatilis Cook; very abundant in accumulated organic debris in arboreal bromeliads; Brazil. Pereira *et al.*, 1960; Pereira & Halffter, 1961. (In these references, this species is wrongly cited as *B. lagopus* Harold).

Bdelyrus laplanadae Cook; especially attracted to *Gouraribae* fallen fruits (Bombacaceae); Colombia. Escobar, 2003.

Bdelyrus pecki Cook; at least fairly specialist of fallen fruits of one species of *Passiflora*; Peru. Larsen *et al.*, 2005.

Four unidentified species of *Uroxys* were collected in traps baited with fermented bananas, but also, and in larger numbers, in traps with carrion and excrement.

Chalcopris hesperus (Olivier); found in a recently cut rotten vine; Brazil. Pereira & Halffter, 1961.

Dichotomius amplicollis (Harold); found in various fallen fruits; Mexico. Halffter & Halffter (original information).

Dichotomius ascanius (Harold); found in guava and pineapple; also frequent in traps baited with fermented banana; Brazil. Luederwaldt, 1911; Julio Louzada (*in litt.* 25/II/2009).

Dichotomius ascanius piceus (Luederwaldt); found in coffee beans; Brazil. Pereira & Halffter, 1961.

Dichotomius aff. *ascanius* (Harold); found tearing apart fruits of *Annona crassiflora* (Annonaceae), and burying their pulp and seeds in gallerys up to 20 cm deep; Brazil. Fernando Vaz de Mello (personal communication).

Dichotomius bicuspis (Germar); found in gallerys under jaca fruits (*Artocarpus heterophylla*), and burying pulp and seeds of piqui fruits (*Cariocas brasiliense*, Cariocaceae); Brazil. Fernando Vaz de Mello (personal communication).

Dichotomius carbonarius (Mannerheim); a copro-necrophagous species, it has been occasionally collected in traps baited with fermented bananas; Brazil. Julio Louzada (*in litt.* 25/II/2009).

Dichotomius fissus (Harold); although it is also attracted to carrion and excrement baits, it is more frequently captured in traps with fermented bananas; Brazil. Julio Louzada (*in litt.* 25/II/2009).

Dichotomius geminatus (Arrow); found beneath oiti fruits (*Licania tomentosa*, Chrysobalanaceae) in storage galleries; Brazil. Fernando Vaz de Mello (personal communication).

Dichotomius glaucus (Harold); found in cut palm; Brazil. Luederwaldt, 1931.

Dichotomius laevicollis (Felsche); found in galleries, beneath jaca fruits (*Artocarpus heterophyllus* – Moraceae); Brazil. Fernando Vaz de Mello (personal communication).

Dichotomius mundus (Harold); found in traps baited with fermented bananas; Brazil. Julio Louzada (*in litt.* 25/II/2009).

Dichotomius muticus (Luederwaldt); collected almost exclusively from traps baited with fermented bananas (the other alternatives were traps baited with carrion and excrement); Brazil. Julio Louzada (*in litt.* 25/II/2009).

Dichotomius satanas (Harold); found in guava and coffee beans; Mexico. Lucrecia Arellano (personal communication).

Dichotomius sericeus (Harold); found in gallerys beneath jaca fruits (*Artocarpus heterophylla*); Brazil. Fernando Vaz de Mello (personal communication).

Copris lugubris Boheman; found in traps baited with bananas, and avocado fruits (*Persea* sp., Lauraceae); Costa Rica. Escobar *et al.*, 2008.

Phanaeus beltianus Bates; found in rotten *Monstera* sp. fruits (Araceae); Costa Rica. Bert Kohlmann (*in litt*, 13/I/2009).

Phanaeus endymion Harold; two individuals buried with an oval mass of fruit; Mexico. Halffter & Halffter (original information).

Phanaeus kirbyi (Vigors); found burying pulp and seeds from piqui fruits (*Cariocas brasiliense* – Cariocaceae) and *Annona crassiflora* (Annonaceae); Brazil. Fernando Vaz de Mello (personal communication).

Phanaeus palaeno Blanchard; found in fruits of *Annona crassiflora* (Annonaceae); Brazil. Fernando Vaz de Mello (personal communication).

Phanaeus pyrois Bates; found in palm fruits and *Gustavia* sp. fruits, but also in carrion and excrement; Costa Rica, Panama. Howden & Young, 1981; Escobar *et al.*, 2008.

*Coprophanaeus bellicosu*s (Olivier); although mainly attracted to carrion baits followed by excrement ones, some specimens have been collected in traps with fermented bananas; Brazil. Julio Louzada (*in litt.* 25/II/ 2009).

Oxysternum festivum (Linneo); beneath guriri fruits (*Allagoptera arenaria*, Araceae); Brazil. Fernando Vaz de Mello (personal communication).

Oxysternon palemo Castelnau; found in *Annona crassiflora* fruits (Annonaceae); Brazil. Fernando Vaz de Mello (personal communication).

Diabroctis mirabilis (Harold); found in *Annona crassiflora* fruits (Annonaceae); Brazil. Fernando Vaz de Mello (personal communication).

Onthophagus acuminatus Harold; found in *Virola* sp. fruits (Myristicaceae), and in traps baited with bananas; Costa Rica, Panama. Howden & Young, 1981; Kohlmann & Solís, 2001; Escobar *et al.*, 2008.

Onthophagus andersoni Howden & Gill; found in citric fruits; Costa Rica. Gill, 1991.

Onthophagus atriglabrus Howden & Gill; found in citrics, bananas, and other fruits; Costa Rica. Gill, 1991; Kohlmann & Solís, 2001.

Onthophagus batesi Howden & Cartwright; found in rotten avocados; Mexico. Lucrecia Arellano (personal communication).

Onthophagus belorhinus Bates; found frequently in diverse range of fallen fruits; Mexico, Guatemala, Panama. Bates, 1886; Halffter & Matthews, 1966; Gill, 1986.

Onthophagus bidentatus Drapiez; found in banana-baited traps; Ecuador. Peck & Forsyth, 1982.

Onthophagus canellinus Bates; found in banana-baited traps; Ecuador. Peck & Forsyth, 1982.

Onthophagus carpophilus Pereira & Halffter; this species is very abundant in zapote mamey fruits (*Calocarpum sapota*, Sapotaceae) as well as in other fruits. However, in these same localities some individuals were occasionally collected in carrion and excrement baited traps; Mexico. Pereira & Halffter, 1961; Halffter & Halffter (original information; see Palenque analysis).

Onthophagus corrosus Bates; found in various fruits; Mexico. Halffter & Halffter (original information).

Onthophagus dicranius Bates; found in *Gustavia*, as well and in some other fruits; Mexico, Panama. Howden & Young, 1981; Halffter & Halffter (original information).
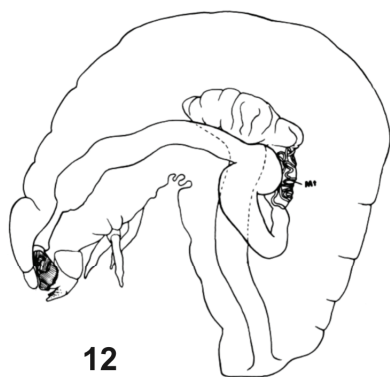
Fig. 12. Digestive apparatus from a Scarabaeinae larva, *Phanaeus quadridens* Say. From Halffter & Edmonds, 1982. **Fig. 13.** Digestive apparatus from an adult Scarabaeinae. From de Halffter & Edmonds, 1982.
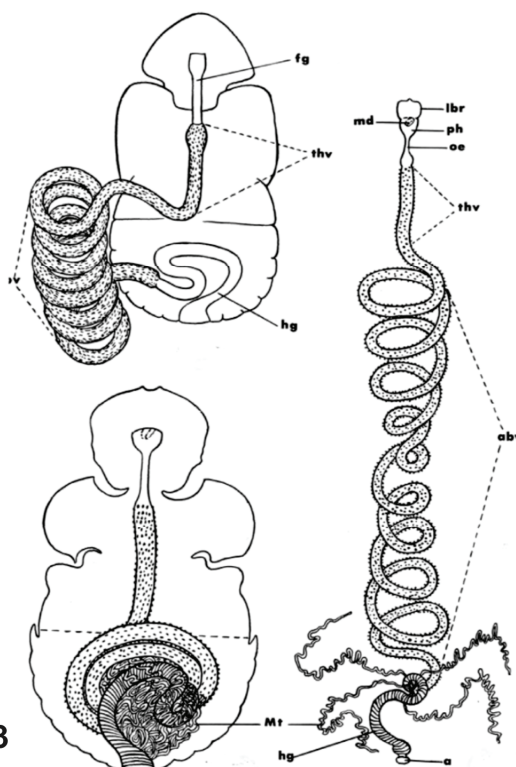
Onthophagus digitifer Boucomont; only collected in freshly cut hearts of palm; Bolivia. Pereira & Halffter, 1961.

Onthophagus genuinus Kohlmann & Solís; found in a variety of fruits; Costa Rica. Kohlmann & Solís, 2001.

Onthophagus incensus Say; collected in a trap baited with rotten fruit; Mexico. Matthías Rös (personal communication)

Onthophagus aff. *lucidum*; found burying pulp and seeds from *Ficus* sp. fruits (Moraceae); Brazil. Fernando Vaz de Mello (personal communication).

Onthophagus maya Zunino; found in a variety of fruits; Mexico. Halffter & Halffter (original information).

Onthophagus mirabilis Bates; found in avocado fruits; Panama. Gill, 1986.

Onthophagus nasicornis Harold; found in various decaying fruits, and even some individuals found in trays containing soy sprouts; Mexico. Halffter & Halffter (original information); Lucrecia Arellano (personal communication); Enrique Montes de Oca (personal communication). Pedro Reyes-Castillo (personal communication) has found numerous individuals of this species, both male and female, among the decaying bracts of a semi-aquatic plant (possibly *Hedichium coronarium*, Zingiberiaceae). Fernando Escobar and Matthías Rös (personal communication) found several specimens of this species apparently feeding on the inflorescences of *Xanthosoma*, probably *robustum* (Araceae), as well as inside the bracts.

Onthophagus nemorivagus Kohlmann & Solís; found in *Gustavia* fruits, and in banana-baited traps; Costa Rica. Kohlmann & Solís, 2001; Escobar *et al*., 2008.

Onthophagus ophion Erichson; solely collected in freshly cut hearts of palm; Bolivia. Pereira & Halffter, 1961.

Onthophagus orphnoides Bates; solely found in semi-rotten avocado seeds; Costa Rica. Kohlmann & Solís, 2001.

Onthophagus praecellens Bates; found in various fruits, including those of palm trees; Costa Rica, Panama.

Howden & Young, 1981; Gill, 1986; Kohlmann & Solís, 2001; Escobar *et al*., 2008.

Onthophagus rhinolophus Harold; found in different localities of east and southeast Mexico with tropical rain forest, abundant in Apocynaceae fruits, mangos, chirimoyas (*Anona cherimola*), zapote mamey, *Philodendron desmarestianus*, and *Syngonium podophyllum* (Araceae). Even found in rotten oranges and coffee beans; Halffter & Halffter (original information), Miguel Ángel Morón (personal communication), Lucrecia Arellano (personal communication), Alfonso Díaz (personal communication), (see Nidification).

Onthophagus sharpi Harold; found in *Gustavia* and maguira fruits, banana-baited traps, other fruits and palm tree bracts; Costa Rica. Howden & Young, 1981; Kohlmann & Solís, 2001.

Onthophagus rostratus Harold; found in chirimoyas (*Anona cherimola*); Mexico. Halffter & Halffter (original information). We maintained this species in the lab, in terrariums with this same fruit. Although the adults did well for some time—and even buried pieces of chirimoya—they did not constructed nests. They did so when offered with dung.

Onthophagus solisi Howden y Gill; appears to be specialized in wild avocado seeds (*Persea* sp.); Costa Rica. Kohlmann & Solís, 2001.

Onthophagus tapirus Sharp; has a high tendency to frugivory. Very abundant in Moraceae fruits, *Pouteria* sp. (Melastomaceae), and banana-baited traps; Costa Rica. Kohlmann & Solís, 2001; Escobar *et al*., 2008.

