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Behavioral evolution of the non-rolling
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(Coleoptera: Scarabaeidae; Scarabaeinae)

Gonzalo Halffter and Violeta Halffter

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**BEHAVIORAL EVOLUTION OF THE NON-ROLLING
ROLLER BEETLES
(COLEOPTERA: SCARABAEIDAE: SCARABAEINAE)***

**Gonzalo Halffter
and
Violeta Halffter**

Instituto de Ecología
Apartado Postal 63
91000 Xalapa, Veracruz
and
Centro de Investigaciones
Biológicas de Baja California
Sur (CIB)
Apartado Postal 128
23000, La Paz,
Baja California Sur

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ABSTRACT

The fundamental ethological display of the Scarabaeinae (Insecta: Coleoptera: Scarabaeidae) is the relocation of food: relocation for the adult's use or for nesting. Relocalization can be either vertical or horizontal. The basic ethological and morphological division of the Scarabaeinae into burrowers and rollers is determined by whether one or the other is done. The rollers relocate horizontally by forming a ball at the food source (dung or carrion), rolling it for a certain distance and then burying it (or not). When the ball is for the adult's food, the process is carried out by one specimen, male or female; when the ball is for nesting, the process is carried out by a bisexual pair and once the ball has been rolled it is transformed by the female into a brood-ball. Both processes are characteristic and unique - in the whole animal kingdom - of the Scarabaeini, the rolling beetles.

This paper is dedicated to the analysis of the origin and evolution of the processes involved in ball formation and rolling and the relationship between the two. In order to do this all the known cases where one or the other of these fundamental behavioral displays are lacking were analyzed. The analysis starts with the reexamination of all the exceptions to rolling and ball formation pointed out in the first synthesis on the biology of Scarabaeinae (Halffter and Matthews, 1966). The Australian examples observed by Matthews (1974) are also examined as well as the observations published subsequently.

The second part of this paper describes the behavior of *Canthon obliquus*, an endemic species from the southern part of Baja California, whose biology was completely unknown up to now. This beetle does not make balls for food, and it does not roll them on the surface, although it can occasionally separate a small fragment of dung and relocate it holding it with the tarsi of the posterior legs, while it walks on the anterior and middle ones. For nesting it makes balls which it immediately burys under the dung pad.

The third part of the paper is a discussion on the processes of ball formation and rolling and their interrelation within the general context of the evolution of feeding and reproductive behavior of Scarabaeinae. The main ideas of the hypothesis (advanced in part by Halffter and Matthews, 1966; Halffter, 1977; Halffter and Edmonds, 1982) are: Scarabaeinae are part of a monophyletic group whose ethological evolution is centered around the ecological problem of the excrement of large vertebrates. A series of important common morphological characteristics (analyzed in detail by Halffter and Edmonds, 1982) reinforce the idea of this monophyletic origin. The tribe Scarabaeini detaches itself early from the common trunk, probably before the end of the Mesozoic era, but not before a fundamental gain regarding the nesting of the subfamily has been established: the formation by the mother of an individual and isolated brood-ball. In the most primitive burying Scarabaeinae, the brood-ball is not present. The most evolved forms of burrowers arrive at the brood-ball by following at least three different behavioral sequences. As far as we know, all rollers

make a brood-ball in a similar way. The brood-ball is considered fundamental as it guarantees the efficient isolation and protection of the egg, larva and pupa. It is accompanied by the lack of ability to make a pupal cocoon at the end of the larval development and by the acquisition of a perfected mechanism of repair; in a similar manner the maternal activity is perfected through the recoating of the brood-ball by a layer of soil and/or the care of the mother during development.

From the analysis carried out in this paper the outstanding fact is that all rollers whose nesting is known make a brood-ball from which we can deduce -until evidence to the contrary is found- that the capacity to execute the complex series of movements necessary to separate the ball is present in the whole tribe, although because of local or regional ecological conditions it may not be used for feeding behavior. We postulate that the capacity to elaborate the ball has evolved simultaneously with the rolling and not independently and after this process as Eric G. Matthews suggests for the Australian forms.

In a certain number of cases in which the non-formation of a ball on the surface has been pointed out, subsequent observations have demonstrated that this is possible when the scarab finds itself before excrement which has the adequate texture and size. There are still some species in which ball formation has never been observed in the feeding processes. We consider that in all cases where ball formation is not present or only manifests itself occasionally, it is because of a derived behavior due to special ecological conditions, such as the lack (during a long evolutionary period - Australia - or because of local or regional conditions) of an abundant and adequate excrement and the presence, on the other hand, of pellets. What really stands out is the fact that, as has been demonstrated in many of these species, the capacity to make a ball has been preserved when the adequate material and conditions are present and that the, up to now universal, permanence of the brood-ball formation is a fundamental part of nesting. The fact that nesting behavior is more conservative compared with feeding behavior is made obvious. In this way, as recent papers on burying species of the subfamily are beginning to point out, the ecological pliability of the Scarabaeinae's behavior becomes evident.

The outstanding aspect of the Scarabaeini's behavior is the importance of bisexual cooperation, essential to the rolling process for the future brood-ball. Two roll better and faster than one. A series of morphological experimental discoveries over the last decade point out the enormous importance of chemical communication through pheromones.

RESUMEN

El despliegue comportamental básico de los Scarabaeinae (Insecta: Coleoptera: Scarabaeidae) es la relocalización del alimento: relocalización para uso del adulto o para la nidificación. La relocalización puede ser vertical u horizontal. El que se siga una u otra determina la gran división

etológica y morfológica de los Scarabaeinae en cavadores y rodadores. Los rodadores realizan una relocalización horizontal que comprende la formación de una bola en la fuente de alimento (estiércol o carroña), su rodaje a una cierta distancia y (o no) su enterramiento. Cuando la bola está destinada a la alimentación del adulto, el proceso es realizado por un solo individuo, macho o hembra; cuando la bola está destinada a la nidificación, el proceso es efectuado por una pareja bisexual y la bola una vez rodada es transformada por la hembra en bola-nido. Ambos procesos son característicos y únicos - en todo el reino animal - de los Scarabaeini, tribu que comprende los escarabajos rodadores.

Este trabajo está dedicado a analizar el origen y evolución de los procesos de formación de la bola y de rodaje, y la interrelación entre ambos. Para ello se analizan todos los casos conocidos en los que no se presenta uno y otro de estos dos despliegues comportamentales fundamentales. El análisis se inicia con el reexamen de todas las excepciones al rodaje y formación de la bola señaladas en la primera síntesis de la biología de los Scarabaeinae (Halffter y Matthews, 1966). Se examinan también los ejemplos australianos anotados por Matthews (1974), así como las observaciones y etogramas publicados después.

La segunda parte del trabajo está destinada a describir el comportamiento de *Canthon obliquus*, una especie de Scarabaeini endémica del extremo sur de Baja California, de cuya biología no se conocía hasta ahora nada. Este escarabajo no hace bolas para la alimentación, ni tampoco las rueda en superficie, aunque excepcionalmente es capaz de separar un pequeño fragmento de estiércol y relocalizarlo sujeto con los tarsos de las patas posteriores, mientras se desplaza utilizando las patas anteriores y medias. Para la nidificación hace bolas que entierra inmediatamente por debajo del mojón de estiércol.

La tercera parte del trabajo es una discusión de los procesos de formación de la bola y de rodaje y de su interrelación dentro del contexto general de la evolución de los comportamientos alimentario y reproductor en los Scarabaeinae. Los puntos fundamentales de la hipótesis que se presenta (en parte avanzada por Halffter y Matthews, 1966; Halffter, 1977; Halffter y Edmonds, 1982) son: Los Scarabaeinae integran un grupo monofilético cuya evolución etológica se centra en torno a la problemática ecológica del excremento de los grandes vertebrados. Una serie de importantes caracteres morfológicos comunes (analizados en detalle por Halffter y Edmonds, 1982) refuerzan la idea de este origen monofilético. La tribu Scarabaeini se separa pronto del tronco común, seguramente antes del fin del Mesozoico, pero no antes de que se haya establecido una conquista fundamental de la nidificación de la subfamilia: la formación por la madre de una bola-nido individualizada y aislada. En los Scarabaeinae cavadores más primitivos no se presenta bola-nido. Las formas de cavadores más evolucionadas llegan a ella siguiendo por lo menos tres secuencias comportamentales distintas. Todos los rodadores hacen bola-nido, en una forma que hasta donde se conoce es muy homogénea. La bola-nido se considera fundamental, ya que asegura a huevo, larva y pupa aislamiento y protección muy efectivos. Va acompañada por la

pérdida por la larva de la capacidad de hacer un cocón pupal al fin de su desarrollo, así como por la adquisición de un perfeccionado mecanismo de reparación; en forma paralela se perfecciona la actividad maternal a través del recubrimiento de la bola-nido por una capa de tierra y/o de cuidados de la madre durante el desarrollo.

Del análisis realizado en este trabajo resalta que todos los rodadores cuya nidificación se conoce hacen una bola-nido, de lo cual se deduce - hasta que no aparezca una evidencia en contra - que la capacidad para ejecutar la compleja serie de movimientos necesarios para separar y redondear la bola es una característica que existe en toda la tribu, aunque por condiciones ecológicas locales o regionales pueda no emplearse en el comportamiento alimentario. Postulamos que la capacidad para elaborar la bola ha evolucionado simultáneamente con el rodaje y no independiente y después de este proceso como sugiere para las formas australianas Eric G. Matthews (1974,1975).

En un cierto número de los casos en que se ha señalado la no formación de bolas en superficie, observaciones posteriores han mostrado que ésta puede ser posible cuando el escarabajo se encuentra ante un excremento de tamaño y textura adecuados. Siguen quedando especies en las que nunca se ha visto formación de bola en los procesos alimentarios. Consideramos que en todos los casos en que la formación de bola no se presenta o se manifiesta sólo en forma ocasional, se trata de un comportamiento derivado debido a condiciones ecológicas especiales: la no existencia durante un largo periodo evolutivo (Australia) o en condiciones regionales o locales de un excremento adecuado abundante, y la presencia por el contrario de pellets. En realidad, lo que es notable es que en muchas de estas especies se conserva la capacidad de hacer una bola cuando se encuentra un material y condiciones adecuados, así como la permanencia hasta ahora universal del proceso de formación de la bola-nido como parte fundamental de la nidificación. El carácter mucho mas conservador del comportamiento ligado a la nidificación en comparación con el alimentario, es puesto de manifiesto. Así mismo comienza a ser evidente una plasticidad ecológica del comportamiento de los Scarabaeinae, que también otros trabajos recientes sobre especies cavadoras de la subfamilia comienzan a señalar.

Aspecto llamativo del comportamiento de los Scarabaeini es la cooperación bisexual, fundamental en el proceso de rodaje de la futura bola-nido. Dos ruedan mejor y más rápido que uno. Una serie de descubrimientos morfológicos y experimentales de la última década señalan la importancia enorme de la comunicación química en esta cooperación, así como confirman el papel de la bola en asociación con la comunicación a través de feromonas.

INTRODUCTION

The exception, in this case the non-rolling ball-rollers, can contribute valuable information towards the understanding of the appearance and development of the rolling process. With this paper we wish to analyze these exceptions and their evolutionary implications.

