THE NATURAL HISTORY OF DUNG BEETLES OF THE SUBFAMILY SCARABAEINAE
(Coleoptera, Scarabaeidae)

by

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INTRODUCTION

The term "dung beetle" (Mistikäfer, bousier, navoznik) has been applied equally to the members of three subfamilies of Scarabaeidae: Scarabaeinae, Aphodiinae, and Geotrupinae, especially in northern latitudes where the latter two groups may be more important than the first as coprophages, but the Scarabaeinae have a more legitimate claim to the apellation, since only in this subfamily is the vast majority of the species coprophagous.

The present work is an attempt to bring together and analyze all available knowledge of the comparative ecology and comparative ethology of the subfamily Scarabaeinae. The idea for this work was conceived as we proceeded with our taxonomic, ecological, and behavioral studies of this group and came to realize that further progress would be difficult without a thorough review of what is already known, both by ourselves and others. The intent of this work is that it serve as a base from which we may depart on our future investigations, and it is our hope that it will serve other investigators in the same way.

We attempted to consult and read completely all the literature on scarab natural history in English, German, Russian, and the Romance languages, including Rumanian. One work in Swedish was also consulted.

1 La información original contenida en este trabajo forma parte de la Tesis presentada por Gonzalo Halffter ante el Colegio de Profesores de la Escuela de Graduados de la Escuela Nacional de Ciencias Biológicas, como uno de los requisitos para obtener el grado de Doctor en Ciencias Biológicas.
Many papers read were found to be repetitive of data previously published, or too vague to be used, and were not cited. A number of older papers, adequately summarized in more recent works, were not consulted. And, of course, it is to be expected that we have overlooked a few papers. For all these reasons, the list of literature cited at the end is not to be construed as a complete bibliography of the subject.

A major proportion of the information presented results from our own observations and much of it is hitherto unpublished. This is particularly true of the ecological data. Also presented for the first time are observations of certain colleagues who generously communicated their field data (see under acknowledgments). Whatever their source, nearly all the data presented result from field observations. This is largely due to a scarcity of experimental studies in this group, but it also stems from an appreciation of the inestimable value of the field lore acquired by the collector through years of experience. This knowledge, a by-product of taxonomic activities, often remains unrecorded and so dies with its possessors.

It is useful at this point to discuss some historical aspects of scarab studies. The term "scarab" is employed in this introduction in reference to members of the subfamily Scarabaeinae only, for the sake of brevity.

Drawings and references to insects are found in human records from the very earliest times, and scarabs were not the first insects to be thus chronicled. This honor probably belongs to the honeybee. But scarabs (especially members of the genus Scarabaeus) do have the distinction of playing a prominent role in early Western theology, and probably the first recorded account of the life history of any insect is that of Horapollo on the "sacred" scarab or Kheper (Weiss, 1927). While admitting the great historical interest of these records, we must not ascribe to the ancient Egyptians any extraordinary powers of scientific observation. The Egyptians' interest in scarabs was theological or simply aesthetic. Furthermore it certainly seems unlikely that their knowledge of astronomy was such that they could see in the scarab's dung ball an image of "the earth and its rotation", as is claimed by Fabre and repeated in a recent textbook of entomology.

The turning point in scarab studies which marks the transition from narratives of purely historical interest to accounts of scientific value, is the publication specifically of the Scarabaei. Fabre's Souvenirs d'un Naturaliste, the first volume of the Escargots et Scarabées, was published in 1883. Fabre's study of these insects was the result of years of patient observation, and his observations were published in numerous papers which appeared in the Revue de Société Entomologique de France. The first paper appeared in 1881, and the last appeared in 1915. The book itself was not published until 1900.

That Fabre's work in this field helped bring about the undeniable fact that scarabs were "Souvenirs d'un Naturaliste? It is impossible to overstate the importance of what Fabre did, whatever the accuracy of his scientific conclusions. The Souvenirs d'un Naturaliste is the most important book ever written on the scarabs, and its influence is still felt today. The book is a classic of natural history, and its publication marks a turning point in the study of the scarabs.