Onthophagus villanuevai Delgado & Deloya; large numbers of individuals found feeding on the decaying succulent parts of Sapotaceae, Cactaceae, and Agavaceae fruits; found some gallerys beneath the fruits, some with adults in them, compacting fruit fragments; found also in carrion baited traps and one individual in an excrement trap; Me-

xico. Delgado-Castillo & Deloya, 1990; Fernando Vaz de Mello (personal communication).

Onthophagus xanthomerus Bates; found plenty individuals in *Ficus* fruits. In the same locality, this species was not captured in excrement-baited traps; Peru. Mario Zunino (personal communication).

Even when the above review of collect data gives a clear vision of the importance of the attraction to Neotropical fruits by Scarabaeinae adults, it does not give quantitative values of the percentage of species with this feeding habit, be it sporadically or on a regular basis by locality. In order to have these values, we analyzed the collected data of the La Selva Biological Station, Costa Rica, published by Escobar *et al*. (2008), and our own unpublished data from Palenque and Los Tuxtlas, Mexico.

Escobar *et al*. (2008) present a list of Scarabaeinae collected in La Selva, Costa Rica, throughout a period of 35 years of collecting campaigns, as well as a cumulative species list for all the known species for La Selva and its surroundings. The intensive sampling was performed using excrement, carrion and fruit baited traps, as well as directly in various types of excrement and fallen fruits. This is the only published work that –due to the intensity and coverage of the sampling—allows to perform a qualitative analysis of the importance of frugivory in a given location (but see the new unpublished data for Los Tuxtlas and Palenque that follows).

In La Selva the following species were found in fruits: *Canthon moniliatus* in decaying *Entada* sp. fruits (Leguminoceae), but more abundant in carrion and excrements. *Copris lugubris*, an especially coprophagous species, was found in decaying avocado fruits (*Persea* sp. – Lauraceae) and in banana baited traps. *Ateuchus candezei* and *Canthidium ardens* were found in palm tree fruits, although the former species was more commonly found in excrement and carrion. *Eurysternus plebejus* was collected in *Gustavia* sp. fruits (Lecythidaceae), as well as in excrement and carrion. *Onthophagus acuminatus* was found in *Virola* sp. fruits (Myristicaceae), and in excrement and carrion. *O. nemorivagus* found in *Gustavia* sp. fruits (Lecythidaceae), in banana baited traps, and excrement. *O. praecellens* found in palm tree fruits, *Spsidum guajara* fruits (Myrtaceae), and Moraceae fruits. However it was also found in excrement and was very abundant in carrion. Although *O. tapirus* was collected in excrement, it was also very abundant in Moraceae fruits, *Pouteria* sp. fruits (Melastomaceae), and banana baited traps. It was the only La Selva species that clearly prefers decomposing fruits to carrion or excrement. The copro-necrophagous species *Phanaeus pyrois* was found in palm tree fruits and *Gustavia* sp. (Lecythidaceae) fruits. Also in La Selva we found two individuals of this species buried with a banana mass.

Of the 50 species that make up the accumulated richness of Scarabaeinae in La Selva and surrounding places, 10 species (20%) have been collected in a variety of fallen fruits. Only one, *O. tapirus*, (2%) displayed a clear preference towards fruits, although not exclusively.

During two intensive collecting campaigns in the tropical rainforest of Palenque, Chiapas, Mexico, we found *Onthophagus carpophilus* (very abundant), *O. rhinolophus* (abundant), *O. dicranius*, *O. maya*, *O. corrosus*, and *Dicho-*

tomius amplicollis inside or beneath more or less rotten mangos, chirimoyas, mameys, Apocynacea, and *Syngonium podophyllum* fruits (Araceae). In the same locality we found a *Phanaeus endymion* pair (male and female) buried with a food oval mass of food beneath a fruit (Apocynacea). We also collected an individual of *Canthidium laetum* in a *Poulsenia armata* fruit (Moracea). Although all these species were also collected in traps baited with carrion or human excrement, the fact that *O. carpophilus* and *O. rhinolophus* were much more abundant in fallen fruits make us suppose that there is a real tendency towards frugivory specialization under the conditions of Palenque. This same conditions are also found throughout other forests in the south of Mexico and Central America.

Of the 35 species that make up the accumulated species list of the Palenque rainforest, seven (20%) have been found in fallen fruits. Of these at least three –and probably four—are true specialists on this trophic resource. This is the highest recorded incidence of dung beetles affinity to fruits in a single locality, not only in the Neotropics, but also in the world.

In different collecting campaigns in the fragments of the tropical rain forest of los Tuxtlas, Veracruz, Mexico, we found the following Scarabaeinae species (new data) in fallen fruits: *Phanaeus endymion*, *Onthophagus nasicornis*, *O. rhinolophus* and *Canthidium laetum*. Of these species, *O. nasicornis* is very abundant in fruits, and only rarely found in carrion or excrement. Most of the reviewed fruits corresponded to *Philodendron* sp. (Araceae), *Pouteria sapota* (Sapotaceae), *Pousenia armata* (Moraceae), and *Syngonium podophyllum* (Araceae).

Of the 33 species collected by us within the Los Tuxtlas forest, [Favila & Díaz Rojas (1997) cite 31 for the forest and its edges], only four (13%) were found in fruits, being *O. nasicornis* an specialist of this trophic resource.

In the former list of adult Scarabaeinae found in fruits and vegetable detritus we do not include those species associated to heap detritus of leafcutter ants' nests of the genera *Atta* Fabricius and *Acromyrmex* Mayr (Formicidae: Attini). The reason is that these detritus—formed by the leftovers of fungus cultivation and by the ants themselves—are not equivalent to other vegetable detritus to which the reviewed Scarabaeinae are associated. However, from a purely mechanical point of view, and its relationship to the mouthparts, there is indeed a coincidence as the texture and size of the detritus, like sawdust, is similar to the others. The most important aspect, however, is that the ecological importance of this detritus as a feeding alternative to the evolution of the Neotropical Scarabaeinae is the same. The Attini are endemic to the Neotropics, so this association is only found here.

Atta ants dump their wastes in special chambers inside their extensive and complex nest, or in the case of two species, in external heaps, next to one or several entrances, taking advantage of the inclination of the terrain. In some old ant heaps, these waste heaps can reach one meter depth. In these heaps, the lower layer of the waste decays and forms a compact mass.

The relationship between Scarabaeinae and detritus, as well as of *Attini* nests and beetles in general was reviewed by two good recent works: Vaz de Mello (1998) and Navarrete Heredia (2001) (see also citations within these works).

Both authors give a list of 32 species associated to detritus, plus one species, *Canthon virens* Mannerheim, with a totally different feeding behavior—predating on impregnated *Atta* females.

Of the genera reviewed, *Dendropaemon* and *Tetramenia* comprise three species that, according to Vaz de Mello (1998), are associated to *Atta* nests. According to the above-cited authors, these species and the closely related genera *Megatharsis* and *Homalatarsus* seem to form a monophyletic group within Phanaeini, which is associated to ants.

Attavicinus monstrosus Bates[1] is a relict species, with a restricted distribution in a small area in Jalisco state, Mexico. It can only be found in the external waste heaps of *Atta mexicana*, where it nests, using this debris.

Although most of the species of *Ontherus* are coprophagous, four species from the brevipennis group are associated to the waste of *Atta* or *Acromyrmex* nests (Genier, 1996). Among the *Onthophagus* species, two species have been accidentally found in the detritus, but *O. rufescens* Bates lives exclusively in the waste heaps of *Atta mexicana* in Mexico, where it nests, using the debris. Of the nine cited species of *Ateuchus*, many live exclusively in these waste heaps throughout the Neotropics. The same is true for *Uroxys dilaticollis* Blanchard and two species of *Anomiopus*.

Of the 31 species of the above-cited reviews, we consider that somewhere between nine and 13 are only accidentally found in these waste heaps, but the other 22 to 19 are permanently associated with them. Of these, two are known to nest only in the detritus, which could also be true with one species of *Ontherus*.

There are two aspects of the relationship between beetles and Attini nests that are worth mentioning. Almost all the known cases of frugivory occur in the tropical rainforest. This is not the case in the relationship with waste heaps —at least in Mexico, where many of the cited cases occur. These relationships do not occur in forests, and they sometimes correspond to highly anthropogenized landscapes. In Mexico there are Attini in the tropical rainforests, but we do not know the Scarabaeinae associated to their waste chambers, which usually are subterraneous. Although there is much yet to be known about this particular interaction, it seems evident that the association between Scarabaeinae and Attini wastes is not modeled by the ecological evolution of the Neotropical forests (see the Discussion for the frugivory cases).

The association between beetles and Attini wastes seems to be more ancestral than frugivory. The following facts support this hypothesis: 1) The number of species of different genera that feed on or nest exclusively in them; 2) Those specialists in detritus—not those that occasionally are found in them—do not conserve coprophagy habits, not even in a small number of cases, as seen in most frugivorous species. *A. monstrosus* and *O. rufescens* have nested in the lab using detritus, and do not use excrement even when offered.

Dry North of Argentina

The tribe Eucraniini is endemic to the Chaco and El Monte biogeographic provinces. One of its four genera, *Anomiopsoides* Blackwelder, feeds on rodent excrements. The beetles transport these pellets from the surface to a previously excavated gallery (see Zunino *et al*., 1989; Ocampo, 2005). Ocampo (2005) cites that two species, *A.biloba* Burmeister and *A. cavifrons* Burmeister, can also feed on small leafs and seeds, although they do not constitute their main source of food.

According to Federico C. Ocampo (*in litt*., 20/VI/2003), the most common way of transporting their food is to grasp it with the anterior tibiae, rise it, and swiftly walk with the medium and posterior legs. At least in *A. biloba*, it has been recorded that the large clypeal processes can be used to cut small pieces of leafs and seeds (using the clypeus as a fork). This author also observed that some individuals took small pieces of dry leaves that they came about in their paths. He considers this occasional herbivory as a response to competition. Usually these species occur in isolated populations, with a high number of individuals, which gives rise to an intense inter- and intra-specific competition. It is not difficult to find somewhere between 100 and 200 individuals foraging in the lapse of one to two hours, in an area no greater than an hectare.

Oriental Region

In the tropical rainforests of Southeast Asia there are many Scarabaeinae species associated to decaying fallen fruits and flowers, although the known cases are much less than that of the Neotropics.

Microcopris reflexus (Fabricius); collected in fallen fruits; Sabah, Malaysian Borneo. Davis, 1993; Davis & Sutton, 1997.

Onthophagus batilliger Harold and *O. mentaveiensis* Boucomont; collected in *Rafflesia pricei* flowers, during the first states of decomposition. These flowers emit a strong smell that resembles carrion. Both species *Onthophagus* have been collected in carrion, while *O. batilliger* is frequently found in fallen fruits in dipterocarp-dominated forests, and *O. mentaveiensis* is rarely found in human excrement baited traps; Sabah, Malaysian Borneo. Davis, 1993; Davis & Lantoh, 1996; Davis & Sutton, 1997.

Onthophagus bonarae Zunino; found in loquat fallen fruits (*Eriobotrya japonica*); Thailand. Masumoto, 2001.

Onthophagus coorgensis Arrow; collected in decaying fruits; Assam, India. Arrow, 1931.

Onthophagus deflexicollis Lansberge; abundant species with an ample distribution throughout southeast Asia, frequently collected in fruits and vegetable detritus; The individuals collected in Sabah were even found in gallerys beneath fallen fruits. It is pertinent to note that neither in this, nor in any other case, the fact that an individual is collected in a gallery—even with food storage—implies nidification. These gallerys and food masses are part of the normal process of food relocation in adults; Assam, India; Sabah, Malaysian Borneo. Arrow, 1931; Davis, 1993; Davis & Sutton, 1997.

Onthophagus duporti Boucomont; collected in decaying fruits; Assam, India. Arrow, 1931.

Onthophagus frugivorus Arrow; collected in decaying fruits; Assam, India. Arrow, 1931.

Onthophagus ramosellus Bates; collected in decaying fruits; Assam, India. Arrow, 1931.