The rich and varied fauna of beetles which attack the excrement of large and medium sized herbivorous mammals is basically made up of three subfamilies of Scarabaeidae: Scarabaeinae, Geotrupinae and Aphodiinae. Within this broad group of insects, the *ball-roller beetles* form a well defined group, with a unique feeding and nesting behavior correlated with a series of morphological characteristics. They all belong to a group that we consider monophyletic: the tribe Scarabaeini of the subfamily Scarabaeinae.

The most distinctive aspect of this group's behavior is the horizontal relocation of food. This relocation is a brilliant solution to the problem of aggregating around a food source which is fought over and perishable (see Halffter and Edmonds, 1982). The formation of a ball at the food source and its rolling is a unique solution of the Scarabaeini and the basis of all its feeding and reproductive behavior.

In order to provide food for the adult, the rolling is done by a single individual; when it is a matter of feeding the larvae, the ball, which is going to be transformed into a ball-nest, is rolled by both the male and female. In spite of a series of variations, the general outline of the feeding and reproductive behavior of the Scarabaeini is one of the most coherent for such an abundant and diversified group of insects.

More than thirty years ago, during the preparation of the monograph on the genus *Canthon* in North America (Halffter, 1961), our attention was drawn towards the rarest species of the region: *C. obliquus* Horn. It is exceptional not only because the number of known specimens is scarce, but also because of its special characteristics which make it easily distinguishable from the rest of the *Canthon*. With the Centro de Investigaciones Biológicas de Baja California Sur (CIB) we have initiated a search for this species and the studies done for the creation of the Sierra de La Laguna biosphere reserve have intensified these efforts. *C. obliquus* is a paleoendemism of the extreme south of Baja California, restricted to the Sierra de La Laguna. It occupies the subdeciduous tropical forest with some expansion towards the lower part of the oak forest.

Different aspects of this species are being studied. Armando Tejas of the CIB, is in the process of doing a detailed study with us of its microgeographical distribution and we are also preparing a taxonomic analysis with the Argentinian entomologist Antonio Martínez, which will make its isolation in relation to the other *Canthon* stand out. This isolation has already been put forward by Halffter (1961) and proven in a cladistic analysis by Kohlmann and Halffter (unpublished). *C. obliquus* has an interesting biology: it is a Scarabaeini that does not roll, it does not roll to eat and it does not roll to nest, although it can occasionally make a "rustic" horizontal relocation. The origin of this article is the detailed and not easy study of the behavior of this species over a period of four years. We did not want to limit it to an ethological description, so we examined all the known cases of roller beetles that *do not roll* for feeding or for reproduction. This is the first time that an overall analysis of this phenomenon in undertaken since the first synthesis by Halffter and Matthews, 1966.

In an evolutionary sense, this phenomenon is extremely interesting. The horizontal relocation of food by Scarabaeini includes two different processes, each composed of a complex succession of behavioral steps: the first, the formation of a ball into a mass of food, the second, the rolling. The second step does not necessarily always involve the previous formation of a ball. Which process within the evolution of behavior precedes the other? What about the cases where there is no ball formation or rolling? When there is only rolling, is it a question of the *conservation* of a primitive expression, or is it the ecological result of a conditioned evolutionary process?

We do not intend to give a definite answer to these questions, but rather to closely analyze the existing information and the hypotheses presented thus far. In the first chapter, "The Scarabaeini that do not roll" we submit the known cases where a ball was not formed or rolled. The second chapter is the ethology of *Canthon obliquus*. The third is devoted to the discussion of the previously presented hypothesis and the introduction of a new one.

The ecological scenario

In the tropics, and the sunny ecosystems of the temperate zones, the most important group of beetles - and of insects - living from the excrement of large and medium sized herbivorous and omnivorous mammals are the Scarabaeinae. In this tropical zone, especially in the neotropics, they also attack carrion and rotting fruit. Excrement (when it is large and moist), carrion and rotting fruit are

food sources which are rich and abundant although they are short lived and greatly vied for. Excrement, when it is left exposed on the ground, dries and hardens rapidly making it unsuitable for food as well as for nesting for most dung beetles. This process is faster in the savannas and sunny prairies and reaches its limits in arid prairies or brushlands and in the ecotones with the desert. In moist pastures, in the forests and especially in the humid tropical forest, dryness becomes irrelevant, but the rapid oviposition and development of fly larvae restricts its use.

The irregular availability of large and medium sized excrement and carrion also fosters intense aggregation and competition. Dindal (1973) defines excrement and carrion as unstable heterotrophic habitats, in which the primary production does not exist or is minimal and the initial energy dissipates exponentially through decomposition. The ethological and morphological evolution of the Scarabaeinae revolves around the ecological situation previously outlined. The most pressing need is to rapidly relocate the food far from the competition and to protect it from drying out and from rapidly deteriorating (see discussion in Halffter and Edmonds, 1982; Edmonds, 1983). Basically, this relocation can be done by two methods: a) *Vertical*, burying a portion of food under or very close to the original source; this procedure is followed by the burrowing Scarabaeinae and the Geotrupinae. b) *Horizontal*, forming a ball at the food source and rolling it, to later (generally but not always) bury it just below the surface. This behavior is found in only one taxonomic group: the tribe Scarabaeini.

There are some cases of convergence in which the horizontal relocation *does not necessarily mean that a ball was previously made*. Thus, groups which are essentially burrowers (or which carry out vertical relocation) could push, or even roll, a fragment which has not been manipulated (for examples in the Scarabaeinae, see Halffter and Matthews, 1966; Halffter, Halffter and López, 1974; for a similar phenomenon in the Geotrupinae, Zunino and Palestini 1986; Howden and Peck, 1987).

Horizontal relocation can also be done via mechanisms which are not pushing or rolling but rather by holding a fragment with the front legs while walking on the other legs (see cases and discussion in I.4). This behavior rather than the dispersion of a food mass, is the recollection of small dispersed fragments.

We do not consider that the objective of transporting food a certain distance is to find an adequate place to bury it, as various authors have suggested. It has more to do with reducing competition (intra and inter-specific), thus avoiding an aggregation around the deposit sites. The biological advantage of maximum

distancing could explain why the beetles stick tenaciously to a straight line during the rolling and take full advantage of the environmental factors such as the inclination of the terrain, the predominant direction of the wind and the position of the sun to maintain their course.

1. THE NON-ROLLING SCARABAEINI

I.1 *Rolling in the Scarabaeini*

When Halffter and Matthews (1966) established Pattern IV, the tribe Scarabaeini included, other than the central nucleus of four subtribes, another three: Eurysterina, Eucraniina and Alloscelina that subsequent research (see current outline in Zunino 1985) has shown to be excludable from Scarabaeini since they demonstrate a convergence of morphological characters: the middle and hind tibiae are not dilated towards the apex. Mostert and Scholtz, 1986, still maintain Eucraniina within the Scarabaeini, without discussing the point too thoroughly as their work is really devoted to the subtribe Scarabaeina. We consider that Scarabaeini is made up of four subtribes: Sisyphina, Gymnopleurina, Scarabaeina and Canthonina, thus establishing a complete identification between rolling beetles and Scarabaeini.

The formation of a ball and its subsequent movement is an ethological process of such importance that it comes with noteworthy morphological modifications: a) the middle and hind tibiae are long and slender, as opposed to the stronger, shorter and dilated towards the apex tibia of the burrowing Scarabaeinae and in general of the entire family. The posterior tibiae are marvelously adapted to function as supports for the spinning ball. The almost straight angle formed by each of the posterior tibia with the femora (which are longer than in the burrowing beetles) during the rolling limits the diameter of the ball according to the beetle's size and therefore the nesting needs and the beetle's possibilities of rolling it; b) a generally oval form which tends to be convex on the dorsum and ventrally flat; c) a very short mesosternum which makes the pronotum articulation with the rest of the body more flexible; and d) the pronotal length is shortened, making the shape rounder. All these characteristics aid the formation of the ball, and above all the rolling.

The burying processes are as characteristic of the Scarabaeini tribe as the ball formation and rolling. When this process is normal, there is no previously

excavated gallery (typical of the burrowing Scarabaeinae). In order to burrow, the earth is dug out from beneath the ball, gradually making the beetle and ball sink¹.

As is characteristic in the broader evolutionary lines of the Scarabaeinae (but not in some of the secondary ones) nesting is a modification of the feeding behavior. The rolling for nesting is performed by a bisexual couple². The male and female place themselves in different positions according to the genera or genus groups and sometimes according to the species. The rolling may or may not be followed by burying; the ball may remain on the surface. Mating takes place at the food mass, during the rolling process or once the ball is buried. The ball is then remodeled only by the female who, after oviposition, converts it into a brood-ball. This is where the larval development, pupation and the first days of the new imago occur.

The brood-ball, which is not unique to rolling beetles, is one of the most interesting evolutionary aspects of Scarabaeinae and it is found in the entire group except for the most primitive burrowing species included in nesting pattern I (see chapter 3. Discussion). The brood-ball performs a complex function of protection. It is usually buried and protected by the soil and in some species it has an additional cover of earth. In Scarabaeini, when the nest contains only one ball the process corresponds to nesting Pattern IV³. Halffter (1977) found that the nest could be compound (i.e. made up of more than one brood-ball) and cared for by the mother sometimes assisted by the father.

This behavior is well known in *Canthon cyanellus cyanellus* LeConte (Halffter, 1977; Halffter, Halffter and Huerta, 1983) on whose ethological basis, nests which had not before been explained are now understood. The compound nest of the rolling scarabs belong to nesting Pattern V (for a discussion of the patterns in the Scarabaeinae subfamily and the importance of the brood-balls, see Halffter and Edmonds, 1982). In the rolling scarabs, the male has a greater participation in the nesting process than in other Scarabaeinae. He is mainly responsible for preparing the ball, rolling it and burying it. In general and as far as is known, unlike the burrowing scarabs, it is the male which attracts the female, especially in connection with the ball and ball rolling activities to which different pheromones are associated. (see 3.2; Favila, 1988).

1.2 *The non-rolling Scarabaeini according to Halffter and Matthews (1966)*

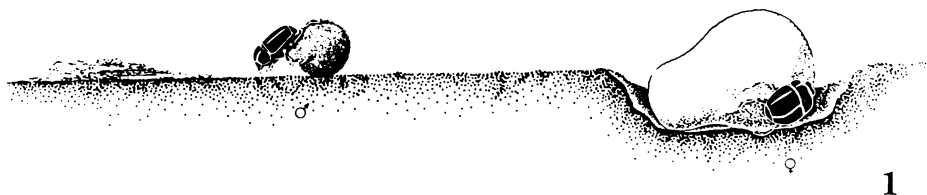
Halffter and Matthews presented a synthesis of the knowledge and of their own experiences gathering together all the cases where the Scarabaeini were not known to roll in variations 2 and 3 of what they called "Aberrant Nesting Behavior".

We have already pointed out that three of the subtribes (Eurysternina, Eucraniina, Alloscelina) which do not roll are not Scarabaeini. This helps to clear up the picture. However there is still the question of the true Scarabaeini, the American Canthonina, in which the behavior observed before 1966 did not include rolling. We shall see how the subsequent observation and research has clarified these cases.