A few of the insects in scarabs. R. E. Fermor (Coccinellidae) and A. E. Rommel (Coccinellidae) in the subfamily Coccinellinae, R. E. Fermor (Coccinellidae) and A. E. Rommel (Coccinellidae) in the subfamily Coccinellinae, R. E. Fermor (Coccinellidae) and A. E. Rommel (Coccinellidae) in the subfamily Coccinellinae, R. E. Fermor (Coccinellidae) and A. E. Rommel (Coccinellidae) in the subfamily Coccinellinae, R. E. Fermor (Coccinellidae) and A. E. Rommel (Coccinellidae) in the subfamily Coccinellinae.
a previously published number of older works were not consulted. I have overlooked a few aspects of scarabs at the end is thus a subject. The results from our exploration are described. This is particularly true for the first time that Fabre's works have been communicated despite their acknowledged value. This is the case with this group, but it is not the case for the value of the field that Fabre established. This knowledge remains unrecorded and has already been mentioned in reference to the importance of Fabre's works since the publication of Jean Henri Fabre's "Souvenirs Entomologiques," more specifically volumes V and VI (1897, 1899), which concern especially the Scarabaeinae. The dung beetles (Scarabaeus and Copris especially) were Fabre's favorite insects:

"Les Scarabées ont été le sujet de prédilection de Fabre. II a consacré aux différentes espèces de cette famille quarante années, afin de percer leur secret, de ne rien ignorer de leur vie intime dont la partie la plus intéressante se déroule dans les ténèbres du sol, à l'abri des regards humains... Même si d'autres chercheurs avaient renouvelé notre connaissance des moeurs des Scarabées, ces pages resteraient encore au nombre des plus belles de la littérature française, grâce à leur style et à leur langue et aussi grâce à la pensée qui les anime." (Jacques Brasse, Collection 10/13, No. 122/123, 1963.)

That Fabre's works achieve heights of literary excellence, and that this helped greatly to popularize knowledge of insect behavior, are undeniable facts. But what about the scientific contributions of the Souvenirs? It became fashionable in the earlier part of this century, whenever an observer encountered some detail different from that given in the Souvenirs, to cast doubt on Fabre's work as a whole (e.g. Siyazov, 1913; Goodman, 1928). In emphasizing differences these critics sometimes made valuable contributions to the important concept of variability in behavior, but often they themselves would not admit the possibility of such variability. In our opinion, and judging from his passages on scarabs, the importance of Fabre's works cannot be overemphasized, quite apart from their popularizing influence, because he alone set up standards of observational patience and accuracy which subsequent workers were then forced to meet.

A few of Fabre's compatriots carried on in his tradition (notably in scarabs. Reneaud Paulian in his well-written book "Les Coléoptères, Fermes—Mœurs—Rôle" (1943). But the true heirs of Fabre, at least in scarab studies, are the various German workers who, with great patience and attention to detail, greatly enriched our knowledge of behavior in the subfamily. Noteworthy among these are F. Burmeister (Onthophagus), R. Heymons (Scarabaeus), H. von Lengerken (Scarabaeus), E. Rommel (Copris), and especially J. Prasse (Gymnopleurus and Sisy-
We owe a special debt to Prasse, whose studies are the most thorough of any yet published so far. The background of detailed, concrete information provided by the German studies has enabled us to place much fragmentary data on many other species and genera in meaningful perspective.

Hanns von Lengerken rendered students of the Scarabaeinae a great service by compiling much information in his book on brood care in beetles (1954, 2nd ed.). However, von Lengerken's bias toward the German and English literature is obvious, and is most clearly shown by the omission of any references to such pioneering works as Sivazov (1913) and Goggi's (1926) account of the biology of *Scarabaeus semiplanatus* Fabricius, a work that preceded by three years Heymons and von Lengerken's much-quoted study of the same subject. Our present work is totally different in scope and concept from that of von Lengerken and, while being restricted to the Scarabaeinae, includes a great deal more information on the subfamily.

Fabre's influence also spread quickly to other parts of the world. In Russia, Sivazov (1913) made some very fine observations on *Synapsis*, *Copris*, and *Scarabaeus* in Central Asia (in what is now Uzbekistan) and, much later, the most extensive experimental study yet done on ball-rolling behavior was published by Puzanova-Malyshova (1956). A very important study of significance to students of Scarabaeidae, in the general sense, is that of Ghilarov (1949) on adaptations of insects to life in the soil.