---

[1] Philips & Bell (2008) created the genus *Attavicinus* for *Liatongus monstrosus* Bates.

According to Davis (1993) and Davis & Sutton (1997), *Onthophagus rouyeri* Boucomont specializes in fallen fruits. It is very abundant in the forest areas where figs are produced, and is absent from areas where no figs are present. Although nothing has been published on the nidification behavior of *O. rouyeri*, its spatial distribution suggests that this species might be solely frugivorous.

Sakai & Inone (1999) describe an extraordinary case of Scarabaeinae found in *Orchidantha inonei* flowers (Lowiaceae, Zingiberales) in Sarawak, Malaysia. These flowers emit a strong smell to carrion. Sakai & Inone (1999) relate these beetles to pollination: "… the only flower visitors that crawled under the lateral petals, where the stigma and anthers were hidden, were dung beetle belonged to two genera, *Onthophagus* and *Paragymnopleurus…*" "The results of our observations revealed that the major pollinators on *Orchidantha inonei* were dung beetles, *Onthophagus*". "*Onthophagus* feeding on pollen was neither observed nor has seen previously recorded. The mucilaginous secretion on the ventral surface of the stigma of *Orchidantha inonei* may function as a glue to hold deposited pollen on the pollinator. *Onthophagus* was presumably deceived by *O. inonei* with its dung or carrion like odor." "Although *Paragymnopleurus* visited with almost the same frequency as *Onthophagus*, they rarely carried pollen … the contribution to pollination by *Paragymnopleurus* in thought to be much smaller than that attributable to *Onthophagus*". The species found were: *O. auriflex* Harold, *O. fujii* Ochi & Kon, *O. vulpes* Harold and *O. waterstradti* Boucomont that has been collected in traps baited with carrion and excrement in different localities of Borneo.

With the data from the work by Davis (1993) we conducted a analysis of the trophic preferences of the Scarabaeinae in the north of Borneo. Of the 50 collected species, the most important trophic group is that of the copronecrophagous species—collected in carcasses and excrements—representing 42% of the total. These are followed by the strictly coprophagous species, collected in various types of excrement, representing 26%. 16% corresponded to uniquely necrophagous species, and 10% those attracted by carrion, excrement and decomposing fruits. Finally only 4% correspond to fruit specialists, one of them found solely in figs.

When we analyzed only the data for *Onthophagus*, seven out of 34 species (21%) were attracted by fruits. All these trophic distributions (including the attraction of *Onthophagus* towards fruits) are very similar to those found in the Neotropical forests.

Ethiopian Region

There is no other region with as many Scarabaeinae as this one, and with as many beetles both in terms of species and individuals per locality. Here most groups are coprophagous. Few species are collected in carrion, and fewer still are found in fruits. Likewise, and contrary to what happens in tropical America, the number of species and individuals in the tropical rainforests are always less than those in the savannas. This is the result of a continuous evolutionary relationship: savannas-big mammals-beetles. Thus, and despite the number of big mammals being higher than that of tropical America, the number of big mammals in African forests is less than that of the savannas.

We have very few data of beetles collected in fruits in Africa. Walter (1978) published the Scarabaeinae of Plateau Bateke, Zaire (current Democratic Republic of Congo). Of 110 cited species, only seven were accidentally attracted to traps baited with decaying bananas and mangoes. Furthermore, in the savanna he reports *Proagoderus speculicollis* Ouedenfold in the fallen fruits of *Laudolphia lanceolata*, Apocynacea, and *Scarabaeus kwiluensis* Janssens rolling balls from the same fruit. He did not find any Scarabaeinae in fallen fruits in the forest.

Cambefort (1982) reviewed the Scarabaeinae fauna from Lamto, Côte d'Ivoire. Of 131 species collected in savannas, tree savannas, and forests, only the adults of one species are attracted to fruits. The species is *Onthophagus callosipennis* Boucomont, found beneath fallen fruits of *Nanclea latifolia*, Rubiaceae, fallen fruits of introduced trees such as *Mangifera* and *Anacardium* among others, and in fungi outside Lamto. The data from Lamto, the ones from Zaire and those that follow from Taï, show a strong dominance of coprophagy in Equatorial Africa, with very few necrophagous species, and even less species attracted to fungi or fallen fruits.

In his review of the Scarabaeinae from the rainforest of Taï, Côte d'Ivoire, Cambefort (1986) cites that only a few species (10.3%) are attracted to carrion, and only one (1.3%) is strictly necrophagous. Only the three *Paraphytus* species in Taï have been found in rotten trees, wood masses, fungi, and excrement from xilophagous insects. The same is true for the *Paraphytus* species of Central Africa (Cambefort & Walter, 1986; see Nidification and Discussion).

Philippe Moretto (*in litt.*, II/2009) has found several species of *Onthophagus* attracted to fruits in the Sudanese-type forests of Senegal. In this type of forests *Cordyla pinnata* trees are very abundant. These trees produce edible fruits, which are specially eaten by the pata monkeys (*Cercopithecus patas*). The monkeys separate in half the leathery skin of the fruit, and without separating both halves, eat the nuts and surrounding pulp, tossing the rest to the ground. Usually both halves shut over one another, so the inside is protected from rain and dehydration. Thus, under the trees it is possible to find fruits in different states, from fresh to various decomposition states; the latter form a type of nutritious compost. Almost all fruits except those that are too fermented, harbor diplopods and or *Onthophagus*. The diplopods arrive first, eat the pulp of the fresher fruits while on the ground, and bury it along their excrements. These excrements play a role in the rapid transformation of the pulp into compost, due to the microbial effect, accelerated by the *Onthophagus* handling.

Moretto wondered what attracted *Onthophagus* the most: the diplopods, their excrement, the fruit pulp or the compost. To answer this question, he set up traps with smashed fresh fruits, and traps with sliced diplopods. Three *Onthophagus* were attracted to the fruits, while, amazingly, 14 *Onthophagus* plus one *Anachalcos aurescens* species were attracted by the sliced diplopods.

Of the species attracted to the fruit, *Onthophagus callosipennis* Boucomont (previously cited in fruits by Cambefort, 1982) was found in great numbers. This species is attracted to snake carcasses, but also and to a greater extent to decomposing fungi and fruits (according to observations in Senegal and Côte d'Ivoire). 56 individuals were

captured under *Cordyla pinnata* fruit peels, which leaves no doubt to their affinity to these fruits, especially after being "potted" by the diplopods.

Onthophagus cupreus Harold is attracted to traps baited with human excrement; however, two females were collected in gallerys beneath a fruit, full of fresh pulp. *O. flaviclava* d'Orbigny is a very abundant essentially coprophagous, but also opportunistic species. It was attracted to leftovers of fruits with excrement of diplopods in great numbers (136 individuals).

The careful observations of Philippe Moretto that we have transcribe, allow us to suppose that for Ecuatorial Africa there is a richer prospect on frugivory and necrophagy (at least the consumption of diplods) than the one known to date. *Onthophagus callosipennis* seems to be a specialist in fruits in a similar degree than the one we have pointed out for the Neotropics. The other species seem to be attracted by fruits with diplopods excrement, or even by the diplopods themselves.

Outside of Equatorial Africa, within the subgenus of *Scarabaeus*: *Pachysoma* formed by wingless beetles endemic to the desert cost strip in southwest Africa, seven species have been found foraging in vegetable detritus (Harrison *et al*., 2003; Scholtz *et al*., 2004). These beetles feed on and nest with excrements of small mammals and vegetables detritus from wind-shaped heaps. The beetles crawl on the soil surface looking for food, and when they find it, excavate a gallery. Each small piece of dung or detritus is transported to the gallery. To do this, the beetle gasps the food in its posterior legs while moving forward. The process is repeated over and over, until enough food is gathered. When this happens, the gallery is further excavated until forming a second chamber, beneath the level of humidity of the ground. The food is then moved to this second chamber, which will function either as a feeding or a nidification one (see Nidification).

Also in the desert of Southern Africa (Kalahari, Bostwana), Adrian L.V. Davis (*in litt*., 21/I/ 2009) captured another Scarabaeini, *Pachylomera femoralis* (Kirby), attracted to smashed monkey orange fruits (*Strychnos* sp.).

Australia

According to Geoff Monteith at the Queensland Museum, Australia (*in litt*., 29-V-2004), the only species that is found in fruits is the rare *Onthophagus vilis* Harold. This species excavates burrows beneath fallen and decaying fruits of different species including *Syzygium suborbiculare*, *S. rubrimolle*, and *Siphonodon pendulus*. The beetles dig inside the fruit and in the ground…"I don't think anyone has dug up the burrows to look at the nest, but it is fairly clear that the beetles are taking the fruit material into the burrow as nidification material". It is quite possible that *O. vilis* uses fruit to nidify as noted by Monteith. However, in this as in other cases cited in this review, we do not consider that nidification using fruits is taking place, unless we have found eggs or larvae in them.

The other Australian species that use vegetable matter are those of *Cephalodesmius*. They prepare an external rumen with excrement and vegetable wastes to build their brood balls, as well as to feed on them while in the nest (see Nidification).

Neartic and Paleartic Regions

After reviewing the literature and consulting distinguished specialists (Mario Zunino, Jean-Pierre Lumaret, Eduardo Galante, and Francisco Cabrero), it is our opinion that the rich Scarabaeinae fauna of the Northern Hemisphere has an exceptional and anecdotic association to fallen fruits. We can now add some further data to the few known cases: M. Zunino (personal communication) found *Furconthophagus furcatus* (Fabricius) in fallen and partly decayed pears in Cuneo, Italy, and *Onthophagus falzonii* Goidanich in a rotten watermelon in Anatolia. In the section devoted to nidification, we also mention the case of *Onthophagus coenobita* (Herbst), which is a clearly coprophagous species, occasionally found in decaying vegetables in France (Lumaret, 1990).

Howden & Cartwright (1963) cite three *Onthophagus* species captured in decaying cantaloupe skins in the United States, as well as in excrements.

Nidification

Due to the significant number of Scarabaeinae species in which adults have been found associated to fallen fruits, some of them too frequently as to point to a true specialization, make us infer that the cases of beetles nidifying using these same materials might be more common than previously thought and published. Even thought in the review that follows the number of known cases is incremented, these are still few. We consider that this might be the result of two reasons: 1) As pointed out in the introduction and the discussion, the transition from coprophagy to frugivory (or necrophagy or mycetophagy) in adults do not imply changes in the structure of the mouthparts, digestive tube, or feeding behavior; in all cases the feeding is microbiotic (juices, small particles and microorganisms). On the other hand, the transition implies important changes for the larvae, including the texture of the food that the mother accumulates for larval development, and the lack of cellulose in such food. Thus—and this is one of the central proposition of this work (see Discussion)—the use of seeds or fruits by the adults of Scarabaeinae adult, even when it coexist in space and time with necro-and coprophagy, is an quick and easy response to local or regional ecological conditions—mainly food availability and competition. However, the transition to using fruits for nidification requires more significant changes 2) The second reason to explain a lesser number of cited cases of fruits used in nidification pertains to data collection. The published cases of adult Scarabaeinae found in fruits are the result of field work, including intense sampling. In the last 15 years, and especially in tropical landscapes, the type of sampling in which the bait in which each individual is collected is recorded has increased, as the Scarabaeinae have been widely used in biodiversity and forest fragmentation studies. On the other hand, verification of nidification—the finding of nests and offspring—requires laboratory work, sometimes for long periods of time. Because the nests are pedotrophic, it is very unusual to find one containing juveniles during field work. Furthermore, we do not consider the finding of a buried fruit mass with one or two beetles but without juveniles as a nidification proof, as there can be a pedotrophic feeding behavior in adults that do not necessarily leads to nidification.

We have grouped the known nidification cases according to the material used: seed and fruit nidification, and other vegetable material nidification. The ecological and geographical processes in which each of them occur are different, as are the nidification mechanisms.

Seed and fruit nidification

Canthidium laetum Harold, was the first species in which nidification in fruits and seeds was found based in field observations by Sofia Anduaga and G. and V. Halffter (Halffter & Edmonds, 1982 – cited as *Canthidium granivorum* Halffter & Halffter). The adults were found Xochitepec, Morelos, Mexico, under *Pithecellobium dulce* trees (Leguminosaceae), feeding on seeds or buried underneath them. Buried cocoons containing pupae were also found.