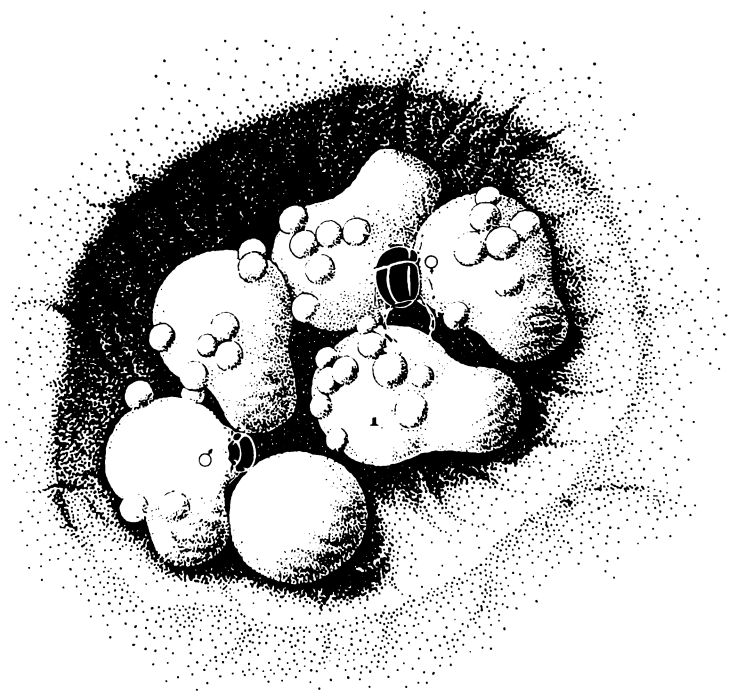
These cases can be gathered into two groups. The first made up of compound nests, precisely described by Judulien (1899), who says nothing, however, about how these nests could have been made. In 1966, before learning about the unusual nesting of *Canthon cyanellus cyanellus*, it was difficult to think about a compound nest which did not include the formation of a great subterranean food cake as a previous step to the making of brood balls, similar to the one observed in *Copris* (a burrowing beetle whose behavior is typical of Pattern III). Thanks to the knowledge regarding the behavior of *C. cyanellus*, we now understand how a rolling beetle can make a compound nest made up of several balls formed successively on the surface and rolled, one by one, independently and at different times until the compound nest is complete (Figs. 1-2).

Supporting Halffter's statement (1977) we included in pattern V several species of American Canthonina which it was assumed could not roll to make compound nests: *Canthon bispinus* Germar, *Canthon muticus* Harold and *Canthon edentulus* Harold. (In *C. bispinus* and in *C. edentulus*, Judulien points out certain aspects of tending for the nest which could be present in *C. muticus*). In *C. muticus* direct evidence of rolling exists, Halffter and Martinez (1968: 280-281) point out that it has been seen many times quickly rolling balls of excrement during the warmest hours of the day. Bisexual rolling has also been seen: one specimen (probably the male) pushing the ball as the other (the female) remains on top.

The second group includes other species which Halffter and Matthews referred to as non-rollers, *Canthochilum oakleyi* Chapin apparently does not make balls, but it can bury a food fragment directly without modifying it. The other Puerto Rican species of *Canthochilum* roll balls only a short distance and then bury them deeply (Matthews, 1965; Halffter and Matthews, 1966; Matthews, 1966). As in other cases which we will comment on later, it is impossible to affirm that this species



1



2

Compound nest in *Canthon cyanellus* - Fig. 1 - The female has covered the first brood-ball with soil; the male conveys a new ball of carrion with which the female will make a second brood-ball. The nest is gradually made by successive rollings. (Taken from Halffter, G., V. Halffter and C. Huerta, 1983)

Fig. 2.- Male and female care for a nest made up of 5 brood-balls and one ball which has neither been transformed nor oviposited. The small globes of the outside of the brood-balls are excretions of larval excrement.

does not make a ball and bury it for reproduction without knowing its nesting behavior.

Feeding behavior is more opportunistic than the reproductive one and depending on the circumstances, certain behavioral traits which are maintained while nesting, can be lost. However, the relation between the lack of rolling and the morphoanatomical proximity of the *Canthochilum* to several primitive genera of Dichotomiina (burrowing beetles of the Coprini tribe) noted by Matthews, 1966, is very interesting.

In another case of non-rolling, *Canthonidia rubromaculata* (Blanchard), subsequent observations show that rolling takes place during a limited time: it rolls with great agility in the morning before the sun comes up but when the sun rises, the beetle disappears under the dung and no longer makes balls (Antonio Martínez, pers. comm.).

The observations of Luederwaldt (1911) continue to be interesting, conveying that special feeling of the observer in the field. Comparing an excellent maker of balls and roller, *Canthon curvipes* Harold, to *C. conformis* Harold⁴, he observes: "...procede primeiro a excavação de seu canal, justamente por baixo da carnica, para so depois tirar a quantidade de carne de que precisa (page 429) ... pude reparar que *C. conformis* nao faz verdadeiras bolas, mas que elle se contenta com boccados de carne que destaca do cadaver" (pages 431-432). ("...first it proceeds to excavate a gallery exactly under the carrion and only later takes the quantity of meat that it needs...it should be pointed out that *C. conformis* does not make real balls, but rather that it is content with small bits of meat which it takes from the carcass").

Much less surprising are the observations made of *C. tristis* Harold⁵, *C. conformis* Harold⁶ and *C. septemmaculatus* Latreille which bury themselves with their balls nearby or even underneath the carrion.

The observations made about *C. virens* (quoted as *conformis*) do not seem so impossible at this point although they do not comply with the three norms of Scarabaeini behavior: to make a ball, roll it and bury it, excavating after the rolling (Luederwaldt clearly points out the previous existence of a gallery). There is an African species *Pachylomera femoralis*, whose behavior is similar although there is no taxonomic relationship. There is also another reference to the non-rolling of balls in *C. virens*, that was not appreciated until the synonym *conformis* = *virens* was established. In Brasil, according to the observations of E. Navajas, *Canthon virens* (Mannerheim) makes 2 or 3 brood balls with the contents of the abdomen of a female mated *Atta* (Hymenoptera: Formicidae) trapped during the bridal flight

and it buries them immediately without rolling. This behavior is exceptional for a Scarabaeinae. *C. virens* acts like a predator, it kills the ant, and immediately takes advantage of its abdominal content. This attack of the *Atta* females has also been mentioned -with much less information- for *Canthon dives* Harold (see Halffter and Matthews, 1966).

1.3 The non-rolling Scarabaeini according to Eric G. Matthews (1974)

At the beginning of the 70s, Eric G. Matthews carried out an important project: the monographic revision of all the Scarabaeinae of Australia. The second part (1974) concerns the Scarabaeini, all of which belong to the Canthonina subtribe. Matthews divides the Australian Canthonina into two groups of genera. The most primitive of which is called "mentophilines". He points out that he has not observed any of the 11 genera which make up this group form a ball at the food source⁷, although many of them have been seen rolling an object which is the right size and shape: a pellet belonging to a marsupial or rabbit. Matthews says (pages 4-5): "...particularly if it is found that all, or a majority, of its elements (the mentophilines) are at a stage of evolution preceding the development of ball-making behavior". The previous phrase clearly indicates Matthews' thoughts regarding the fact that rolling evolutionarily precedes the formation of a ball at the food source, he writes: "...Halffter and Matthews (1966, page 102) proposed that ball-rolling ability evolved in this manner (that is, that rolling preformed pellets preceded ball making in evolution), without at that time having known of any living examples still at this primitive stage".

In chapter 3 we will analyze whether Matthews' hypothesis can still be maintained or not. We can now see some of the most striking aspects of the mentophilines. On their antiquity or primitiveness, Matthews considers that they represent the most ancient element of all the Australian Scarabaeinae fauna. They are morphologically similar to *Cryptocanthon* Balthasar (a neotropical Canthonina whose biology we know nothing about) and to *Canthochilum* another neotropical Canthonina which, as we have mentioned, is neither a good roller, nor an agile maker of balls. These two genera which appear to be primitive, have been proposed several times as a bridge joining Canthonina (Scarabaeini) to Dichotomiina (Coprini).

Additional evidence of the antiquity of the mentophilines is the small distribution areas of many species and the importance of the wing reduction. In Australia 45% of the Canthonina have reduced wings, the highest percentage by far

compared to any other of the region except South Africa, whose extraordinary canthonine fauna has just been studied by Scholtz and Howden, 1987 *a* and *b*; Howden and Scholtz, 1987. Of the eight Australian genera totally without wings, all except one are mentophilines.

With the exception of some very preliminary observations on *Cephalodesmius* and an unusual *Aulacopris* nest in 1974, Matthews had no knowledge of the mentophilines' nesting habits. We insist on this point as it affects the evolutionary interpretation of several field observations regarding the existence (or not) of rolling. The fact that a ball is not formed during the feeding process does not mean that a ball is not formed during nesting. If the deviation from the general patterns affects only the feeding process, this can be interpreted as an adjustment to the specific ecological conditions (in this case the only or dominant presence of excrement in the form of pellets) and not necessarily as a primitive characteristic.

What knowledge do we have up to now regarding the non-formation of a ball in the Australian mentophilines? Apart from *Cephalodesmius*, whose behavior is now well known, we have observations on six of the other ten genera. Only one nest has been found and this was under exceptional conditions; it belonged to *Aulacopris maximus* Matthews. It was a compound nest, evidently made at different periods because the larvae were at various stages of development and the brood-balls were made of an unusual material: bat dung. This is the only time that this species (or any other Australian Scarabaeinae) has been found in a cave making nests with bat dung.

We quote Waite's original description (1898) he refers to the species as *Aulacopris reichei* White (= *A. maximus*): "Under great piles of bat dung we found two scarabs..." each had excavated a small hollow wherein the dung balls were deposited. One beetle was discovered with seven balls and the other with nine. On examining some of the series it was seen that while the ball at the time of being formed contained an egg, others were in various stages of development, indicating that considerable time is absorbed in forming the whole series of balls."

What Waite is clearly describing is a Pattern V nest. However, the fact that the compound nest had been formed under the pile of bat dung does not make it clear whether the ball was formed on the surface or not. Storey's (1986) observations do make it clear: *Aulacopris maximus* has been observed forming balls of human excrement and *Aulacopris matthewsi* Storey forming balls of horse excrement. The formation of the ball does not differ in general from a *Canthon* (for the latter see Halffter and Matthews, 1966).

Canthonosoma was observed by Matthews (1974) rolling marsupial pellets. Storey (1986) refers to *C. castelnaui* Harold as making balls of bovine excrement and rolling them. There are also Matthews' observations of ball formation and rolling in *Amphistomus*.

At the moment, since there is no additional information, it may be considered that the mentophilines (or some of them) only occasionally make balls on the surface and *in order to do so, they need an excrement of an adequate size and plasticity*. From an evolutionary point of view they are ancient beetles with a long association with marsupial pellets. What is unusual is that, at least in the case of four species, they have not lost the ability to make a ball when they find the appropriate excrement. We know the nesting behavior of *Aulacopris* and *Cephalodesmius*, and it belongs to Pattern V.