In South America, scarab studies got off to an early start with the interest shown by Jean Bréthes (Père Jodulien), who collaborated closely with Fabre by correspondence. In the early part of this century two German investigators came to South America, attracted by the very rich and varied scarab fauna of the continent: Friedrich Ohms, who made two "Studienreise" in Ecuador and Brazil, and Hermann Luederwaldt, who came to Brazil penniless and took a job as a gardener in the grounds of the Museo Paulista. His now legendary activities include voluminous studies of many aspects of the flora and fauna of the Sao Paulo region, and the amassing of a great insect collection now in the Department of Zoology. His principal interest quickly turned to the Passalidae and Scarabaeinae, in which he published a few papers of biological interest. The most important later workers in scarab natural history in South America are those on scarab balls, a very particular experience and interest that will be followed up in an extraordinary paper (Eisenschelz) in his forthcoming work (1926). However, our workers, and Prasse in particular, are the best known of these but a great deal more is needed.

The English-speaking natural historians in Hindustan, Volume 3 of the *Ecological Revision of North America*, is short but significant with a great deal. A great deal of progress has been made since the publication of Lindquist. A great deal more is needed, however, in the extensive original work.

The field of scarab natural history is superior to that of beetles in general, and the factors governing it are more closely related to the factors governing the behavior of insects and their behavior. The field of scarab natural history is superior to that of beetles in general, and the factors governing it are more closely related to the factors governing the behavior of insects and their behavior. The field of scarab natural history is superior to that of beetles in general, and the factors governing it are more closely related to the factors governing the behavior of insects and their behavior.
studies are the most detailed. Consequently, we have been able to place much of the history in meaningful perspective.

For the Scarabaeinae a great deal more research on brood care in particular, and a bias toward the Neotropics, is clearly shown by the work of Sivazov (1913) and Martínez (1929). The present work is heavily dependent on Langerken and Martínez, and a great deal more research on brood care is needed in the Neotropics. In their respective "Fauna" volumes, and in their respective "Fauna" volumes, and V. Baltašar, in his recent monograph covering the Palaeartic and Oriental regions, invariably show a strong awareness of ecological factors in describing and discussing distributions. Finally, one of us (Halffter, 1959) was the first after Kolbe to attempt a comprehensive survey of the ecology, palaeontology, and economic importance of the Scarabaeinae on a worldwide basis. The present work arises out of this latter paper.
In spite of the tremendous wealth of Scarabaeinae on the African continent, studies there have so far been exclusively taxonomic, with the exception of a study of Onitis caffer Boheman by J. J. Oberholzer (1958) and some collection notes on Onthophagus published by G. Frey (1961) and other Scarabaeinae by M. C. Ferreira (1962), both in reference to the Garamba National Park (Congo). Australia, which has an apparently archeaic scarab fauna of great interest, is even more poorly studied. Even minimal behavioral and ecological data on the commonest genera from these two continents are lacking and would be of great value.

A fine natural history study of forest-inhabiting scarabs, the techniques of which could be applied elsewhere in the tropics, is that of Vinson (1951 and previous papers) on the species of Nesositsalpbus of Mauritius. A similar study was made by one of us (Matthews, 1965) on the canthonines of Puerto Rico.

Some of the greatest gaps in our knowledge of the biology of Scarabaeinae concern the physiology, soft anatomy, and histology of both adults and larvae. We have tried to collect as much data as possible on these aspects, but very little seems to have been done. The studies of Heymons (1930) and Willimzik (1930) on the female reproductive system are particularly significant and point the way to some very interesting further studies. Crucial nutritional investigations have not been made. We have no idea what elements of the excrement food are utilizable by larvae and by adults, whether different excrements differ importantly in composition, in what ways decaying vegetation and carrion are similar to excrement, whether symbiotic microorganisms play any part in digestion, and so forth. Studies of great potential taxonomic significance on the chromosome cytology of several genera of Scarabaeinae were begun by Nilo Virkki in a series of papers.