Sofia Anduaga & Carmen Huerta (unpublished data, personal communication) raised this beetle in their laboratory, in order to study their nidification process. They set up three sets of terrariums—with three to six couples each. In one set of them the beetles were only offered seeds, in the other only cow manure, and in the last one both seeds and cow manure, but physically separated. The adults fed indiscriminately on both types of food. They ate mature—not rotten—seeds, while they were lying on the surface and after being shallowly buried. Some of the buried seeds were not used and germinated. Both males and females used the seeds, and in all cases they opened it from the micropile, separating the cotyledons. Using the clypeus and the anterior tibiae, they scrapped the cotyledons, forming a mass, which was later consumed.

Even when cow manure was continually available, the beetles only used seeds for the nidification. The female scratches the seeds as previously described, and transport the well packed mass to the previously dug oblique gallery. Once in the gallery, she mixes the mass with her own excrements to form the brood ball. In the upper part of the brood ball she prepares an egg chamber, which she covers with a thin layer of soil. It is in this chamber where she deposits the egg, in a vertical position, glued to the surface with a white substance. The chamber is then sealed, using concentric layers of soil mixed with her own excrement.

The maternal excrement produces a microbial fermentation of the brood ball, and transforms the stored food from a light orange color at the time of ovoposition, to black by the time the larvae reaches its third developmental stage. At the end of this third stage, the larvae builds a spherical pupal cell, which thin but resistant wall is internally smoothed out with the anal plate of the larvae (Fig. 14). As previously mentioned, Solís & Kohlmann (2004) found this species in legume seeds in Costa Rica, but did not find nidification evidence.

Thanks to the careful observations of Anduaga and Huerta on the nidification process of *C. laetum*, we can do some inferences about other cases of nidification using seeds and fruits for which we have less information. From their work, we can draw three interesting points: 1) At least in the Xochitepec populations, the beetles nest only using seeds. 2) The nidification process does not show any functional or structural change in relation to other *Canthidium* species that nest using excrement. 3) There is an external rumen in which the mass of food comprised by seeds is fermented by the microbes inoculated by the female's own excrement.

Julio Louzada (personal communication) raised in his laboratory a non identified *Canthidium* species that is frequently attracted by fruits of the forest in Brazil, and provided them with fermented bananas. During the first few days, each couple excavated a simple burrow, about 20 cm deep (Fig. 15), and relocated the banana pulp and part of the peels to it. The mass remained at the bottom of the burrow two or three days, during which it changed color due to the effect of microbial fermentation. After this period the adults dug secondary gallerys (Fig. 15), and produced one brood mass with one egg in each one of them. The broods mass were dark, and contained a mix of soil, fermented fruit, and previously manipulated excrement form the parents. The egg lies in the upper chamber. The complete development, from the offering of fermented bananas to the emerging of the new adults, took from 18 to 22 days.

For *Onthophagus orphnoides* Bates, Kohlmann & Solís (2001) indicate: "we have found this species nesting beneath semi-rotten avocado seeds (*Persea americana*). They use some of these as back up food for their larvae, and perhaps even for themselves. When they find a suitable seed, they cover it with soil by digging underneath and around it. Then they carry small potions of it to the newly constructed nest beneath it". In Costa Rica, *O. orphnoides* is a true fruit specialist—as it has only been captured in *Persea* seeds. At the same time, its nidification in seeds has also been proved.

We were able to achieve nidification in our laboratory of *Onthophagus rhinolophus*, from individuals captured in Coatepec, Veracruz, Mexico. We offered figs, pineapple and decomposing orange to the adults. In burrows of up to 14 cm deep, we found brood masses formed by concentric layers of fruit, and an external surface mixed with hardened soil. These brood masses were individually placed, isolated from one another. Each mass had a big ovipositon chamber (5 mm) on the top, with the erect egg glued to its base. In addition to eggs, we found larvae and pupae.

In her laboratory (Instituto de Ecología, A.C.), Rosario de Ma. Ribeiro Sarges (personal communication) has achieved the nidification of *Onthophagus rhinolophus* offering as food kinkajou (*Potos flavus*) and spider monkey (*Ateles geoffroyi*) excrement, as well as mature *Ficus yoponensis* fruits. In all cases the beetles constructed brood masses, and live offspring were obtained.

Onthophagus (*Paleonthophagus*) *coenobita* (Herbst) is distributed in Europe and Asia Minor, as far as Turkestan. It is mainly collected in human excrement, but it is possible to find it in other types of excrement, as well as in small carcasses, fungi and decaying vegetable remains. According to Lumaret (1990), this species mainly uses excrement for its nidification, and to a lesser extent, decaying vegetable remains.

In Chiapas, Mexico, Miguel Angel Morón (personal communication) found two brood balls of *Deltochilum pseudoparile* next to some seeds and rests of breadnut fruits (*Brosimum alicastrum*). One of the balls contained an adult, while the other had rests of a larva or pupa. The balls were found at 2-3 cm deep in the ground, among leaf litter—just as those of several other species of *Deltochilum*—beneath a breadnut tree. According to Morón, it is possible that they were constructed using fruit pulp. If this were the case, this would represent a case in which a typical coprophagous

Fig. 14. Pupal cocoon from *Canthidium laetum* Harold. Explanation in text. Original from S. Anduaga y C. Huerta. **Fig. 15.** Nidification process of *Canthidium* sp. Explanation in text. From an original ilustration by J. Louzada.
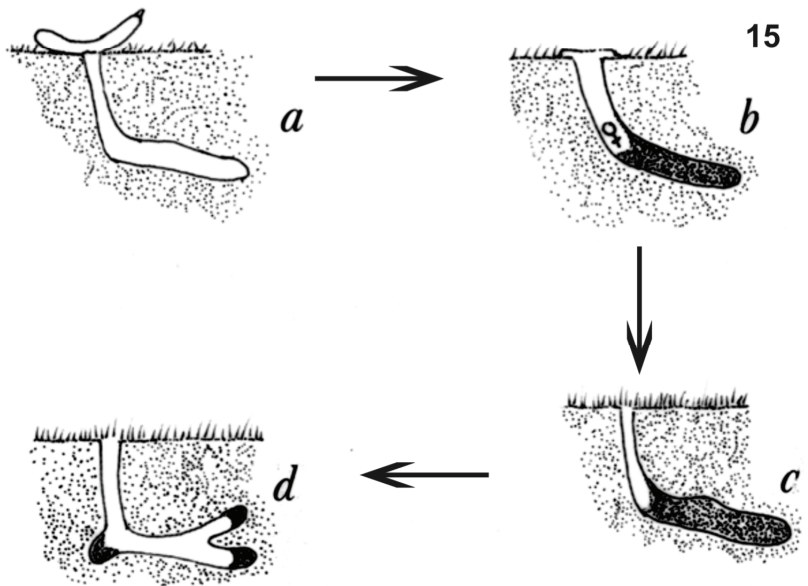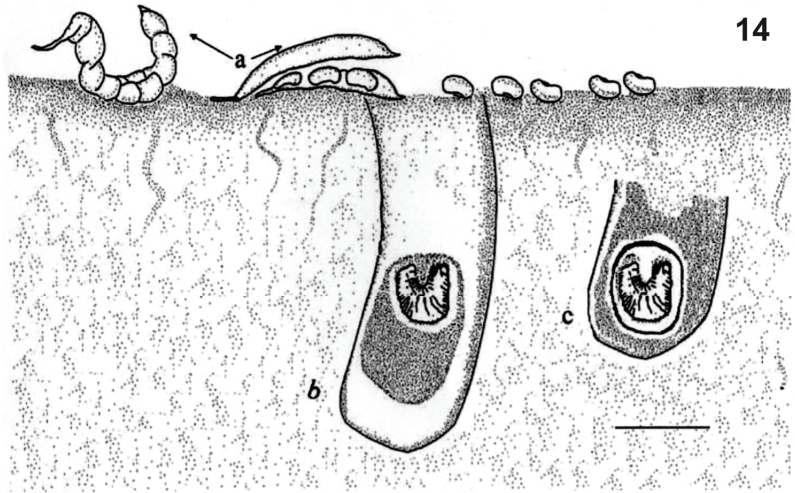
species sporadically construct its brood balls from fruit pulp. The same would be the case with *Copris lugubris* Boheman. Deloya (1988) described a set of brood balls (this is a species with multiple nests) found in the waste products of an *Atta* nest, made of these same material. The relevance of these two cases is not the fact of the construction of the brood balls, but the fact that the larvae were able to develop in brood balls constructed from these new and uncommon materials.

Nidification using vegetable detritus and waste products from ant nests.

Cambefort & Walter (1985) described the nest of *Paraphytus aphodioides* Boucomont, a species distributed in Gabon and Côte d'Ivoire, and one of the possible cases of primitive saprophagy. The nest consists of a poor-defined chamber, dug among debris of wood and saproxylophagous insects excrements, in a rotten tree. The chamber contained an ovoid brood mass formed by debris, and the mass contained a larva. This is a subsocial species, and the female remains in the nest until nymphosis.

Pachysoma is a subgenus of *Scarabaeus* that includes 13 wingless species, endemic to the southwest African shoreline. In those species for which nests have been found, or that have been raised in the laboratory, [*Scarabaeus* (*Pachysoma*) *striatus* (Castelnau) y *S.* (*P.*) *gariepinus* (Ferreira)], nest provisioning was based on pellets, and dry rests of excrements and plants (Scholtz, 1989; Harrison *et al.*, 2003; Scholtz *et al.*, 2004). Preference towards one type of food or another varies within species, and sometimes even among individuals. For instance, of 17 excavated nests of *S.* (*P.*) *gariepinus*, nine contained only dry pellets, three only vegetable detritus, and five contained both detritus and pellets. The chosen food is picked up and relocated to a previously excavated burrow, grasped with the posterior legs while walking forward (a similar way of locomotion is found in another roller, *Canthon obliquus* Horn; see Halffter & Halffter, 1989). In *Pachysoma* as in the Argentinean *Anomiopsoides*, relocation allows to concentrate in a previously excavated gallery and in favorable humidity conditions, small portions of dry food, spread over a significant area.

In *Pachysoma* food relocation takes place over and over again, until there is enough material in the burrow to feed the adults and for the nidification process. When this happens the beetles deepen the burrow, preparing a second chamber bellow ground humidity level. The entrance to the burrow is sealed with sand, and the food is relocated to the

second chamber; here it becomes humid and transformed, becoming either a feeding or a nidification chamber.

Pachysoma does not build brood balls to nidify. Instead, larvae roam freely throughout the food, representing a unique behavior among Scarabaeinae (Harrison *et al*., 2003; see also López-Alarcón *et al*., 2009).

Also in desert conditions, but in northwest Argentina, the Eucraniini a group related to the burrowers Scarabaeinae, display a similar behavior of picking up dry excrement. They gasp the excrement fragment with the anterior tibiae, and walk forward with the medium and posterior legs, relocating the food to a previously excavated gallery. In two species of the genus *Anomiopsoides* (*A. biloba* and *A. cavifrons*), food provisioning occurs partially of completely with vegetable fragments, even directly cut from the plant (see Frugivory and Saprophagy in Adults). Although happening in a different manner, the relocation of dispersed food and the use of vegetable detritus in these *Anomiopsoides* species is similar to the aforementioned *Pachysoma* ones. Convergence is due to purely ecological reasons (extreme aridity), because these two genera are not closely phylogenetically related.

The nidification process of *Attavicinus monstruosus* (Bates) and *Onthophagus rufescens* Bates is well known. They live and breed in the external waste product heaps of *Atta* (see Frugivory and Saprophagy in Adults). *O. rufescens* builds ovoid brood masses in burrows underneath the ants' waste products (Halffter & Edmonds, 1982). Each individual brood mass is provisioned with debris, just as in other *Onthophagu*s that nidify using excrements.