1.4 The case of *Cephalodesmius*

In the absence of ethological information about the Australian Canthonina, the genus *Cephalodesmius*, whose biology is well known, stands out. It is a canthonine -mentophiline that does not make balls on the surface nor does it roll them. Its nesting is one of the most complex within the Scarabaeinae, not only for the subsocial level reached, but also for the very specific food which requires special microbiological handling when used by the adult and larvae.

The ethology of the *Cephalodesmius* has been studied by the Australian researchers G. B. Monteith and R. I. Storey. The first publication was by Halffter (1977) based on data received from these authors, who later published (1981) an excellent detailed analysis. *Cephalodesmius* includes three species with reduced wings restricted to the humid forests of New South Wales and the southeast of Queensland; *C. armiger* is studied in detail with complementary observations being made about the two other species.

In synthesis, the ethology of *Cephalodesmius* is the following: the recently emerged adults (end of summer) excavate individual galleries. Gradually the whole population joins together as pairs (beginning of winter) in larger galleries which they will keep for the rest of their lives. At the beginning of spring the scarabs forage outside their nests for various types of *vegetal detritus* which they take to a chamber -now enlarged- at the end of the gallery.

Foraging soon becomes the male's only activity while the female remains in the chamber *making a cake with the foraged material*. In this cake, the leaves, flowers and some small pellets, all contaminated with the scarab's excrement,

undergo an intensive microbiological transformation into an external "rumen". The resulting substance looks like dung. The female begins the construction of small brood-balls with the cake material. In each of them she deposits an egg. As the larvae develop the mother places more material on the outside of the brood-ball, increasing their size, at the same time the external foraging of the male continues and the cake continues to grow.

This continuous provision for the larvae during their development is a unique process in Scarabaeinae and probably in Coleoptera. The stridulant mechanisms in the larvae and the adults, plus the fact that the mother and father eat the cake and sometimes larval excrement from the exterior of the brood-balls, maintain the cohesion of the family.

Towards the middle of the second summer the majority of the larvae are fully developed and they begin to pupate in the brood-balls now enlarged and constantly attended to by the female. The male ceases to forage and leaves the nesting chamber. A short time later the new generation emerges.

In *Cephalodesmius* as opposed to the typical Scarabaeini, the feeding galleries later become nests. In this way the nests are excavated before being supplied with detritus. This change in the normal sequence is because of the nature of the food material and the requirement of the microbiological process.

Foraging during nesting is done almost exclusively by the male. The female forages for herself briefly at the beginning, but once the cake is made she rarely leaves the nest. To forage the insect chooses the object, holds it with the anterior legs and pressing it against its head returns to the entrance of the gallery by walking backwards in a straight line. As it approaches the gallery, it turns around and walks forward, placing the plant fragment in it. This horizontal relocation, instead of being a dispersion of concentrated material is a concentration of dispersed material.

For short distances from the gallery, the burrowing scarabs' behavior is similar to the one just described. For greater distances (meters) this form of transportation is found in Eucraniina for fragments of excrement or dry pellets (Halffter and Matthews, 1966) and in *Coptorhina* (Coprini: Dichotomiina) for fragments of mushrooms (Tribe, 1976); and also in some Geotrupinae (Zunino and Palestini, 1986).

There is an interesting similarity with position I (pulling) in the rolling process. In this position, the beetle places its head and front legs on the upper part of the ball and makes it roll towards him, while he walks backwards.

In *Cephalodesmius*, as in all Scarabaeinae, the construction of the brood-ball is the work of the female. The way in which the ball is separated and handled by surrounding it with the middle and hind legs, and then retouched with the anterior legs is typical of a roller (Scarabaeini). The mating on the top of the ball (though it can also be observed on the surface) is also typical of a roller.

The Australian Canthonina-mentophiline *Cephalodesmius*, is the Scarabaeinae with the most bizarre nesting, even if it displays a mechanism of horizontal relocation that is not very different from Position I of joint rolling and it retains the ball formation mechanism of the Scarabaeini. The progressive supply of the brood-ball, is clearly associated to the external rumen (cake) and to the type of material that it generates. This type of supplying is a phenomenon usually limited to insects with advanced brood care, such as in various Hymenoptera.

1.5 Other examples

The observations made by Gordon and Cartwright (1974) in North America show up to what point the dominant type of excrement influences the making (or not) of a ball before rolling. *Canthon (Boreocanthon) praticola* LeConte is associated in North Dakota and Colorado with the pellets of the prairie dog *Cynomys ludovicianus ludovicianus* (Ord.). Ball formation was not observed: "Here *praticola* was extremely common feeding on and in prairie pellets, which were usually buried in the mound. In addition to feeding, in three instances pairs of *praticola* were observed rolling whole pellets away from a mound, making no attempt to fashion a ball. Two identical observations were made at a prairie dog town in...North Dakota". In spite of the fact that bison excrement was available in Colorado, there was no *praticola* found in it. The dependence of *Canthon (Boreocanthon) praticola* on the local conditions represented by the type of food is obvious. It is the only *Canthon* in the area between the southeast of Utah and the southwest of North Dakota and in this whole region it uses prairie dog excrement (Gordon and Cartwright, 1974). In other areas where this excrement is also available, it is the only species of *Canthon* that uses it. However, the dispersion area of *praticola* is larger than that of the prairie dog, so when the prairie dog excrement is not available, it uses human and cattle excrement by making balls and rolling them.

We have been able to study *praticola* in the south of Bolson de Mapimí, in the state of Durango, Mexico, in what is the southern limit of its range. There are no prairie dogs here, and although other rodents are plentiful, we found *praticola*

attacking cow, pig and human excrement. We have also kept this species in the laboratory for more than a year and a half feeding it cattle dung. The formation of balls was not observed during the autumn, winter and beginning of spring. The beetles ate on the surface or on the inside of the dung, or else they were superficially buried, (under natural conditions during the cold, dry period the presence of beetles on the surface is merely accidental). Towards the end of spring and during the summer, as sexual activity starts so does ball formation and rolling. Half the balls end up as brood-balls, the other half are abandoned. Sexual activity during this period is extremely intense: they roll balls in pairs, copulation is seen (even several by the same pair) and displays such as the dispersion of pheromones with frequent movements of the hind tibiae similar to those which have been described by Tribe (1975, 1976) and Bellés and Favila (1983) are frequent. The formation of the ball and rolling in pairs are both carried out in the normal manner for a *Canthon* (see Halffter and Matthews, 1966).

It has been found that *praticola*, a well studied species, forms balls during the reproductive period, when the temperature is high and when it is in the presence of adequate excrement. As the beetle tends towards the prairie dog pellets, when it avails itself of this resource, it rolls the pellets (even as a pair) without preparing a ball at all. This is a clear behavioral modification in response to local ecological conditions. We do not know how it nests with the pellets.

Gordon and Cartwright (1974) point out other cases of pellet rolling in the United States: *Melanocanthon bispinatus* (Robinson) and *Canthon (Boreocanthon) probus* (Germar) roll deer pellets in New Jersey; the second species also rolls rabbit pellets in South Carolina. Close species and possibly the ones mentioned above also form a ball with different excrement and roll it. They also refer to a species which we know to be a ball maker and roller for feeding and nesting purposes: *Canthon (Glaphyrocanthon) viridis viridis* (P. de B.) which has been observed rolling a rabbit pellet in Tennessee.

Canthon (Boreocanthon) simplex LeConte had been referred to as associated with the prairie dog (Linsley, 1942: 166) in Yosemite National Park, there were plenty of them rolling pellets near the entrance to nests of *Citellus beecheyi*. The same species has collected in other places on cow excrement, with which the situation of *praticola* is repeated.

Behavior which is equivalent to the rolling of a pellet has been communicated to us by Dr. P.B. Edwards, CSIRO, Canberra: "...I have observed in Mkuzi Game Reserve (South Africa) on many occasions the behavior of *Scarabaeus*

galenus. This species carries a piece of dung in its hind legs, lifted off the ground, while walking backwards to its burrow".

The feeding behavior of two species of the African genus *Pachylomera* has been described by Tribe (1976). On one of them, *Pachylomera femoralis* Kirby, there are some observations by Walter (1978, 1980) which coincide with the previous descriptions. According to Tribe, 1976: "Both *Pachylomera* species are strongly modified morphologically for digging, possessing enormous forelegs with shortened, weakly developed hindlegs... *P. femoralis* and *P. opaca* have only occasionally been observed to roll dung-balls in the field but do so often in the laboratory, *P. opaca* rolling with astonishing speed. In the field, feeding normally occurs at the dung pad... (*Pachylomera femoralis*) under laboratory conditions they have been observed repeatedly rolling dung-balls in a similar manner to that of the *Kheper* and *Scarabaeus* genera. But both *P. femoralis* and *P. opaca* differ from the latter two genera in that in proportion to their sizes, a smaller amount of dung is rolled... The typical behavior in the field is to construct an unbranched tunnel within 30 cm. of the dung pad by digging with the foretibiae and clypeus and then turning around in the burrow and pushing out the loosened soil, using the broad prothorax as a shovel. The tunnel is long, approximately 120 cm., and slopes gently downwards to a maximum depth of approximately 20 cm. depending on the hardness of the soil. The loose excavated soil is used to build a ramp which leads to the dung pad... The *Pachylomera* burrows are provisioned with dung by the beetle making several trips to and from the dung pad. Pieces of dung are detached using the clypeus and foretibiae by means of an action similar to that of a dog digging - the pieces of dung being passed between the legs. The pieces are either butted with the head *or rolled* (our underlining) to the burrow entrance and pushed inside with the head..." (according to Walter, the piece of dung is transported by pushing, in the manner of a bulldozer)"... Once the end of the burrow has been provisioned with dung the beetle returns to the entrance and takes up a pheromone release stance... No beetles have been observed to pair off at the dung pad and the construction of the burrow is completed by a single beetle." Unfortunately a *Pachylomera* nest has not been seen.

The provisioning process of *Pachylomera* requires a previously constructed gallery, into which the food is introduced in small successive fragments (the same as a burrowing beetle). It has a similar background to the behavior described by Luederwaldt for *Canthon virens*. This way of provisioning the tunnel is, together with the behavior of *Cephalodesmius*, the greatest deviation found up to now

from the behavior typical of a roller. In *Pachylomera* the possibility of making and rolling a ball is present, although in the field it is not frequent.

The typical roller excavates immediately beneath the rolled ball, *Pachylomera*, on the other hand, digs an oblique tunnel, and removes the sand (both species are found in sandy parts of South Africa) by pushing it with the front part of the body, until the sand is a certain distance from the entrance. This form of digging is not unique to the *Pachylomera*. Matthews (1974) notes that the Australian Canthoninae *Stenophilus hollandiae* does the same in loose sand; in other types of ground it buries the pellet in the "normal" manner of the rollers.