Finally, studies on the comparative ethology and ecology of a group must rest on a solid taxonomic basis, and although the taxonomy of the Scarabaeinae is in better shape than that of some other groups, there is a need for a fundamental re-examination of the higher categories especially (subtribes and tribes). The type of comparative biological information discussed in the present paper will contribute importantly to such an eventual re-examination.
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Coprophagy is seen in a few species of Scarabaeinae, but the behavior, distribution, and the presence of the factors of the Scarabaeinae abounds probably been been found primarily to groups.

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in many cases other excrements, carrion, or decomposing plant matter are used does not detract from the importance of the above-mentioned excrements as the basic food materials of the subfamily.

Scarabaeinae feed copiously in the adult stage, ingesting large quantities of fecal materials, which contain undigested food residues, products of secretion and excretion, bacteria, yeasts, and molds. In man, between 10 and 25% of the fecal mass consists of bacteria. The microbial content of the dung of herbivorous animals is probably equally high. Like the maggots of coprophagous flies, the Scarabaeinae must depend to a large extent on the microbial products which are ingested with the excrement (Miller, 1961: 739).

Ceprophagy in the Scarabaeinae directly determines their relative abundance in various biomes. Even though the tropical forest is without doubt very rich in species, and contains a greater morphological and ecological variety of Scarabaeinae, it is in the pasture land, savanna, or other equivalent open grassland association that the role of these beetles is of the greatest importance, and the number of individuals probably the greatest. In grassland biomes the herds of bovids are a continuous source of supply of excrement which, once buried, eaten, or dispersed by Scarabaeinae and Aphodiinae, plays an extremely important part in the biological cycle of these biomes.

One demonstration of the importance of the role of Scarabaeinae in grasslands with large herds of bovids is provided by those pasture lands where these insects are scarce or absent — lands where there were no indigenous large herbivores. With the introduction of bovids by man, the absence of Scarabaeinae brings about a deterioration of the pastures through accumulated excrement, which kills or impedes the growth of grass (Bornemissza, 1960). This does not happen in areas with indigenous bovids, where grassland Scarabaeinae have had an opportunity to evolve and where their presence now permits a renovation of the pasture (see section on parasitological and economic importance).

In relative extent, grasslands have been very important — in many areas predominant — since the middle Cenozoic. In recent centuries man has greatly expanded their area by creating artificial pastures and clearing forests for cultivation. Bovidae, especially Bovinae, are an expanding group (at least in numbers of individuals). Consequently the Scarabaeinae adapted to gr

Halfher in the Northern Hemisphere (and as preceded) in some cases the excrement the eucalyptus coleopterum, such it has no reference may not.

It should be noted that the common type of excrement, the insect's excreta, is an indiscriminate use of excrement. For example, fruits (euryphilous) and the excrement of some insects (e.g., the European earwig) are used, e.g., in the case of the Carrier beetle, such could be on many occasions.

Important note

We have included the excrement of the Otomops' common excreta is used in a few rare for such a situation. Onthophagus and Scarabaeinae are relatively abundant, although the pattern in some cases.
adapted to grassland formations and to coprophagy are also an expanding group, in many cases spreading at the expense of the expense of forest species.

Halfiker (1959:168) considers that coprophagy is not a primitive character in the Scarabaeinae, but is rather the result of a process of specialization. We continue to maintain the same opinion here, but point out at the same time that the subfamily did not acquire the characteristics which distinguish it today until it became, not only coprophagous, but specialized for coprophagy on large-mammal dung in grassland biomes. This broad specialization must have occurred very early in the history of the subfamily and colored all its subsequent evolution.

In general, the excrement most utilized in the temperate prairies of the Northern Hemisphere is that of cattle, followed (or in a few cases preceded) in importance by that of man. There follows in order of preference the excrement of sheep and (much further behind) horse, donkey, camel, and goat. This order of preference is a generalization, and as such it has its exceptions. Furthermore, within the same species the preference may vary according to the types of excrement locally available.

It should also be noted that certain species come to only a certain type of excrement (stenophagous species), while a larger number feed indiscriminately, or with a low degree of preference, on the various types of excrement available, and sometimes also on cadavers and decaying fruits (euryphagous species). The stenophagy of a species could be a de facto stenophagy, determined by local conditions — the absence or rarity of excrements other than that consumed — or it could be a true or intrinsic stenophagy — feeding on one type of excrement regardless of the presence of other types in the locality —. In some cases stenophagy could be only apparent, being due to the incompleteness of the field observations of the authors reporting it.