Both *Attavicinus monstrosus* and *O. rufescens* are *Atta* waste-obliged species; the adults feed and nidify using debris from the nest (Figs. 16 to 18). The nest of *A. monstrosus* (Anduaga *et al*., 1976; Halffter, 1977; Halffter & Edmonds, 1982) consists of a main tunnel that can be unique or branch into two to five lateral ones. It is excavated and provisioned by the female beneath the debris mass, and can reach between 50 to 80 cm deep, with galleries 2.5 to 3 cm wide. Once there is enough debris, the female proceeds to build the brood-masses, beginning at the end of the main gallery or that of each branch. In all cases, an initial 10 cm brood mass is formed, and ovoposition follows within a simple ovoposition chamber. A second identical brood mass and egg follow, and space permitting, a third one. At the end, the tunnel or branch is provisioned with an extra 5 to 10 cm of debris. Thus, each compound nest contains, at 10 cm intervals, a cylindrical mass of debris with an egg. Each branch, if the nest has more than one, will contain between one and three eggs, and the whole nest complex will have between 8 to 11. Once the whole process is finished, the main gallery is partially filled with debris.

A primitive feature of this kind of nidification is that the brood-masses are not separated by any barrier other than the excess of debris. This overabundance of debris guarantees that each of the larvae will complete its development. The larvae eat the debris, producing a microorganism-rich excrement that is deposited among the provisions. As in all other Scarabaeinae, this excrement will be eaten along the rest of the food. At the top of the space created by the consumption of the debris, the mature larva builds the pupal cocoon around itself, using its own excrement. As in *Onthophagus rufescens*, the nidification process of *A. monstro-*

sus is similar to that of other burrower coprophagous Scarabaeinae (nidification pattern I).

The nidification process of the Australian genus *Cephalodesmius* is meticulously described in a masterwork by Monteith & Storey (1981), with some advances presented by Halffter (1977). Halffter & Edmonds (1982) reviewed and synthesized the process. The behavior in general and particularly the nidification of these beetles are known thanks to the careful field and laboratory observations by Monteith and Storey of *Cephalodesmius armiger* Westwood, plus some other isolated field observations of the other two species of the genus: *C. laticollis* Pascae and *C. quadridens* MacLeay. These observations suggest a similar behavior, except that *C. laticollis* relocates mainly excrement, while *C. quadridens* only relocates vegetable remains. Because the remarkable of this process, and because it clarifies to a great extent the process of microphagic feeding based on fermented vegetable remains, we include a detailed description of it, based on Monteith & Storey (1981).

The adults of *C. armiger* emerge at the end of the summer, and take up individual feeding galleries, in which they accumulate a few leaves and a small fermentation mass made of leaves and beetle excrement. During the day they forage on leaves, and by night they roam the surface attracted by excrements. Towards the winter, the adults group themselves in bisexual pairs, each of them with its own gallery that ends in a chamber (Fig. 20). These galleries are gradually widened and transformed into nests. The pair bonds for life, occupying the same nest-gallery, which main attraction will be a mass of fermented vegetable remains, constantly supplied with new material (Fig. 20).

The adults spend winter in the galleries, with few feeding excursions to the surface. In the spring, foraging becomes active, collecting vegetable matter, mainly partially decayed leaves, but also small fruits and flowers, seeds and occasionally fragments of excrement (Fig. 19). Initially both sexes forage, but eventually it turns into a mainly male activity. Each fragment is carried to the nest held by the anterior legs, while the beetle walks backwards until reaching the gallery (Fig. 19).

The female manipulates the material, mixing it with both hers and the male's excrement into the fermentation mass. In the mass, a microbial process—due mainly to fungi according to Monteith and Storey—takes place, transforming the gathered material into one similar in appearance and consistency to fresh dung; it is therefore, a very efficient external rumen. As Monteith and Storey point out, these beetles "synthesize" all the food they will require for the rest of their adult lives, as well as for their larvae. Throughout their entire lives, the fermentation mass is continuously replenished through the aforementioned division of labor, so that it never runs out.

The construction of brood balls begins when the female takes a portion of food and models it into a small ball. Using its feet, she then transforms the ball into a cup, in which she deposits one egg. She then closes the cup, bringing it to the original spherical shape. Between four and ten brood balls are thus constructed, at a pace of one per day. Once the process begins, it does not end until all brood balls are finished. If the female leaves one of the brood balls without an egg, its material is reincorporated to the fermentation mass. Copulation occurs frequently, especially
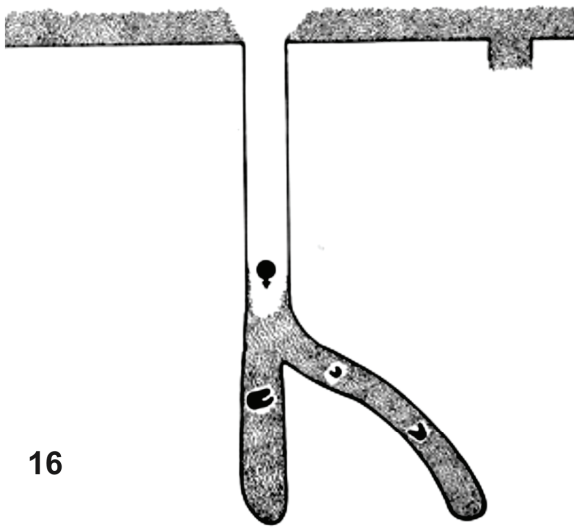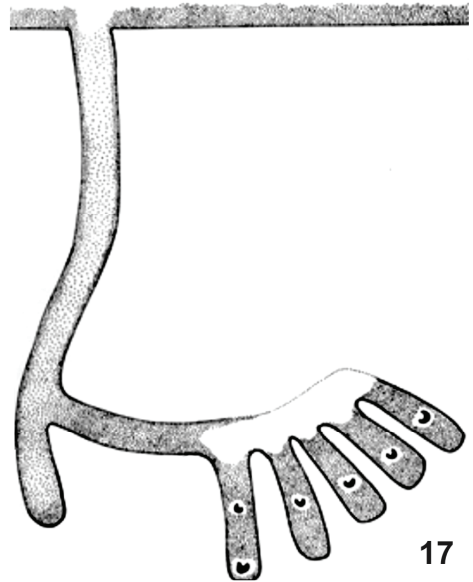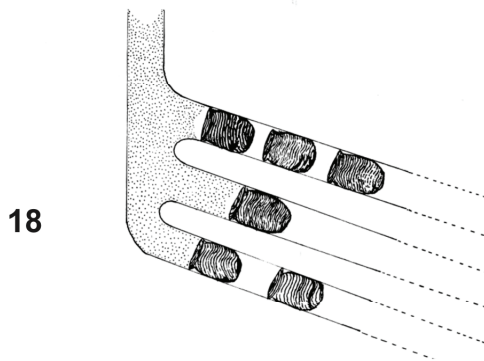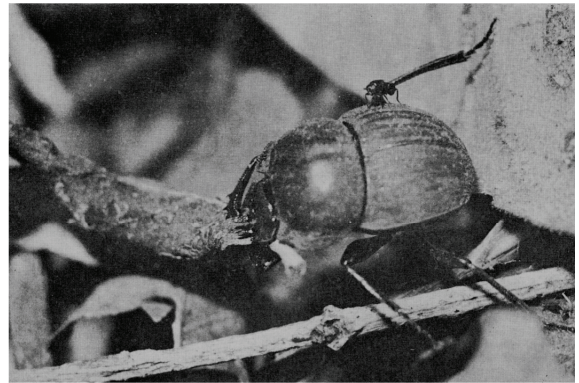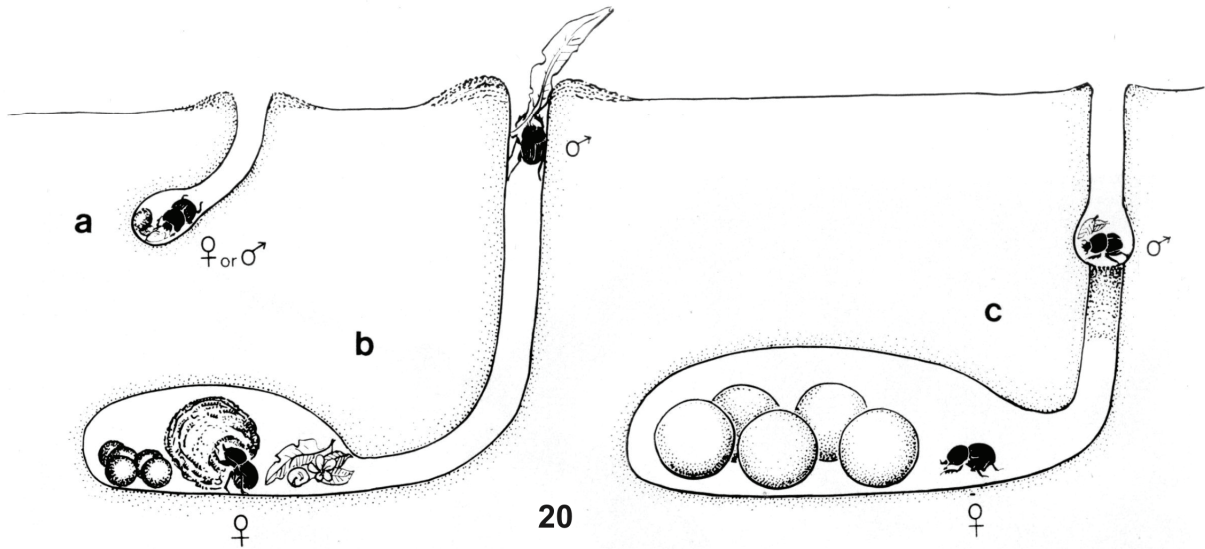
Fig. 16-18. Nidification in *Attavicinus monstrosus* (Bates). Explanation in text. From Halffter & Edmonds, 1982. **Fig. 19.** *Cephalodesmius* carrying a leaf to the nest. From Halffter & Edmonds, 1982. **Fig. 20.** *Cephalodesmius* nidification process. Explanation in text. From Halffter & Edmonds, 1982.

throughout the brood ball construction process. Once the brood balls are finished, the female rarely leaves the nest. Moreover, she will only nidify once in her lifetime. The male continues to provide material from the exterior, which the female will incorporate to the fermentation mass. As provisioning continues and brood balls are constructed, the nest chamber is expanded to accommodate the increase of volume (see Fig. 20).

As the larvae emerge, each in its own brood ball, they begin to eat from the small initial balls. When the food runs out, and the walls of the brood ball become very thin, the female adds material from the fermentation mass to its exterior, causing it to grow. This continuous cycle of provisioning from the outside and consumption from within, maintains the walls with a thickness of about 2 mm. Each brood ball acts as a second external rumen (the fermentation mass being the first), in which the food provided by the mother mixes with the excrement from the larva.

During early larval development, the material added to the brood balls comes from the fermentation mass, and thus, is completely fermented. Further in the process, the mother adds to the exterior of the brood balls vegetable matter only partially fermented, directly from the provisions brought by the male, without going through the fermentation mass. The developing larvae stridulate. Although the function of this sound has not been established, Monteith and Storey suggest that as it transmits through the brood ball wall, it informs the mother of its thickness and of the urgency of adding more food to it.

Once the larvae has completed its development, the female covers the external wall of each brood ball with a mix of excrement from both adults and larvae, the latter eyected through cracks on the brood ball. When dry, this layer becomes very hard. The female continues tending the brood balls throughout pupation, while the male isolates itself in the upper part of the entrance gallery through a soil plug. Usually, by the time the new generation emerges, both parents have died.

In the forests where the three species of *Cephalodesmius* live, the excrement is scarce and with irregular distribution, but leaves and other vegetable materials are abundant on the ground. The development of foraging habits and food concentration into a fermentation mass, allow *Cephalodesmius* species to thrive in large populations, with abundant nests per surface area. Nidification time in this genus is the longest known for any Scarabaeinae, with the bisexual pair bonded for more than a year. This is undoubtedly associated to the type of food, the continuous foraging, and the presence of a fermentation mass.