We have observed the same behavior in *Scarabaeus pius* Ill., in Azerbaidjan, USSR, on the shores of the Caspian Sea, in sandy-clayish soil. *S. pius* makes and rolls balls, but if, as it is rolling (individually in the cases observed) it happens to reach an undulation in the terrain, it starts the excavation of an oblique-almost horizontal gallery immediately. It uses the clypeus and the forelegs to dig, leaving the ball near by. The loose sand is pushed out by inverting its position and using its head and pronotum like a bulldozer, ending each trip with an abrupt movement of the clypeus producing an audible "clip" sound. After several trips, the beetle has managed to excavate a short tunnel and a chamber. It tries to insert the ball, if it does not fit it enlarges the gallery. It pushes the ball in a rolling position, supporting it with the hind legs - occasionally with the middle ones, and with the front ones on the ground, it can change position and push with the pronotum, or it can pull the ball towards itself when it is inside the gallery (Figs. 3-8 and 9-10).

2. FEEDING AND REPRODUCTIVE BEHAVIOR OF *CANTHON OBLIQUUS* HORN

2.1 *Material*

Until the beginning of these studies (and the related collections of Professor Antonio Martínez), *C. obliquus* was a rare species in museums; there were probably no more than half a dozen specimens in all of them put together. This shortage of such a taxonomically interesting species which has been known for more than a hundred years, is due to its extreme endemism as well as the difficult access to the area in which it lives. *C. obliquus* is restricted to Sierra de La Laguna (also previously called Sierra El Chinche) in the southern tip of the Baja California



Rolling and burrowing in *Scarabaeus pius*, Azerbaidjan, USSR. Fig. 3.- The specimen rolls a ball of dung in the usual way of a ball-roller. Fig. 4.- Finding a vertical obstacle, he starts digging a burrow, leaving the ball of dung to one side. Original photographs.

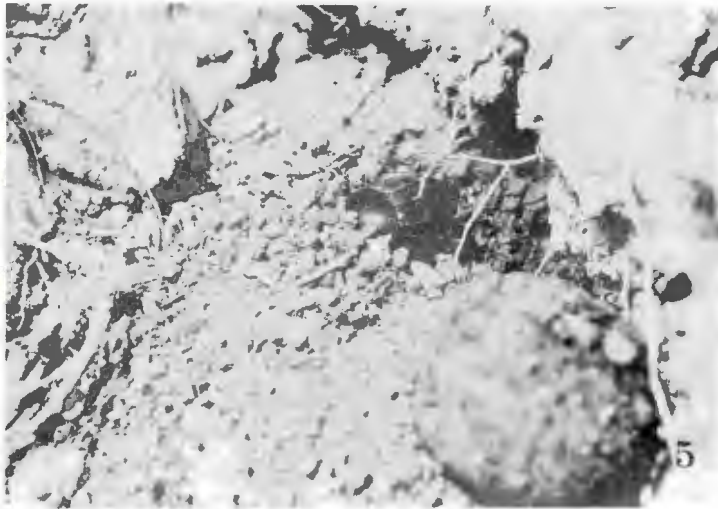


Fig. 5 and Fig. 6.- *Scarabaeus pius*. Acting like a bulldozer he removes the soil from the tunnel. In Fig. 6 one can see the moment in which with an abrupt movement he detaches the soil he has extracted. Original photographs.

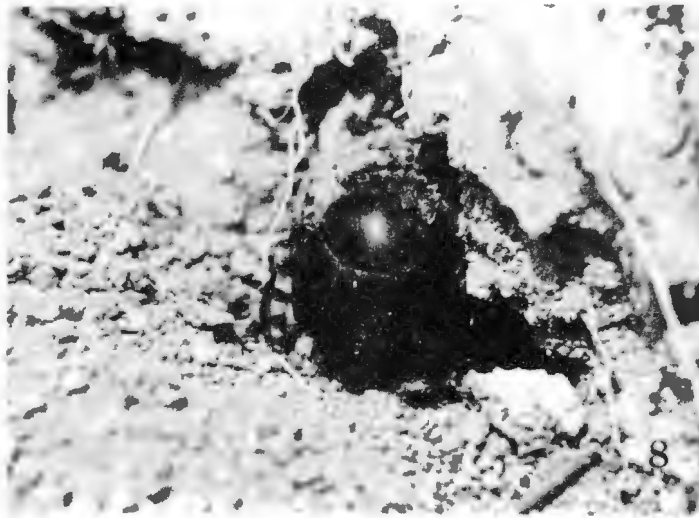


Fig. 7 and Fig. 8.- *Scarabaeus plus*. Pushing, the scarab introduces the ball in the burrow he has made. Original photographs.



Fig. 9 and Fig. 10.- *Scarabaeus cicatricosus*, Reserva de Doñana, Spain. Two aspects of the "bulldozer" action which the scarab develops to excavate a gallery before he introduces the ball he is rolling. Original photographs.

Peninsula. It lives in the canyons of the Pacific and the Gulf of California slopes, usually at an altitude of between 400 and 750 m. but whose outer limits can be between 350 and 1620 m; the altitude varies with the temperature and humidity determined by the insolation and the dominant winds. It lives in a Baja California relict plant formation: the tropical subdeciduous forest and in the lower part of the oak forest. It is not found in the upper parts of the Sierra covered by desert brush. Within this limited area, it exists only in some canyons whereas in other places, which are apparently favorable, it does not. The very reduced wings could be related to this restricted distribution. In Australia, in the *Canthonina*, the reduced wing is frequently present in ancient endemics of limited distribution (Matthews, 1974).

Not only is the range reduced but also the number of individuals is scarce. We have not found even a moderate number of *C. obliquus* in traps of human excrement or in different excrements in the field. This is why, in its distribution area, most of the cow pads dry up with no sign of activity.

C. obliquus has collected in the excrement of coyotes, cows, humans, horses and even lizards, it is a non specific coprophagous insect which can also be found on small carrions. Regarding its circadian cycle of activities, it is not restricted either as in most cases it is diurnal but can be found at night. This range of activity is not frequent in Scarabaeinae, particularly in species made up of small populations. This can be associated, as many characteristics of *obliquus* are, with the lack of competition in Sierra de La Laguna.

The presence of cows on the steep slopes of the Sierra de La Laguna is scarce and they do not seem to have been there any earlier than the 18th century. The presence of human beings, although they were there before, is not enough to explain the isolated survival of the species. Man is not only a relatively new element in the area, but it also seems that he was never numerous. *C. obliquus*, surrounded by desert and sea, has survived in isolation since the separation of the southern part of Baja California from the continent ten million years ago (Miocene). The only other Scarabaeinae occurring in the area is *Onthophagus cartwrighti* Howden. The reduced range and the scarceness of *obliquus* contrasts with the only Scarabaeinae of the surrounding lower semi-desertic areas, *Canthon (Boreocanthon) puncticollis* LeConte, which has a wide distribution in the Baja California Peninsula and in the Sonora Desert, where it is abundant and has a continuous distribution between sea level and an altitude of 400 m.

This research was done with material collected during 1984-1988. It was continued in laboratory terraria with soil as similar as possible to that of the original

habitat and in rooms with controlled (27° C, 70% humidity) or variable temperatures and humidity. On the rare occasions when nesting sequences were obtained, they were in the rooms with controlled temperatures. At the time when there was the most material in the laboratory, there were 19 terraria with one pair each and three terraria with several pairs. They were all kept until they died. There were five nesting sequences: four consisting of one to three brood-balls with one to two balls in process and the fifth nesting sequence had a total of 13 brood balls and five unfinished balls. In all, 20 finished brood-balls were examined. Also, two or three terraria with a pair or more of *obliquus* have been continuously maintained for observation since 1985.

They were feed on cow dung. Every 3 or 4 days new material was added on top of the old, which was left untouched, so there was fresh dung on top and partially hard below. All the dung was removed when the terrarium was examined every 30 days. The *obliquus* used the dung which was several days old and which had lost humidity and was therefore more compact for food and above all for the formation of balls.

2.2 Feeding and resting behavior

Ball formation on the surface of the cow dung was never observed, nor was any type of rolling. All the balls, not only those transformed into brood balls but also those which had not reached this stage, were found when the female was nesting. We therefore assume that the formation of balls is not necessarily part of the feeding behavior. The scarab frequently eats in the dung-earth interface. Here the scarab "gnaws" (eats away) the interior surface of the dung pad, leaving a hollow which is sometimes quite large and well defined, going from the border towards the center always horizontally the length of the interface. On the surface it "gnaws" in small circular areas which can be up to 1 cm in depth. After several days the surface of the dung pad is covered with hyphae and fructiferous bodies of mushrooms, except in the "gnawed" areas, leading to the conclusion that there may be a fungicidal/fungistatic substance in the mouth of the beetle. The male and female never eat together and do not participate in any joint activity except copulation. Remember that the only roller observed up to now which neither jointly rolls nor subsequently cooperates is *Megathoposoma candezei*. It is normal also for the burrowers to cooperate even in a limited way in the preparation of the nest or in the prereproductive stage (for the latter see Halffter, Halffter and López, 1974).

After 5 years of continuous observation in the laboratory and numerous field trips without seeing a well defined sign of relocalization, on day in 1988, our collaborators, Armando Tejas and Rosalía Servín from the CIB, observed several examples of a very primitive form of horizontal relocalization on Sierra de La Laguna (Sierra de San Lazaro). While the insect moved forward with the middle and anterior legs, a small fragment of dung was being taken by the tarsi of the posterior ones. The fragment was not being rolled as it did not touch the ground. It was small in relation to the insect's body, it had been separated from a cow pad using the clypeus and the anterior part of the pronotum and it had not been remodelled with the anterior legs (Fig. 11). Of all the forms of relocalization known, the only one which is comparable is the behavior of *Scarabaeus galenus* pointed out in item 1.5.

This relocalization was observed in the field, however, there was no similar activity by specimens of *C. obliquus* from the same area in the laboratory terraria. This form of relocalization seems to be exceptional. In 16 periods of careful observation in the field, only very occasionally (3) had Armando Tejas observed the taking of small fragments of dry dung and even, once, a specimen dragging a small pebble.

The observations at Sierra de San Lazaro were done towards the end of the rainy season. On this occasion a greater concentration of *obliquus* was found (up to 15 specimen per pad). As is the case in most of Sierra de la Laguna, the terrain where the observations were made is very rugged, this seems to be related to the type of horizontal displacement observed. The *obliquus* easily went up steep walls of granitic rock, where the usual rolling would have been impossible. The dragging, although irregular in its course, did cover distances of more than 10 meters.

We do not consider that there is any relation between the dragging observed and nesting. In the first place because of the small size of the fragment which would not have the volume for a brood-nest and also because it was observed in a period immediately before but not coincidental with, the nesting observed in the laboratory. There was no dragging by pairs and the displacement was done by males as well as females. There is still the doubt as to whether this is a very primitive form of relocalization or a response to topographical conditions of the Sierra (with deer pellets, this type of relocalization could be very effective, although the lack of pressure due to the scarce density would not make it frequent).