Importance of Coprophagy in Different Geographical Regions

We have already indicated the sequence of preferences in types of excrement consumed in the pastures of the Northern Hemisphere. This sequence is followed by practically all the Scarabaeinae of Eurasia (a few rare forest species may eat other types of excrement). Only in the Onthophagini, especially in Onthophagus, are there some important deviations, although even here the majority of the species follows the above pattern. In North America, including the Mexican Plateau, this same
preference sequence is displayed by the majority of the species of the genera Canthon, Boreocanthon, Melano- 
canthon, Dichotomius, Ontherus, Capris, Phanaeus, Ateuchus histeroides Weber and some other species 
of the genus, and about half the species of Onthophagus.

An important feature of the Scarabaeinae of the Northern Hemisphere, to be discussed later, is that they are not important in the temperate deciduous forests, and even less so in the taiga. As we advance north­ward, we see an increasingly strict restriction to open habitats, which are exposed to full insolation. In the forests, the coprophagous scarabs are mostly Geotrupini (a predominantly Holarctic group), whose species show, aside from coprophagy, strong tendencies to mycetophagy and saprophagy. Thus, in Sweden all the species of Scarabaeinae are both coprophagous and inhabitants of open, preferably sandy, terrain (Landin, 1957).

Leaving the temperate Northern Hemisphere, we will pass now to the African savanna, where the consumption of bovid excrement maintains its basic importance, but where the diversity of large herbivores (until recently present in large herds) greatly widens the range of excrements utilized.

In 1961 Frey made a taxonomic study of the Onthophagini of the Congo and (something very unusual in works dealing with the Ethiopian fauna) he recorded the collecting data completely, giving us information on the excrement in which each species had been captured. This enables us to present the following analysis.

The numbers of species of Onthophagini captured in each type of excrement are as follows: elephant 27; buffalo 23; rhinoceros 22; waterbuck 15; wart hog 11; giraffe 7; antelope 2; hippopotamus 1.

The category of most-preferred excrements includes that of elephant, rhinoceros, and buffalo. Of the 27 species collected in elephant dung, 14 were also collected in rhinoceros and buffalo dung, seven in only one of these, and the remaining six in neither rhinoceros nor buffalo dung. Of these six species, Onthophagus jadavata d'Orbigny was also found in wart hog dung and O. cyanomelas d'Orbigny in that of waterbuck; the remaining four species (O. atrocaudatus d'Orbigny, O. moquetti d'Orbigny, O. tajutuillians d'Orbigny, and Caeolabus punctatissimus Harold) were found only in elephant dung.

Of the 22 species found in rhinoceros dung, only four were not also collected in elephant and buffalo dung. Of these four, Onthophagus flavicollis d'Orbigny was also found in wart hog dung, while the remaining three (O. victorii Ericsson, O. cyanomelas d'Orbigny, and O. macedon d'Orbigny) were found only in rhinoceros dung.

All the species of scarabs were also collected in wart hog, and giraffe, and even in the dung belonging to various species of antelopes and buffaloes. Two species should be mentioned: Onthophagus d'Orbigny and O. bicornis bicornis, whose excrements of these animals were collected together.

Of the 14 species also in excrement of the Heteromorphini (Caccobius) were found in wart hog, elephant and other excrements of the same colonies. More species of Onthophagini were collected in wart hog and elephant dung.

Of the seven species collected in elephant dung only one is not also found in this type of excrement.

Finally, it is interesting to note that of antelope dung, wart hog and wart hog dung, there are no species exclusive to this type of excrement.

There are no species of Onthophagini that are completely common in the remaining habitats.

The data obtained by Frey clearly show the importance of excrement. Evidently some species are associated only with the dung of certain herbivores, and it is clear how much information is obtained by examining faunal assemblages of animal excrement.