Discusion

The study of the transition from coprophagy to frugivory or necrophagy in Scarabaeinae requires an analysis of the ecological evolution of this subfamily, as well as of its adaptations to different environments, especially to rain forests. It is generally accepted (see Cambefort, 1991), that the Scarabaeinae originated from primitive saprophagous Scarabaeoidea, whose extant equivalent would be families such as Chironidae and Orphnidae. This was probably an adaptive response to the widespread availability of big excrements from dinosaurs and later from large and medium herbivorous mammals.

According to fossil records, Scarabaeinae first appeared in the Cretaceous (see Krell, 2004). Chin & Gill (1996) describe bioperturbed dinosaur's fossilized excrements next to dung-stocked galleries. Although is possible that this remains could also belong to Geotrupinae nests, it is very possible that they are Pattern I Scarabaeinae nests (see Halffter & Edmonds, 1982). If indeed this group has a Cretaceous origin, then the fossil brood balls found in Uruguay (Late Cretaceous – Early Eocene, see Genise, 1998) would be the most ancient ichnofossils of its kind. The presence of clearly Gondwanian lineages in the two most basal Scarabaeinae groups, Canthonini and Ateuchini (see Vaz de Mello, 2008) would constitute a strong biogeographic support to the Cretaceous origin.

The Scarabaeinae went through a true evolutionary explosion in the Cenozoic—especially from the Eocene onwards—clearly associated to the expansion of medium and large size herbivorous mammals in grasslands (Genise *et al.*, 2000). This explosion was so significant, that in Argentinean paleosols, fossilized brood balls are the most abundant fossils (see Genise & Laza, 1998; Genise, 1999; Genise *et al.*, 2000; Krell, 2000, 2004; Laza, 2006). Fossilized brood balls though to belong to Scarabaeinae, both burrowers and rollers, are of at least three different types (Genise, 2004; Laza, 2006). Furthermore, there are also fossilized brood masses similar to those from extant burrowers with nidification pattern I.

Authors agree in considering the Scarabaeinae as a monophyletic group that shares many clearly plesiomorphic morphological characters, such as the mouthpieces in adults, adapted to manipulate a thick and microorganism-rich food (see Introduction). According to Holter *et al.* (2002) and Holter & Scholtz (2005), adults only ingest particles between 4 and 85 microns, which include juices, microorganisms, and rests of epithelial cells. Larvae can ingest and digest vegetable fiber in the excrement, along with a great amount of microorganisms. Moreover, a series of adaptations appear in larvae, such as a C shape, dorsal hunchback, and flattened caudal end, which allows them to live in a confined space, i.e., the brood mass or ball.

Adults exhibit behavioral adaptations, paired with morphological ones, towards the relocation and protection of food for larvae (nidification) and themselves (see Halffter & Edmonds, 1982). Furthermore, all Scarabaeinae exhibit an extreme reduction in the female's reproductive system, which consist in only one ovary with one ovariole. This is one of the most significant plesiomorphic characters of the entire subfamily, and is associated to an efficient nidification.

In conclusion, Scarabaeinae constitute a monophyletic group, which evolved around coprophagy, perhaps from a saprophagous Scarabaeiform ancestor, or an ancestor with a feeding behavior based on fungi and microorganism associated to humus and vegetable detritus (see Cambefort, 1991; Scholtz & Chown, 1995; Philips *et al.*, 2004). We will further discuss whether examples of this primitive saprophagy are still present in the group.

The use of other types of food, such as fruits and vegetable detritus by adults, and sometimes for nidification, are relatively recent evolutionary processes. However, we consider this saprophagy as derived, as it takes place in clearly coprophagous lineages, and as a response to very specific

local conditions. In fact, in many cases, some individuals of the same species are actively or potentially coprophagous. Moreover, this change does not imply morphological or functional modifications, as adult are still microbiontic.

It is worth noticing that in all documented cases in which seeds, fruits or vegetable matter are used in the nidification process an external rumen (i.e., outside the beetle's body) is present. The rumen is formed with accumulated food, which in the first stage of the brood mass or ball preparation is planted with the mother's or both parent's excrement, which ferments the food, making it easier to manipulate and even richer in microorganisms than the original material. There is also a second external rumen, formed by each mass or brood ball during larval development. In this second rumen the fermented material of the first rumen is mixed by the larva with its own excrements, and eaten repeatedly. Lastly, there is an internal rumen, formed by the fermentation chamber within the larval intestine. All this process produces an extremely microorganism rich material, which means that the larva feeding mode is really microphagic.

The first external rumen has been reported from Scarabaeinae that nidify with dung (see Halffter, 1991). The fact that this external rumen is also found in those species that use fruit pulp, seeds or vegetable detritus to nidify, is another proof indicating that in Scarabaeinae the use of new types of food is achieved conserving the morphological and behavioral structures associated to coprophagy.

Does any Scarabaeinae retain basal saprophagic habits? Halffter & Matthews (1966: 34-36) were the first ones to raise this question, by summarizing the existing information on the Scarabaeinae found in vegetable detritus. Of the several cases cited therein, that of *Bdelyrus* seems to correspond to basal saprophagy. Further studies have suggested the genera *Bdelyrus*, *Bdelyropsis* and *Paraphytus* as probable basal saprophagy cases.

Paraphytus lives in the humus layers between the cortex and the trunk in decaying trees (see Nidification). A question that remains unanswered is whether this species eats humus, fungi hyphae, excrement from xilophagous insects or all these elements.

As we have presented, two species of *Bdelyrus* have been systematically collected in detritus accumulated in bromeliads, as well as in other sites (see Frugivory and Saprophagy in Adults). However, several other species in the genus have been collected in dung and other materials. According to Vaz de Mello (*in litt.*), *Bdelyropsis* is coprophagous, and can be collected in great numbers in excrement-baited taps.

The current state of knowledge, which includes some phylogenetic studies, precludes that *Bdelyrus* and *Paraphytus* retain the basal saprophagy. Philips *et al.* (2004) explain: "In summary, the ancestral food of the Scarabaeinae based on this analysis is equivocal. It may be dung, but could actually be fungi, based on *Coptorhina* appearing as most based in this study. The near basal position of *Bdelyropsis* (± *Bdelurys*) is slight evidence than the oldest ancestral Scarabaeines were saprophagous…".

According to the results of a phylogenetic analysis done by Vaz de Mello (unpublished, *in litt.* 13/II/2009), *Bdelyrus* is close to *Onychotechus* (unknown habits) and *Paraphytus*. Vaz de Mello suggests that the feeding habits

of the aforementioned genera might have derived from an ancestral generalist detritivory, with a second branch that would include fungi feeders such as *Coptorhina*, and a third one including all the rest of Scarabaeinae. If these ideas were confirmed, they would constitute the most comprehensive approach that present saprophagy as basal within a phylogenetic context.

We now present an analysis of frugivory and secondary saprophagy in Scarabaeinae by biogeographical region, as they constitute adaptive responses to the historical biogeography and to the current ecological conditions of each region.

Neotropical Region

Gill (1991) lists 35 Scarabaeinae species found in fruits or recently cut plants. We present 100 species (not counting the ones from northwest Argentina), including in many cases repeted citations of species captured in fruits. Of this list, 51 cases belong to new, unpublished data of species that had not been cited as collected in fruits.

Most citations correspond to Neotropical rainforests (mostly from Mesoamerica), which are the biomes with the highest number of frugivorous Scarabaeinae in the world. This relationship with one vegettion type is interesting, as it is also found in Southeast Asia, and, although in less numbers, in Equatorial Africa.

The Neotropics not only comprise the highest number of frugivorous species, but also the highest number of frugivorous genera. On the other hand, most other cases of frugivory in tropical regions correspond to the genus *Onthophagus*. Neotropical frugivorous and saprophagous Scarabaeinae are distributed in 16 genera; *Onthophagus* has the highest number of cases with 29 species, followed by *Canthidium* and the burrower genus of medium to large beetles *Dichotomius*, both with 14 species.

These numbers correspond to all species found once or several times in fallen fruits or vegetable remains. In most cases these species are coprophagous or copronecrophagous species, where the adults turn to fruits as an alternative trophic resource. As fruits and vegetable remains are very abundant, they decrease the intense competitions that surround scarce and ephemeral resources of the tropical forests, such as excrement and small corpses. However, in some cases this species are true fruit or vegetable specialists, although occasionally collected in carrion or excrement-baited traps. This is the case of *Canthidium laetum*, a true legume seed specialist in Mexico and Costa Rica, which even nidifies using this resource. In the same situation are *Canthidium* aff. *lucidum* and other species in the same genus, *Bdelyrus* species associated to humus accumulated in bromeliads, several species of *Dichotomius* (*D. ascanius*, *D. bicuspis*, *D. fissus*), *Eurysternus hirtellus*, and several species of Mesoamerican *Onthophagus* (*O. belorhinus*, *O. carpophilus*, *O. dicranius*, *O. nasicornis*, *O. rhinolophus*, *O. rostratus*, *O. solisi*, *O. tapirus*, and *O. villanuevai*), plus the Peruvian species *O. xanthomerus* (for complete information, see Frugivory and Saprophagy in Adults). Besides *O. rhinolophus* that is known to nidify in fruits, it is possible that some of the other mentioned species do it too. All the Mesoamerican *Onthophagus* species that are fruit specialists belong to the clypeatus group (Zunino & Halffter, 1997). This phylogenetic unit further support the notion that frugivory within this

17

group constitutes a significant and recent biogeographic and evolutionary phenomenon.

Quantitatively, what is the relevance of frugivory in adult Scarabaeinae of the Neotropical forests? In Frugivory and Saprophagy in Adults, we mentioned that in the biological station La Selva (Costa Rica), 20% of adult Scarabaeinae are attracted to fruits. In Palenque, (Mexico), the percentage is the same, but three and maybe four species specialize on this resource, whereas in La Selva only one species is a specialist. The only other Mesoamerican forest with quantitative data, Los Tuxtlas (Mexico), has a lesser percentage of species attracted by fruit (13%).

Of the 37 *Onthophagus* species listed for Costa Rica by Kohlmann & Solís (2001), adults of 10 species (27%) have been found in different rotten fruits or in avocado seeds. Of these, three (8%) seem to be fruit specialists: two associated to avocado seeds, and the third one to rotten fruit. These percentages show the importance of frugivory in adult Scarabaeinae (mainly in *Onthophagus*) in Tropical America, mainly in areas with forests. Many of the *Onthophagus* found in fruits or seeds, with the exception of those that specialize in fruits, have also been collected in carrion and excrement baited traps, occasionally even in large numbers.

What are the reasons behind the importance of frugivory in Neotropical forests? The answer is the same that explains the significant number necrophagous or copronecrophagous beetles in this region, the highest in the world, and is related with the low number—compared to other regions—of mammals of medium and large size, and thus the lack of their excrements.

Halffter & Matthews (1966:16) suggested the following reasons to explain the importance of necrophagy—and accordingly of frugivory—in the Neotropics: 1) The abundance of rainforests is higher than in other tropical regions, with the exception of Southeast Asia; 2) The lack of large mammals in the interior of the forests in comparison to other regions; 3) The relatively less importance of other necrophagous insects such as flies and Silphidae.

The close relationship between Scarabaeinae and Mesoamerican forests, from Mexico to Panama, has been empirically "proved" in recent times. As forests have been cut down and substituted with grazing pastures, the rich Scarabaeinae faunas (from 32 to more than 40 species per site) that characterize these forests, including several frugivorous and necrophagous species, have been replaced by a small ensemble of around five coprophagous species, that includes some remains of forest fauna, and a few isolated open landscape species.

Why are Neotropical forests, including those in Mesoamerica, so rich in Scarabaeinae species, when there are so many factors against it? The answer can be found in the historical biogeography of the region, and especially, to the capacity that Scarabaeinae (mainly adults) process to use alternative sources of food.

Until about 10,000 years, the Neotropics, including Mesoamerica, had mammal megafauna as rich as the current fauna in some protected areas of Africa (Janzen & Martin, 1982). With the mass extinctions of the end of the Pleistocene-beginning of the Holocene (see Janzen & Martin, 1982; Martin & Klein, 1989) more than 19 genera of large mammals, and more than 75% of the whole number of species became extinct. It is evident that this extinction caused a significant impact, only partially compensated by the introduction of large species after the Spanish conquer. Although the number of Scarabaeinae species is less than in Africa (where the relationship large and medium mammals-cophrophagy-Scarabaenae richness has been continuous), the richness in Tropical America is still high. We consider that its survival and current richness can be explained by the capacity of many Neotropical Scarabaeinae to partially or completely adapt to a necrophagous and frugivorous feeding habit.