Exceptional for a roller (Scarabaeini), although it has been observed in *obliquus*, is the presence of resting galleries. At the edge of the dung pad they

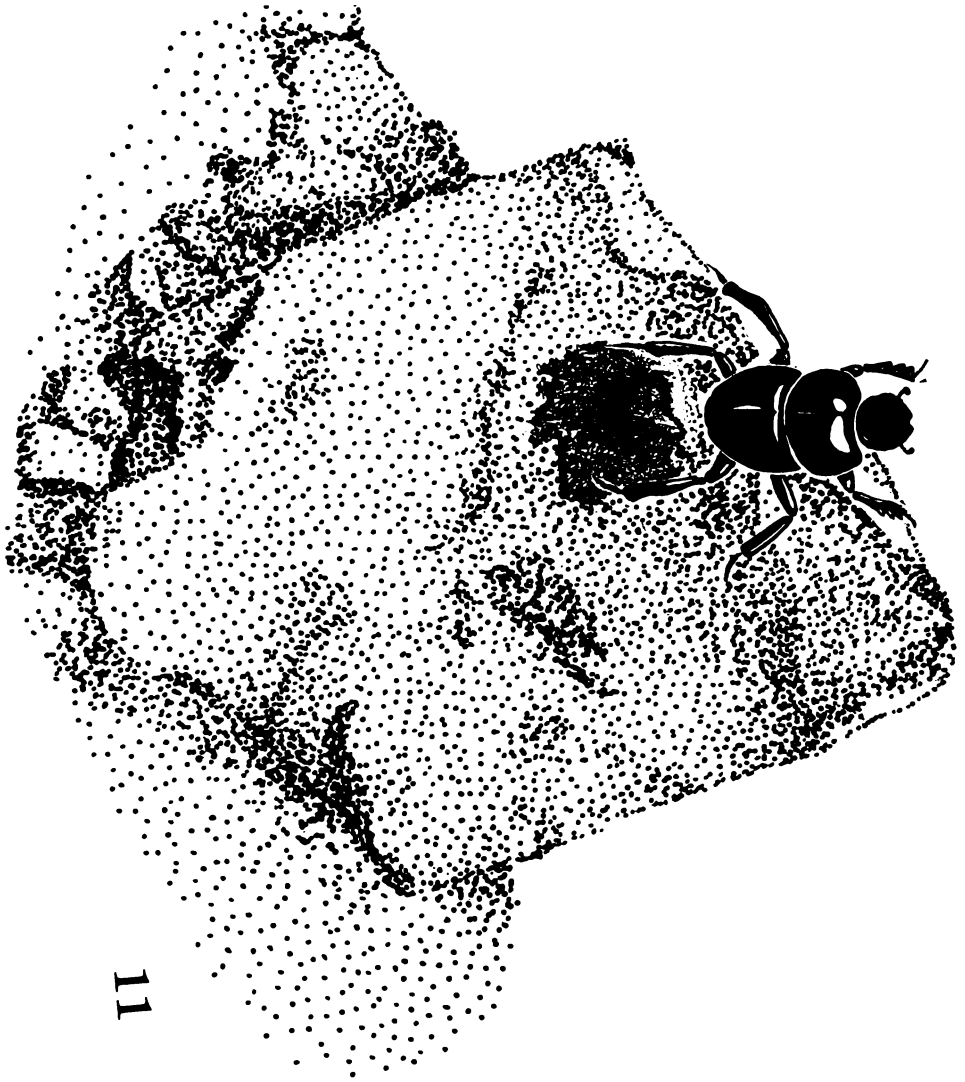


Fig. 11.- Relocalization by *Canthon obliquus*. The specimen is climbing a vertical wall dragging a small unmanipulated fragment of dung with the posterior tarsii. The drawing was done from a photograph belonging to Armando Tejas and Rosalía Servin.

excavate one or two shallow (2 to 4 cm) almost vertical galleries which end up in a slightly larger area. Only once was the gallery under the dung pad, close to the edge, there were no balls or left over food in these galleries which were always open. We found a beetle on several occasions either entering, leaving or just staying close to the entrance. These galleries are for resting and protection and they are the only ones found up to now for the Scarabaeini. Up to what point the dung in the terraria, which was not removed and was periodically added to and which obviously lasted longer, influenced the existence of these galleries is still to be determined. Although, Armando Tejas has also found these galleries in the field. The galleries which have been found in the prenesting stage of burrowing Scarabaeinae (Halffter and Matthews, 1966; Halffter, Halffter and López, 1974) are also for resting and protection, but they are, above all, places where they can peacefully consume food. In the rollers, the rolling and burying of a food ball performs the same function. The fact that in *obliquus* the gallery does not have a feeding function could be due to the exceptional lack of competition, a condition which is present in the Sierra de La Laguna and which is stressed in the laboratory where the food is stable and abundant. The resting galleries have been found at the same time when nesting occurs and they are always occupied by one individual, never a pair.

2.3 Nesting

We refer to the nesting sequence or time as the active reproductive period during which the female periodically makes brood-balls.

In *obliquus* we found two types of balls which are no more than stages in a process. The brood-ball has a papilla which makes it look like a pear. The center is made up of a spherical mass of dung covered with soil, or dried dung mixed with soil which has a width of about 1 mm. The chamber for the egg is towards the papilla, which communicates with the exterior by a well defined channel for ventilation containing some loose straws which protrude slightly (width 9.5-11 mm, (10.2); height 11-13 mm, (11.7)). The other type of ball is a naked sphere of cow dung. We once found a ball like this which contained an egg, this is understandable if we consider that oviposition precedes both the formation of the papilla and the deposit of the earth cover. Between 30 and 50% of the balls found are spherical and without papillae. They are abandoned before the brood-ball forming process has finished (this is not unusual in Scarabaeini).

From the moment the larvae reach the third stage, excretions of solidified larval excrement appear on the outside of the ball. These excretions have been found in other *Canthon* whose nesting has been followed with care (see Halffter, Halffter and Huerta, 1983).

The balls remain buried under or a short distance from the dung pad, at different depths (maximum 10 cm). The burying appears to have been done in the manner of a Scarabaeini (that is, excavating immediately under the ball) as no evidence of a gallery has been found. The balls which were not exactly in the neighborhood of the dung pad, were buried obliquely. In three of the five nesting sequences, the balls were immediately under the dung pad, at the interface with the ground. These balls (2 or 3) were found more or less close to each other, giving the false impression that the nest was of the compound endocoprid type, emphasized in one case by the fact that the female was found with the balls (one ball was in the spherical stage and lacked one egg). The concentration of balls is probably due to the way in which they are extracted from the dung mass. It is a true extraction, creating a well defined spherical hollow. This, together with the extended time when the female is eating and active in a circumscribed area in the under part of the dung pad, creates a concavity which is enlarged by the compacting of earth due to the movement of the insect (mainly face up) and by the removal of soil for the outer layer of the brood balls. The end result is that the balls stay more or less close, in a hollow which gives the impression of a compound nest. The presence of the female is explained by the concentration of activity in a limited area due to the special conditions of the terrarium: all the brood-balls were made using a single dung pad topped with additional fresh dung. The female, found with two brood-balls, was working on a third which was at the time in the spherical stage.

At other times in the laboratory and possibly always in the field, one or several balls were buried independently, away from and below the food source.

The balls are always made by the female from the under side of the dung pad, mainly from the middle part. In two out of thirty cases the balls were made from the peripheral area of the dung pad but always with the area which rests on the ground.

2.4 *Ball formation*

We have said that the ball is extracted from the under side of the dung pad. Contrary to the normal process of *Canthon* and other Scarabaeini (see Halffter

and Matthews, 1966) in which the beetle cuts and separates a portion where it is standing and to which it adds complementary fragments giving the ball a spherical form with the hind legs, *C. obliquus* appears to make balls as does *Eurysternus* (Halffter, Halffter and Huerta, 1980). That is, the beetle, face up, enters the base of a dung pad which is firm enough and with the anterior legs and the clypeus separates a ball with circular movements.

When this process is over, the ball simply detaches itself. This mechanism would explain why *C. obliquus* balls are found under the dung pad, why there are extraction marks under it and why the ball has a spherical shape without having been remodeled or rolled. To move within the dung mass, *Eurysternus* uses the middle legs which are long and extended most of the time. *C. obliquus* also has long and extended legs and it probably uses them in the same way as *Eurysternus*.

Mating has been observed on the surface, 15 cm from the dung pad, unrelated to any ball. We do not know if copulation occurs in the interface between the dung and the ground.

3. DISCUSSION: THE BALL FORMATION AND ROLLING PROCESS

This discussion is aimed at placing the ball formation and rolling processes within an outline of the evolution of feeding and reproductive behavior in the rolling beetles.

3.1 Background

The first theoretical outline of the evolution of Scarabaeinae behavior was proposed by Halffter and Matthews, 1966, in the context of: 1) Scarabaeinae behavior, distribution, morphology and development as related to coprophagy and the derived necrophagous and saprophagous habits; and 2) nesting seen from an evolutionary point of view. Halffter and Matthews (1966) recognized several nesting patterns (or groups)⁸. Within these patterns, three are characteristic of the burrowing beetles and one (Pattern IV) to the rollers (Scarabaeini). According to Halffter and Matthews, the behavior in Pattern IV is completely different from that of the burrowers; rollers do not pack the food into a previously constructed gallery and the brood-ball is prepared by remodelling a ball initially made on the surface, something that the burrowers never do. These two characteristics, and the habit of rolling, unknown outside of the Scarabaeini, lead the

authors to believe that very early in the evolutionary process, this tribe was separated from the common and basic trunk of the entire subfamily.

Halffter (1977) proposes a general hypothesis regarding the evolution of the subfamily's nesting behavior. We quote (page 231): "There are two evolutionary lines of nidification in the Scarabaeinae and, on the basis of each one, there is a response to the ecological problems of exploiting excrement of large herbivores... Nidification patterns in both lines are expressed as differences in food handling processes by adults." The first evolutionary line refers to the burrowing beetles. "The second evolutionary line has as its starting point the rolling (and in the majority of the cases the previous making) of a ball of excrement, that is carried a certain distance and buried in a shallow excavation. Pattern IV is basic, which presents variations in the method of rolling and collaboration between sexes. The group V pattern is derived from this group, with formation of multiple nests cared for by the female and well marked bisexual collaboration in nidification."

In this same paper, Halffter describes two new nesting patterns, Pattern V which corresponds to compound nests made by rollers, tended to by the mother with a certain amount of collaboration from the father; and Pattern VI, exclusive of *Eurysternus* in which, although rolling is not found, a massive formation of balls on the surface prior to nesting is and only a few of these are transformed into brood balls. *Eurysternus* nesting habits are complex and in some species include a stage in which both parents destroy one or several provisional compound nests before preparing the final one, which is also compound and which is cared for by the mother with different degrees of cooperation from the male.

Halffter (1977) thinks that the formation of balls in Pattern IV, V and VI is related to the particular features of the large herbivore excrement; these are masses which are sufficiently large so that even if the surface hardens, the middle stays plastic for days. The coprophagy of the entire subfamily may have originated with this type of excrement. According to this paper, the affinity towards pellets is due to certain ecological conditions: the abundance of rodents in the dry areas of North America and an abundance of sheep in certain areas but above all the native fauna of marsupials in Australia. The loss of ball formation is due to the fact that the pellets either dominate or are exclusively available.

Halffter and Edmonds (1982) reaffirm the correlations between feeding and nesting behavior and tie their evolution to the environment. The characteristics of excrement determine the basic points of the ethological responses in nesting ("...more than anything else, nesting behavior is just one of several adaptive responses to an unusual set of ecological circumstances." *op. cit.*: 9). Halffter and

Edmonds (1982) insist on the importance of the relocation of food, as much for the feeding of the adult as for nesting. "Because of their early appearance of food relocation behavior in response to an increase in competition, the evolution of Scarabaeinae was committed toward development of complex nesting behaviors. Moreover, their ecological characteristics collectively centered upon reduction of competition, increase in brood care and reduction of fecundity that is, upon a clear K - strategy." (op. cit.: 26)

The same authors think that the Scarabaeini represent an independent evolutionary line within the monophyletic Scarabaeinae. The differences between rolling and burrowing beetles can be established by the fact that the former form a ball at the food source, roll it and bury it (or not). The burrowers stock a previously excavated gallery. In the present paper, we have focused the discussion on the known exceptions to typical Scarabaeini behavior.

3.2 *Ethological evolution of the rolling beetles*

- 1) We think that the Scarabaeinae (a monophyletic group, see point 2) probably appeared in the lower of middle Mesozoic, when the excrement of the large vertebrates arose as an abundant ecological niche. The group derives from a Scarabaeidae trunk (the family considered in a broad sense) which has a general saprophagous habit as a response to the new possibilities that coprophagy opens. From the beginning, Scarabaeinae specialize in handling a particular food: excrement. Consequently the morphology and behavior respond to the needs of this process, especially regarding food relocation behavior.
- 2) Some important features, shared by all Scarabaeinae, place its monophyletic origin out of doubt (see discussion in Halffter and Edmonds, 1982).
- 3) In an evolutionary context, the isolation of food belonging to each offspring, such as a brood-mass in the case of the burrowing beetles of primitive nesting or such as a brood-ball in the evolved burrowing beetles and in the rollers, is significant. The isolation of food belonging to each offspring in a brood-mass is also found in Geotrupinae and exceptionally in Aphodiinae, however none of these subfamilies makes a brood-ball. The Scarabaeinae are the only group in which the important evolutionary step from the brood-mass⁹ to brood-ball¹⁰ has been taken.

The step from brood-mass to brood-ball is accomplished by the burrowing Scarabaeinae following two fundamental tendencies which originate Pat-

terns II and III and a secondary tendency which originates Pattern VII. All the rollers (Scarabaeini) whose nesting is known, including those who do not roll (*Cephalodesmius*, *Canthon obliquus*) or who only do it occasionally (*Aulacopris*) make a brood-ball. We can deduce that the entire tribe, as far as we know, has these derived characteristics. In other words the formation of a brood-ball is evidence that Scarabaeini separated from the common trunk once this very special process had been mastered.

However, we know nothing about the nesting of the most primitive Scarabaeini which, because of their morphology, are closer to the Dichotomiina (burrowing beetles of the Coprini tribe). If these genera (*Canthochilum*, *Agamopus* or *Cryptocanthon*) or others with distinctive primitive features, are found to nest without including the formation of a brood-ball we will have to conclude that its elaboration is a process that Scarabaeini developed independently and parallel to the rest of the subfamily. Under these circumstances, the presence of the brood-ball in rollers and in evolved burrowers as a final product of the evolutionary process, would be a convergence.

- 4) The formation of the brood-ball is the latest evolutionary and functional advance to isolate the offspring and its food. This isolation may be perfected by two processes: the recoating of the brood-ball with a layer of earth and the protection by the mother during the larval development.

The advantages of the brood-ball, protection and isolation, offset one disadvantage: the quantity of available food for the larva is limited (this limitation is especially obvious in the rollers, where the size of the ball depends on their capacity to roll). This limitation is overcome by the increased nourishing efficiency of the larva. It supplements the food stored by the mother with its own excrement. In this way, the material passes through its intestines several times.

- 5) The appearance of the brood-ball in the evolution of Scarabaeinae reproductive behavior coincides with the loss of the larva's ability to prepare the pupation chamber. The brood-ball is in itself a pupal chamber. The larva, which matures inside a brood-ball, does not need a pupal cocoon, although it does need to develop efficient methods to repair fissures or cracks in the wall of the brood-ball. This repairing method is a prerequisite for the evolutionary step from brood-mass to brood-ball¹¹. The presence of this trait is also additional evidence of the rollers derivation from the primitive trunk of burrowers, as the repairing methods are similar in both lines. (Figs. 12 - 13).

- 6) In the rollers, the brood-ball exists right from the beginning of each nesting process, when it is separated from the food source.
- 7) The formation of the brood-ball implies that the mother has acquired the ability to make it, in the Scarabaeini and *Eurysternus*, directly from the food source and, in the burrowers, from a previously buried mass of food (in the exceptional case of the Oniticellini of Pattern VII, directly from the interior of the dung mass as a modification of burrowing behavior). In Scarabaeini, the movements used to make a ball on the surface and those used to make a brood-ball are the same.
- 8) The existence of brood-balls with the appropriate repairing mechanisms evolutionarily precedes, or is simultaneous with, the development and use of horizontal relocation for nesting, an activity which always includes the preparation of brood-balls.
- 9) In the rollers, bisexual cooperation around the ball is a universal process with only two known exceptions. The first is *Megathoposoma candezei* (see footnote 2). The second is apparently *Canthon obliquus*, the only species where rolling is not known to be associated with nesting.

In the rollers the greatest effort in the nesting is exerted by the male. He prepares the ball which will become the brood-ball, he rolls it and buries it. The female plays a secondary or nonexistent (*Scarabaeus*) part in the rolling. The female - as in all the Scarabaeinae - transforms the ball which has already been buried into a brood-ball after oviposition. When there is a compound nest (as in *Canthon cyanellus cyanellus*). While the female cares for the nest in formation, the male goes to the food source and forms and rolls the additional balls, one by one, until the nest is complete (Fig. 1-2). The male roller is the one who attracts the female, mainly through his activity of forming and rolling the ball or through the release of pheromones. This process is being studied and, thus far, seems to be important to the reproductive success of Scarabaeinae.

It is interesting that in the tribe where the male attracts the female, the morphological sexual dimorphism is minimum or nonexistent.

The significant cooperation of the male Scarabaeini could be interpreted as a scheme to improve its fitness. "Males become better helpmates, but poorer lovers; emphasis falls on more efficient nesting, not on elaborate courting for available mates." (Halffter and Edmonds, 1982: 64). This is also ecologically important as the size of the ball (and therefore the food for the



Fig. 12 and Fig. 13.- Mending of the brood-mass by *Onthophagus gazella*, College Station, Texas. Fig. 12.- The larva places fragments of dung and its own excrement around an artificially opened "window" using its mouth pieces. The hole gradually closes. Fig. 13.- The hole is practically closed and the brood-mass is isolated once more. Original photographs.

larva) depends on the rolling capacity. Rolling in itself is a critical moment: the ball can be stolen or the beetles preyed upon; *two roll better and faster than one*.

- 10) *Cephalodesmius* represents a case which is extremely specialized. These beetles do not, however, lose the movements characteristic of a Scarabaeini to make their brood-balls.
- 11) The appearance of the brood-ball is an old phenomenon in the Scarabaeinae. There are fossils of early and late Oligocene (see synthesis in Halffter and Matthews, 1966). A series of recent discoveries (Laza, 1986) could lead to even older nests. This evidence as well as other recorded fossils (Halffter and Edmonds, 1982: 51) could imply that the formation of brood-balls had begun in the Cretaceous.
- 12) A biogeographical confirmation of the antiquity of this ethological development comes from the Gondwanian distribution of *Canthonina*, without a doubt the most primitive and at the same time the most diverse subtribe of Scarabaeini. In the *Canthonina* all the known nests end up as brood-balls.
- 13) The sequence of ball formation on the surface and rolling is shared by the four subtribes of Scarabaeini. The evidence thus far seems to indicate that this sequence is a basic feature common to all rolling beetles, and its absence is a derived characteristic. This conclusion does not coincide with that of Matthews (1974; outlined in Halffter and Matthews, 1966). We admit that we are missing a certain amount of information regarding the most primitive *Canthonina*.
 - We will individually analyze the two processes involved in the sequence of ball formation - rolling, as the facts gathered thus far about *C. obliquus* clearly indicate that not only ball formation, but also rolling can be absent.
- 14) In order to explain the lack of ball formation on the surface by the Scarabaeini, there are two alternatives: a) either the process never existed; or b) the process has been lost. If the process never existed, the Scarabaeini was separated as a group, *before* developing the ability to form balls, therefore this is not a universal characteristic, some (or many) lines have since acquired this ability in the evolutionary process. This is Matthews' alternative and evolutionarily places rolling before ball formation.

On the other hand, if the process has been lost, its loss is a derived characteristic, a specialization.

As we reexamine the cases where a ball is not formed, in several we find new evidence indicating that they can, in fact, make balls, although this activity

may be exceptional (several mentophilines and *Pachylomera*). What must be considered is that such a complex process as ball formation cannot be improvised. This idea reinforces alternative "b" and forces us to consider that when ball formation has not been observed we must face a lack of information¹² and/or a response to very precise ecological conditions: such as the mentophilines and the marsupial pellets, *Canthochilum* and the lack of significant dung, *Boreocanthon* associated with prairie dogs. These ecological considerations should not be doubted because other rolling beetles respond to similar local conditions as good ball formers and rollers; for example, non-mentophiline *Canthonina* in Australia, *Canthonella* in the West Indies as opposed to *Canthochilum*, etc.. We are inclined to consider that when they do not form balls, it is because this process was lost and the rolling was retained. We favor the idea that the loss deals with a derived characteristic shared by the primitive beetles such as the Australian mentophilines and *Canthochilum*, with others which are not primitive such as *Canthon virens*. There is no common element tying all the known cases together, although in the majority there are special ecological conditions, of which the extreme case would be *Cephalodesmus*. Luederwaldt's observations regarding *Canthon virens* are still difficult to explain.

However, everything we know about its nesting (attack and use of the *Atta* abdomen) indicates that it makes balls.

- 15) What is the origin of rolling? Eric G. Matthews supposes that it appears with the presence of dung in a suitable form; i.e. the pellet independently or before, the ability to make a ball was developed. In the discussion of point 14, we saw that the cases of mentophilines, which make balls occasionally, contradicts this thesis. It does not contradict, however, the relationship between rolling and pellet, but rather the evolutionary sequence of rolling - ball formation as two different events developed at different times^{13/14}.

There is a case, in which there is ball formation without rolling: *Canthon obliquus*. This species does not roll, and the formation of balls is limited to nesting. The lack of rolling in *obliquus* is a derived characteristic, possibly the result of lack of competition not only among individuals, but also among species.

- 16) Pluot-Sigwalt (1982, 1983, 1986, 1988 a and b) and Paulian and Pluot-Sigwalt (1984) describe the morphology of the tegumentary glands of the Scarabaeinae. Among these glands are those placed in the abdominal tegument: sternal and pygidial glands are absent in the majority of burrowers,

which only have dispersed glandular units in the abdomen. The simultaneous presence of all these glands has not been found in any burrower but is, however, characteristic of the rolling genera which were studied with the exception of *Sisyphus*.