In order to have a complete perspective of the deviation from coprophagy in the Neotropics, we most include the rich Scarabaeinae fauna associated to detritus of *Atta* and *Acromyrmex* ants from Mexico to Brazil, as well as the uncommon use of vegetable remains in Northwest Argentina.

Detritus from the Attini nests are a very special food, composed by fine fragments of the remains of fungi farms, as well as by the own ant bodies that are accumulated in internal or external deposits, where it decomposes. In this medium 31 Scarabaeinae species have been found (see the list in the Frugivory and Saprophagy in Adults section). Some of these species are occasional in such detritus, but 19 to 22 seem to be specialists of this type of food or have been only found in ant nests. Evenmore, the nidification of two species occurs only in *Atta* detritus.

In contrast to the great majority of species that use seeds of fruits as food, those species that specialize in detritus from Attini's nests are not attracted to carrion or excrements. This fact, in conjunction with the high percentage of specialists, seems to suggest that this trophic adaptation might be even older than frugivory or necrophagy.

In the arid Northwest of Argentina, *Anomiopsoides biloba* and *A. cavifrons* can use small leaves and seeds as food, which is deposited in galleries (see the Frugivory and Saprophagy in Adults section). This is an extraordinary response to arid conditions, similar to the one that has been described for Southafrica (see the Frugivory and Saprophagy in Adults, and the Nidification sections).

In summary, throughout the Neotropics, we have found deviations from coprophagy to the consumption of seeds, fruits, and non-animal detritus in 133 species, which is, by much, the highest number in the world.

Oriental Region

Although less than in the Neotropics, several Scarabaeinae species have been found in fallen fruits and flowers in the tropical rainforests of Southeast Asia (see Frugivory and Saprophagy in Adults). Of the 15 species listed, 13 belong to the genus *Onthophagus*; of them, only two seem to be true fruit specialists.

Ethiopic Region

As we mentioned in Frugivory and Saprophagy in Adults, coprophagy is dominant in Africa. This region possesses the highest number of specialists within this trophic resource, i.e., species attracted to a specific kind of excrement. The explanation to this "faithfulness" to coprophagy is evolutionary and biogeographical, and resides in the continuous relation that exists since the Cenozoic between the abundance of medium and large size mammals and Scarabaeinae richness and coprophagy.

However, in Frugivory and Saprophagy in Adults, we present a number of interesting cases of associations with fruits and vegetable detritus: 17 species, of which all but the

three *Paraphytus* species are generalists. To this number we must add the seven *Scarabaeus* (*Pachysoma*) species that gather and storage, among other things, vegetable detritus in their galleries, similarly to *Anomiopsoides* in the arid Northwest of Argentina.

Australian Region
Besides truly exceptional feeding and nidification modus in *Cephalodesmius* (see Nidification) in Australia, we only have reference of one species that is attracted to fruits.

Neartic and Paleartic Regions.
In the immense extension of the Northern Hemisphere, rich in Scarabaeinae fauna in its temperate regions, coprophagy is dominant. Attraction by fruits is rare among the clearly coprophagous species (see *Onthophagus coenobita* in Nidification). Also necrophagy lacks ecological relevance.

Conclusions

1) In adult Scarabaeinae, the use of seeds, fruits and vegetable detritus as food, and even in some cases for nidification, have a greatest ecological significance than previously noted. This significance varies a lot among the different biogeographic regions; the Neotropics hold the greatest number of cases, followed, to a lesser extent, by the Oriental and Ethiopic Regions. In Australia there is only one known case besides the highly specialized *Cephalodesmius*. In the Neartic and Palearctic regions, the change from coprophagy to frugivory or saprophagy are casual and non-significant.

2) In the Neotropics, changes towards these derived feeding habits are associated to the extension of the tropical rainforests, as well as to the low abundance of medium and large size mammals in them. These same reasons explain the regional importance of necrophagy.

3) The low abundance of medium and large size mammals in the Neotropics is a relatively recent evolutionary phenomenon, dating from 10,000 years to date, that has been partially compensated during the last five centuries by the introduction and expansion –by the Spanish and Portuguese—of domestic species. We propose that in order to cope with the drastic reduction of available excrement, a change to necrophagy and frugivory-saprophagy allowed a rich Scarabaeinae fauna to survive in the Neotropical forests.

4) In the arid Northwest of Argentina and in the desert of Southwest Africa, phylogenetically unrelated beetles use vegetable detritus, relocating and storing them in underground galleries, bellow soil humidity level. These convergent adaptive processes allow the survival of beetles in extremely arid areas, with very little available excrement.

5) In adults and larvae, the use of seeds, fruits, and vegetable detritus is accomplished without morphological or functional changes of the buccal-digestive apparatus, feeding or nidification behaviors, all them closely related to the coprophagous-microphagic feeding habit.

Bibliography

ARROW, G.J. 1903. On the Laparostict lamellicorn Coleoptera of Grenada and St. Vincent (West Indies). *Transactions of the Entomological Society of London*, **1903**: 509-520.

ARROW, G.J. 1931. Coleoptera Lamellicornia. Part 3 (Coprinae). In *The Fauna of Brithish India, including Ceylon and Burma*. Taylor and Francis. London.

BATES, H.W. 1886. Pectinicornia and Lamellicornia. In: *Biologia Centrali-Americana*, Insecta, Coleoptera. Vol. 2, part 2. London.

CAMBEFORT, Y. 1982. Les Coléoptères Scarabaeidae s. str. de Lamto (Côte d'Ivoire): structure des peuplements et role dans l'écosystème. *Annales de la Société Entomologique de France* (N.S.), **18**(4): 433-459.

CAMBEFORT, Y. 1986. Les Coléoptères Scarabeidae du Parc National de Taï (Cote d'Ivoire). *Revue Francaise d'Entomologie* (N.S.), 7(5):337-342.

CAMBEFORT, Y. 1991. From saprophagy to coprophagy. In: I. Hanski & Y. Cambefort (Eds.) *Dung Beetle Ecology*. Pp 22-35. Princeton University Press. Princeton, New Jersey, USA.

CAMBEFORT, Y. & P. WALTER 1985. Description du nid et de la larve de *Paraphytus aphodioides* Boucomont et notes sur l'origine de la coprophagie et l'evolution des Coléoptères Scarabaeidae s. str. *Annales de la Société Entomologique de France* (N.S.), **21**(4): 351-356.

CHIN, K- & B.D. GILL 1996. Dinosaurs, dung beetles and conifers: participans in a Cretaceous food web. *Palaios*, **5**(11): 280-285.

COOK, J. 1998. A revision of the Neotropical genus *Bdelyrus* Harold (Coleoptera: Scarabaeidae). *The Canadian Entomologist*, **130**: 631-689.

COOK, J. 2000. Four new species of *Bdelyrus* (Coleoptera: Scarabaeidae: Scarabaeinae) and a redescription of *Bdelyrus lagopus*. *The Canadian Entomolgist*, **132**: 551-565.

DAVIS, A.J. 1993. The ecology and behaviour of rainforest dung beetles in Northern Borneo. Ph. D. Thesis. University of Leeds. 147 pp.

DAVIS, A.J. & S. LANTOH 1996. Dung beetles collected from *Rafflesia pricei* Meijer at the Tambunan Reserve, Sabah, Malaysia. *Malayan Nature Journal*, **50**: 39-41.

DAVIS, A.J. & S.L. SUTTON 1997. A dung beetle that feeds on fig: implications for the measurement of species rarity. *Journal of Tropical Ecology*, **13**: 759-766.

DELGADO-CASTILLO, L. & C. DELOYA 1990. Una nueva especie mexicana de *Onthophagus* Latreille, 1802, del "grupo clypeatus" (Coleoptera: Scarabaeidae: Scarabaeinae). *Annales de la Société Entomologique de France* (N.S), **26**(2): 211-216.

DELOYA, A.C. 1988. Coleópteros Lamelicornios asociados a depósitos de detritos de *Atta mexicana* (Smith) (Hymenoptera: Formicidae) en el sur del estado de Morelos, México. *Folia Entomológica Mexicana*, **75**: 77-91.

ESCOBAR, F. 2003. Feeding habits and distributional records of 11 species of Neotropical Scarabaeinae. *The Coleopterists Bulletin*, **57**(2): 131-132.

ESCOBAR, F., G. HALFFTER, A. SOLÍS, V. HALFFTER & D. NAVARRETE 2008. Temporal shifts in dung beetle community structure within a protected area of tropical wet forest: a 35-year study and its implications for long-term conservation. *Journal of Applied Ecology*, **45**: 1584-1592.

FAVILA, M.E. & A. DIAZ-ROJAS 1997. Escarabajos coprófagos y necrófagos. In: E. González Soriano, R. Dirzo y R.C. Vogt (Eds.). *Historia Natural de Los Tuxtlas*. Pp 383-384. Universidad Nacional Autónoma de México.

GENIER, F. 1996. A revision of the Neotropical genus *Ontherus* Erichson (Coleoptera: Scarabaeidae: Scarabaeinae). *Memoirs of the Entomological Society of Canada*, 170, 169 pp.

GENISE, J.F. 1998. Fossil bee cells from the Asencio formation (Late Cretaceous – Early Tertiary) of Uruguay, South America. *Proceedings of the First International Palaeoentomological Conference*, Moscow, pp. 27-32.

GENISE, J.F. 1999. Paleoicnología de insectos. *Revista de la Sociedad Entomológica Argentina*, **58**: 104-116.

GENISE, J.F. 2004. Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols attributed to coleopterans, ants and termites. In: D. McIcroy (Ed.) *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*. Geological Society, London, Special Publications, 228: 419-453.

GENISE, J.F. & J.H. LAZA 1998. *Monesichnus ameghinoi* Roselli: a complex insect trace fossil produced by two distinct trace makers. *Ichnos*, **5**: 213-223.

GENISE, J.F., M.G. MANGANO, L.A. BUATOIS, J.H. LAZA & M. VERDE 2000. Insect trace fossil associations in paleosols: the *Coprinisphaera* ichnofacies. *Palaios*, **15**: 49-54.

GILL, B.D. 1986. *Foraging behavior of tropical forest Scarabaeinae in Panama*. Ph. D. Thesis, Carleton University, Ottawa, Canada.

GILL. B.D. 1991. Dung beetles in Tropical American forests. In: I. Hanski & Y. Cambefort (Eds.) *Dung Beetle Ecology*. Pp 211-229. Princeton University Press. Princeton, New Jersey, USA.

GOIDANICH, A. & C.E. MALAN 1962. Sulla fonte di alimentazione e sulla microflora aerobica del nido pedotrofico e dell apparato digerente delle larva di Scarabei coprofagi (Coleoptera, Scarabaeidae). *Atti della Accademia delle Scienze, Torino*, **96**: 575-628.

GOIDANICH, A. & C.E. MALAN 1964. Sulla nidificazione pedotrofica di alcune specie di *Onthophagus* Europei e sulla microflora aerobica dell' aparato digerente della larva di *Onthophagus taurus* Schreber (Coleoptera, Scarabaeidae). *Annali della Facoltá di Scienze Agrarie della Universita degli Studi di Torino*, **2**: 213-378.

HALFFTER, G. 1961. Monografia de las especies norteamericanas del género *Canthon* Hoffsg. *Ciencia (México)*, **20**(9-12): 225-320.

HALFFTER, G. 1977. Evolution of nidification in the Scarabaeinae (Coleoptera: Scarabaeidae). *Quaestiones Entomologicae*, **13**: 231-253.

HALFFTER, G. 1991a. Historical and ecological factors determining the geographical distribution of beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Entomológica Mexicana*, **82**: 195-258.

HALFFTER, G. 1991b. Feeding, bisexual cooperation and subsocial behavior in three groups of Coleoptera. In: M. Zunino, X. Bellés & M. Blas (Eds.). *Advances in Coleopterology*. Pp 281-296. Asociación Europea de Coleopterología, Barcelona.