The sternal glands do not have an equivalent in other Coleoptera because of the large surfaces they cover and their acute sexual dimorphism. They have two periods of activity: one is presecretory before the beginning of reproduction (and rolling in couples), and another secretory during the reproductive period. Several experimental and case studies (Tribe, 1975, 1976; Bellés and Favila, 1983; Favila, 1988 a and b; Burger *et. col.* 1983; Edwards and Aschenborn, 1988) and the previously mentioned morphological studies, allow the association between several of these sternal glands in both sexes and formation of the brood-ball, its protection against other organisms, joint rolling, attraction of the female for the male and sexual recognition.

There is one type particular to the female which is found in rolling and in burrowing beetles such as *Dichotomius* and *Phanaeus*. These glands may be active during the making or remodelling of the brood-ball, and its secretion could have an antibiotic or fungistatic effect.

The sternal glands are present in the 17 examined species of rollers (according to a list provided by Mme. Pluot-Sigwalt) including *Canthon obliquus* which has the glandular structure typical of a *Canthon*. They are lacking (totally or partially) not only in the burrowers, but also in the examined Australian mentophilines (*Cephalodesmius* and *Tesserodon*) and in a series of genera of *Canthonina* from New Zealand, Madagascar and New Caledonia whose biology we do not know. In the studied neotropical fauna, they are missing only in the primitive *Cryptocanthon paradoxus* Balthasar, and are very underdeveloped in *Canthochilum*. The pygidial glands are also characteristic of rollers and are missing in the majority of burrowers studied, they are similar in both sexes and are associated with a repelling role to prevent depredation.

- 17) The process of digging and burying is as characteristic as ball formation in the Scarabaeini (item 1.1) but there are exceptions. Three genera of mentophilines from western Australia, which is extremely arid, are capable of burying one of several pellets so deeply that they arrive at a level of humidity. The burying is done by digging underneath the ball, in the Scarabaeini manner, but when it has more than one ball, the following ones have to be placed in a gallery by pulling with the anterior legs and walking backwards,

or pushing with the anterior part of the body (Matthews, 1974) as do burrowers (see other cases and discussion in item 1.5).

- 18) Species without wings or with reduced wings are more frequently found amongst the Scarabaeini that do not roll (or roll very seldom) (mentophilines, *Canthon obliquus*, *Canthochilum*). This can be interpreted as an association between non-rolling and reduced aggregation problems.
- 19) Always within a pattern, the Scarabaeinae behavioral traits may lead to changes with ecological conditions. This kind of flexibility was difficult to visualize some years ago when we thought Scarabaeinae, and for that matter all insect behavior, was more rigid and stereotyped. In addition to the examples of behavioral flexibility included in this paper, there are others which refer to burrowing scarabs. D. and C. Rougon (1980, 1982 a and b, 1987) have studied the architectural adaptability of nesting according to the nature of soil; in the cleptoparasites there is a loss of nesting behavior regarding the use of a strange brood-ball (Hammond, 1976; Rougon and Rougon, 1980; Halffter and Matthews, 1966); there is also the adjustment to the aridness in Australia related to pellet burrowing (Matthews, 1972, 1974, 1975); and the noteworthy adjustments of *Uroxys gorgon* Arrow and *Trichillum adisi* Ratcliffe (Ratcliffe, 1980; Young, 1981) to the sloth's (*Bradypus* spp.) excrement and its particularities: periodicity of the defecation and the way the beetle handles it.

One must not see the persistence of primitive characteristics in every divergence or simplification of the general norms of behavior of the group. It may be that the most probable (but not the only) explanation is a new ecological adjustment, giving the term "new" great flexibility regarding time.

3.3 Semantic note

In the text we found we had to use names for different levels of taxonomic groups, derived from the genus *Scarabaeus* plus the ending which corresponds to each category. For the reader who is not a taxonomist, we summarize the names and their meaning.

Family *Scarabaeidae*, in the same rank as *Passalidae* or *Lucanidae*.

Subfamily *Scarabaeinae*, in the same rank as *Geotrupinae*, *Aphodiinae*, etc.

- Tribe *Scarabaeini* (the ball-rolling beetles), the same rank as tribes of burrowing beetles (*Coprini*, *Onthophagini*, *Oniticellini*, *Onitini*) and *Eurysternini*.
- Subtribe *Scarabaeinae*, in the same rank with the rollers *Canthonina*, *Sisyphina* and *Gymnopleurina*, or as *Dichotomiina* or *Coprina* within the burrowing beetles.

And, of course, *Scarabaeus* as genus.

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The definite version of this paper was written in 1988 during a sojourn of two months in the Centre d'Ecologie Fonctionnelle et Evolutive Louis Emberger in Montpellier, France, provided by the scientific cooperation agreement between Consejo Nacional de Ciencia y

Tecnología (México) and Centre National de Recherche Scientifique (France). During this sojourn we received all the working facilities from the director of the center, Dr. Francesco di Castri. We had the opportunity of consulting different aspects of the biology of roller beetles and especially *Scarabaeus* with Dr. Jean-Pierre Lumaret from the Université Paul Valéry, Montpellier.

The observations made on *Scarabeus galenus* were provided by Dr. Penelope Edwards of CSIRO, Australia. The observations on the behavior of *Scarabaeus*, partly used for this article, already used for past articles and which will still be used in the future, were possible thanks to the sojourns in the field in the Republics of Turkmenia (1978) and Azerbaidjan (1981) sponsored by the USSR Academy of Sciences through the Institute of Evolutionary Animal Morphology and Ecology. The director of this Institute, Academician Vladimir Sokolov, provided us in all aspects with our very beneficial sojourns in the Soviet Union. On both occasions we were accompanied by Dr. Leo N. Medvedev to whom we are deeply grateful for his friendly support and patience.

FOOTNOTES

- 1 Because of convergence, three species of burrowers use this method to bury complete pellets (that is, non-manufactured balls). In Australia, it is done with pellets from kangaroos, wallabies and wombats, by *Onthophagus compositus* Lea (Bornemissza, 1971) and *Onthophagus parvus* Blanchard (Matthews, 1972); in Europe, with pellets from rabbits or small sheep by *Onthophagus emarginatus* Mulsant (J.P.Lumaret, pers. comm.).
- 2 The only known exception is *Megathoposoma candezei* Harold (Wille, 1973; Wille *et al.*, 1974), where the female rolls alone after mating on the food source. However, these observations made in the tropical forest still have to be confirmed in the laboratory.
- 3 When Halffter and Matthews (1966) define the types of nesting which exist in the Scarabaeinae, they use the term "group". Halffter also uses the same term in a paper (1977) in which he establishes two new nesting groups and revises the previous ones. In the summary of this paper, however, "group" as well as "pattern" are used. Halffter and Edmonds (1982) deliberately substitute the term "pattern" for "group". The meaning has always been the same but by using the

term "pattern" Halffter and Edmonds have wanted to emphasize that the types of nesting behavior have no taxonomic meaning or rank and that the characteristics assigned to it are general of a pattern, within which there are a series of variations due as much to the ecological heterogeneity as to a response to very specific pressures. The use of the term "pattern" underlines the meaning of a general framework of comparison.

Several authors have used these terms, sometimes without really understanding the sense with which they were created. The majority give it the original meaning, Zunino (1986:205) writes "...se trata de patrones a los que corresponden rasgos etológicos de gran valor adaptivo. Las relaciones filogenéticas entre los distintos taxones no afectan necesariamente a la pertenencia de sus representantes a uno u otro, o a varios de los mismos patrones."

- 4 *C. conformis* Harold is actually a synonym of *Canthon (Canthon) virens chalybaeus* Blanchard (Halffter and Martínez, 1977:89).
- 5 *C. tristis* Harold is now *Canthon unicolor tristis* Harold (Halffter and Martínez, 1977:72).
- 6 We literally transcribe Luederwaldt. In the case of *virens* (quoted as *conformis*) whether it deals with a truly elaborated ball or a fragment should be clarified.
- 7 Nevertheless, in the same paper Matthews mentions a ball made of human excrement and its movement in *Amphistomus*, a mentophiline.
- 8 For a detailed up-to-date description of the seven nesting groups of the Scarabaeinae, to which we continually refer, see Halffter and Edmonds (1982), Cambefort (1982 and 1983), and Monteith and Storey (1981).
- 9 Brood-mass: a quantity of food stored at the end or in an enlargement of the gallery which holds one or several eggs.
- 10 Brood-ball: a ball formed by the mother in the interior of which only one egg is deposited.
- 11 The Geotrupini (Klemperer, 1978; Gonzalo Halffter, unpublished observations with *Megatrupes cavicollis* Bates) have a certain ability to repair fissures in the brood-mass using fragments of the accumulated dung which the larva manipulates with its mouth parts. This system works if the mending material has an obstacle to support it such as the layer of earth around the brood-mass. When this layer does not exist, the mending material has no support and the fissure is not closed. The larva can die from dehydration or from the intrusion of a foreign animal. In the Scarabaeinae, even in the most primitive ones who make brood-masses, the larva closes the fissure with its own excrement which it

places in an orderly manner in the fissure or hole until it is closed. This ability is useful, although not indispensable in the case of a brood-mass which fits tightly in the gallery and is completely surrounded by hard earth. However, in the brood ball which is not tightly surrounded by earth, this ability becomes fundamental to the survival of the larva.

- 12 We must insist on the fact that we do not know the nesting process of the majority of Scarabaeini who supposedly do not form balls.
- 13 In Europe, *Scarabaeus* and *Gymnopleurus* are able to make a ball not only by removing it from larger excrement, but also by joining sheep pellets which they shred and join together. To do this, they place themselves firmly on top of a first ball and with the forelegs they pull another (or others) towards themselves. They can also roll one ball towards another and then work it the same way. We should point out that these pellets must be close to each other. *Kheper nigroaeneus* (Boheman) behaves in a similar way in Africa with pellets from wild ruminants (Edwards and Aschenborn, 1988)
- 14 Matthews (1975) expresses his ideas regarding the formation and rolling of a ball. We have synthesized the principle thoughts. The burying of a whole large dung pad *in situ* is impossible as there is just not enough room underneath it for all the necessary galleries. Under these conditions, the efficient exploitation of excrement requires that some of the beetles be capable of transporting a portion of the excrement to another site, which they normally do by making and rolling a ball. Today's marsupials (referring to Australia) deposit their excrement in dispersed pellets, hardly ever in piles. The native beetles are adapted to look for these in wide areas. The pellet is frequently eaten on the surface because it is so small that there is no time to bury it before it loses its moisture. These tactics are the complete opposite of those which the beetle must use in order to exploit cow dung.

In Australia, many of the native species that can roll pellets cannot, however, make a ball. They can only roll balls of excrement which are more of less spherical or oval pellets. As they have always lived from the pellets produced by marsupials, there was no ecological reason to develop the ability to make a ball from part of a large mass of food (Matthews, 1975).

In another paper, Matthews (1974) recognizes two groups of *Canthonina* in Australia: the oldest, the mentophilines, capable of rolling, but not of making balls, and the less old, the non-mentophilines, which follow the general behavior of making a ball and rolling it. The first fauna must have been isolated

in Australia before the development of the ball formation and rolling mechanism.

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