HALFFTER, G. & W.D. EDMONDS 1982. *The Nesting Behavior of Dung Beetles (Scarabaeinae). An Ecological and Evolutive Approach*. 176 pp. Instituto de Ecología, A.C. México, D.F.

HALFFTER, G. & V. HALFFTER 1989. Behavioral evolution of the non-rolling roller beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Acta Zoológica Mexicana* (N.S.), **32**: 1-53.

HALFFTER, G. & E.G. MATTHEWS 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomológica Mexicana*, **12-14**: 1-312.

HALFFTER, G. & E.G. MATTHEWS 1971. The natural history of dung beetles. A supplement on associated biota. *Revista Latinoamericana de Microbiología*, **13**: 147-164.

HALFFTER, V., S. ANDUAGA & G. HALFFTER 1976. Etograma de *Liatongus monstrosus* (Bates) (Coleoptera, Scarabaeidae). *Folia Entomológica Mexicana,* **36**: 48-49.

HARRISON, J. DU G., C.H. SCHOLTZ & S.L. CHOWN 2003. A revision of the endemic south-western African dung beetle subgenus *Scarabaeus* (*Pachysoma*) MacLeay, including notes on other flightless Scarabaeini (Scarabaeidae: Scarabaeinae). *Journal of Natural History*, **37**: 305.355.

HATA, K & D. EDMONDS 1983. Structure and function of the mandibles of adult dung beetles (Coleoptera: Scarabaeidae). *International Journal of Insect Morphology and Embryology*, **12**: 1-12.

HOLTER, P. & C.H. SCHOLTZ 2005. Are ball-rolling (Scarabaeini, Gymnopleurini, Sisyphini) and tunneling Scarabaeinae dung beetles equally choosy about the size of ingested dung particles? *Ecological Entomology*, **30**: 700-705.

HOLTER, P., C.H. SCHOLTZ & K.G. WARDHAUGH 2002. Dung feedings in adult scarabaeines (tunnellers and endocoprids): even large dung beetles eat small particles. *Ecological Entomology*, **27**: 169-176.

HOWDEN, H.F. & O.L. CARTWRIGHT 1963. Scarab beetles of the genus *Onthophagus* Latreille North of México (Coleoptera: Scarabaeidae). *Proceedings of the United States National Museum*, **114** (3467): 1-133.

HOWDEN, H.F. & O.P. YOUNG 1981. Panamian Scarabaeinae: Taxonomy, distribution and habits (Coleoptera, Scarabaeinae). *Contributions American Entomological Institute*, **18**: 1-204.

HUERTA, C., S. ANDUAGA & G. HALFFTER 1980. Relaciones entre nidificación y ovario en *Copris* (Coleoptera: Scarabaeinae). *Folia Entomológica Mexicana*, **45**: 61-63.

HUERTA, C. & G. HALFFTER 2000. Factores involucrados en el comportamiento subsocial de *Copris* (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Entomológica Mexicana*, **108**: 95-120.

HUIJBREGTS, J. 1984. *Bdelyrus geijskesi*, a new scarab (Coleoptera: Scarabaeidae) from Suriname associated with Bromeliaceae. *Zoologische Medelingen*, **59**(6): 61-67.

JANZEN, D.H. & P.S. MARTIN 1982. Neotropical anachronisms: the fruits the Gomphotheres ate. *Science*, **215**: 19-27.

KOHLMANN, B. & A. SOLIS 2001. El género *Onthophagus* (Coleoptera: Scarabaeidae) en Costa Rica. *Giornale Italiano di Entomologia*, **49**(9): 159-261.

KRELL, F.T. 2000. The fossil record of Mesozoic and Tertiary Scarabaeoidea (Coleoptera: Polyphaga). *Invertebrate Taxonomy*, **14**: 871-905.

KRELL, F.T. 2004. *Catalogue of Fossil Scarabaeoidea (Coleoptera: Polyphaga) of the Mezozoic and Tertiary*. Electronically published. Lincoln, Nebraska. 61 pp.

LARSEN, T., A. LOPERA & A. FORSYTH 2005. Extreme trophic and habitat specialization by Peruvian dung beetles. *The Coleopterists Bulletin*,**60**(4): 315-324.

LAZA, J.H. 2006. Dung-beetle fossil brood balls: the ichnogenera *Coprinisphaera* Sauer and *Quirogaichnus* (Coprinisphaeridae). *Ichnos*, **13**: 217-235.

LÓPEZ-ALARCÓN, D., G. HALFFTER & F. VAZ-DE-MELLO 2009. Nesting behavior in *Trichillum* Harold, 1868 and related genera (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini: Scatimina): a primitive process or a loss of nidification?. *The Coleopterists Bulletin,* **63**(3): 289-297.

LOPEZ-GUERRERO, I. 2007. Análisis de las piezas bucales en *Canthon virens* Mannerheim (Coleoptera: Scarabaeinae: Canthonina) en relación a sus hábitos tróficos. In: Mario Zunino & Antonio Melic (Eds.). *Escarabajos, Diversidad y Conservacion Biológicas. Ensayos en Homenaje a Gonzalo Halffter. Monografías 3er. Milenio*, M3M, vol. 7: 131-142. Sociedad Entomológica Aragonesa, Zaragoza.

LUEDERWALDT, H. 1911. Os insectos necrofagos Paulistas. *Revista Museu Paulista*, **8**: 414-433.

LUEDERWALDT, H. 1931. O gênero *Ontherus* (Coleopt.) (Lamell. – Coprid. – Pinot.) com una chave para a determinaçao dos pinotides americanos. *Revista Museu Paulista*, **17**(1): 363-422, 1 pl.

LUMARET, J.P. 1990. *Atlas des Coléoptères Scarabeides Laparosticti de France*. Museum National d'Histoire Naturelle, Inventaires de Faune et de Flore. Paris.

MARTIN, P.S. & R.G. KLEIN (Eds.). 1989. *Quaternary Extinctions: A Prehistoric Revolution*. Second printing. The University of Arizona Press, 892 pp. Tucson, Arizona.

MASUMOTO, K. 2001. A food habit of *Onthophagus bonarae* (Coleoptera, Scarabaeidae). *Elytra*, Tokio, 29 (1): 140.

MILLER, A. 1961. The mouth parts and digestive tract of adult dung beetles (Coleoptera: Scarabaeidae) with reference to the ingestion of helmith eggs. *Journal of Parasitology*, **47**: 735-744.

MONTEITH, G.B. & R.I. STOREY. 1981. The biology of *Cephalodesmius*, a genus of dung beetles wich synthesizes dung from plant material (Coleoptera: Scarabaeidae: Scarabaeinae). *Memoirs of Queensland Museum*, **20**(2): 253-277, pls. 1-3.

MORON, M.A., C. DELOYA & L. DELGADO 1988. Fauna de coleópteros Melolonthidae, Scarabaeidae y Trogidae de la región de Chamela, Jalisco, México. *Folia Entomológica Mexicana*, **77**: 313-378.

NAVARRETE-HEREDIA, J.L. 2001. Beetles associated with *Atta* and *Acromyrmex* ants (Hymenoptera: Formicidae: Attini). *Transactions of the American Entomological Society*, **127**(3): 381-429.

NORIEGA, J.A. & J.C. CALLE 2008. Comsumption of *Gustavia hexapetala* (Aublet) Smith (Lecythidales: Lecythidaceae) by the dung beetle *Eurysternus plebejus* Harold (Coleoptera: Scarabaeidae). *The Coleopterists Bulletin*, **62**(4): 455-460.

OCAMPO, F.C. 2005. Revision of the southern South American endemic genus *Anomiopsoides* Blackwelder, 1944 (Coleoptera: Scarabaeidae: Scarabaeinae: Eucraniini) and description of its food relocation behavior. *Journal of Natural History*, **39**(27): 2537-2557.

PECK, S.B. & A. FORSYTH 1982. Composition, structure and competitive behavior in a guild of Ecuatorian rain forest dung beetles (Coleoptera: Scarabaeidae). *Canadian Journal of Zoology*, **60**(7): 1624-1634.

PEREIRA, F.S. & G. HALFFTER 1961. Nuevos datos sobre Lamellicornia mexicanos con algunas observaciones sobre saprofagia. *Revista Brasileira de Entomologia*, **10**: 53-66.

PEREIRA, F.S. & A. MARTINEZ 1956. Os gêneros de Canthonini Americanos. *Revista Brasileira de Entomologia*, **6**: 91-112.

PEREIRA, F.S., M.A. VULCANO & A. MARTINEZ 1960. O gênero *Bdelyrus* Harold, 1869. *Actas y Trabajos del Primer Congreso Sudamericano de Zoología*, **3**: 155-164.

PHILIPS, T.K. & K.L. BELL 2008. *Attavicinus*, a new generic name for the myrmecophilous dung beetle *Liatongus monstrosus* (Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin*, **62**(1): 67-81.

PHILIPS, T.K., E. PRETORIUS & C.H. SCHOLTZ 2004. A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling and evolutionary history. *Invertebrate Systematics*, **18**: 53-88.

SAKAI, S. & T. INONE 1999. A new pollination system: dung beetle pollination discovered in *Orchidantha inonei* (Lowiaceae, Zingiberales) in Sarawak, Malaysia. *American Journal of Botany*, **86**(1): 56-61.

SCHOLTZ, C.H. 1989. Unique foraging behaviour in *Pachysoma* (*Scarabaeus*) s*triatum* Castelnau (Coleoptera: Scarabaeidae): an adaptation to arid conditions? *Journal of Arid Environments*, **16**: 305-313.

SCHOLTZ, C.H. & S.L. CHOWN 1995. The evolution of habitat use and diet in the Scarabaeoidea: a phylogenetic approach. In: A.F.J. Pakaluk & S.A. Slipinski (Eds.). *Biology, Phylogeny*

and Classification of Coleoptera. Pp. 335-374. Museum i Instytut Zoologii PAN, Warzawa, Polonia.

SCHOLTZ, C.H., J. DU G. HARRISON & V.V. GRABENNIKOV 2004. Dung beetle (*Scarabaeus* (*Pachysoma*)) biology and immature stages: reversal to ancestral status under desert conditions? (Coleoptera: Scarabaeidae). *Biological Journal of the Linnean Society*, **83**: 453-460.

SOLIS, A. & B. KOHLMANN 2002. El género *Canthon* (Coleoptera: Scarabaeidae) en Costa Rica. *Giornale Italiano di Entomologia*, **10**: 1-68.

SOLÍS, A. & B. KOHLMANN 2004. El género *Canthidium* (Coleoptera: Scarabaeidae) en Costa Rica. *Giornale Italiano di Entomologia*, **11**(52): 1-73.

UMEYA, K. 1960. A comparative morphology of the alimentary tract in the adults of Lamellicorn beetles (Coleoptera). *Memoirs of Faculty of Agricultural Sciences, Hokkaido University*, **3**: 60-113.

VAZ-DE-MELLO, F.Z. 2008. Sinopsis of the new subtribe Scatimina (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini) with descriptions of twelve new genera and review of *Genieridium* new genus. *Zootaxa*, **1955**: 1-75.

VAZ-DE-MELLO, F.Z., J.N.C. LOUZADA & J.H. SCHOEREDER 1998. New data and comments on Scarabaeidae (Coleoptera: Scarabaeoidea) associated with Attini (Hymenoptera: Formicidae). *The Coleopterists Bulletin*, **52**(3): 209-216.

WALTER, P. 1978. *Recherché écologiques et biologiques sur des Scarabéides coprophages d'une savane du Zaire*. Ph. D. Thesis. 366 pp. Université des Sciences et Techiques du Languedoc, Montpellier.

ZUNINO, M. E. BARBERO & M. LUZZATTO 1989. Food relocation behavior in Eucraniina beetles (Scarabaeidae) and the constraints of xeric environment. *Tropical Zoology*, **2**: 235-240.

ZUNINO, M. & G. HALFFTER 1977. Sobre *Onthophagus* Laterille, 1802 americanos (Coleoptera: Scarabaeidae: Scarabaeinae). *Elytron*, **11**: 157-178.