Nonetheless, the most important fact is that the scarabs are associated with a fauna of considerable importance, even if the extent that we understand today is very limited. It also shows the importance of the study of coprophagy in the insect world. However, this phenomenon is not restricted to the most important species of excrements. It is possible that the study of the association of coprophagous species with euryphagous species of the families Cetoniidae, Buprestidae and Scarabaeidae would be important in understanding the dynamics of these assemblages.
The species of the scarabaeids: *Onthophagus reticulifer* d'Orbigny and *Caccobius sericus* Frey were also collected in elephant dung, and the remaining six in the dung of the *Hippotragus pygargus* d'Orbigny: *Onthophagus pygargus* d'Orbigny, *Caccobius pygargi* Landin, *Caccobius reticulifer* d'Orbigny, *Caccobius curtipes* Landin, and *Caccobius truncatus* Landin were also found in elephant dung.

In this way, we can divide the faunas into three groups of excrements, which are classified as: (1) dung of wart hog; (2) dung of wart hog and giraffe; (3) dung of wart hog, giraffe, and elephant. However, this last category of excrements is much greater than the others. Moreover, it is evident that the histogram of scrophulids in *Onthophagus pygargus* d'Orbigny is that of wart hog dung; *Onthophagus pygargus* d'Orbigny and *Caccobius sericus* Frey. The sum of the four species of the second group is that of wart hog dung; *Onthophagus pygargus* d'Orbigny and *Caccobius sericus* Frey. And *Onthophagus sericus* d'Orbigny and *Caccobius sericus* Frey are found in elephant dung.

The second group of excrements includes that of wart hog, wart hog and giraffe. The 15 species found in dung of wart hog are also found in dung of wart hog and giraffe. Of these 15 species, two are apparently exclusive to wart hog dung: *Onthophagus pygargus* d'Orbigny and *Caccobius sericus* Frey, and only one was found exclusively in the dung of this animal: *Phalops coerulatus* d'Orbigny.

Of the 11 species which came to excrement of wart hog, four were not found also in excrement of the first order of preference. Of these four, two species (of *Caccobius* Frey) were also found on wart hog dung, and two are apparently exclusive to wart hog dung: *Onthophagus pygargus* d'Orbigny and *Caccobius sericus* Frey. More species of *Caccobius* (three) come to wart hog dung than to any other kind.

Of the seven species found on giraffe dung, six are also found in that of the first group and only one (*Onthophagus pygargus* d'Orbigny) was collected exclusively on this type of excrement.

Finally, in the least-visited kinds of excrement, we have two species exclusive to that of antelope (*Onthophagus pygargus* d'Orbigny and *Caccobius sericus* Frey), and one exclusive to that of hippopotamus (*O. solitarius* d'Orbigny).

There are no records of species collected in the excrement of carnivores, which are common in the region.

The data we have analyzed are not to be taken entirely at face value. Evidently some results are due to the technique of collecting — we do not know how many deposits of each type of excrement were examined, nor is there any information on the relative abundance of each type of excrement.

Nonetheless, our analysis does show that there are types of excrement with a fauna of *Onthophagus* much greater than that of others, to the extent that we can divide the types of dung into three grades of preference. It also shows us that there is a majority of euryphagous species, together with a minority of stenophagous ones. However, this stenophagy occurs in the African savanna, the biome richest in mammals, where many and varied types of excrement are found simultaneously. It seems therefore that in at least some faunas there are species demonstrating stenophagy to a greater or lesser extent, coexisting with euryphagous species. Stenophagy thus appears to be a reality for a certain number of species in certain biomes and is not, as some authors maintain, a phenomenon without importance. In any case, we cannot
extend the observations made on one species or group of species to the rest of the subfamily.

There are also a few data on the relationships between other Scarabaeinae (not Onthophagini) and different types of excrement in the Ethiopian region. Many species are recorded from buffalo dung, Onitissanguineus Felsche and Oniticellus (Eunoticellus) inequalis Reiche have been collected in rhinoceros dung (Balthasar, 1960), and Onitissulcipennis Felsche (Balthasar, 1960). Helicopris etrus Fabricius, and Copridaspis peregrinus Harold (Paulian, 1943:235) have been found in elephant dung. In these cases it does not appear that there is a marked specificity toward one type of excrement. Most of the records refer to isolated collection data and we cannot exclude the possibility that other types of large-herbivore dung are utilized. Nevertheless, according to Janssens (1939:47), the distribution of the species of Helicopris is closely linked to that of the largest mammals: certain species of large size, notably H. colossus Bates, are specialized for the exploitation of elephant droppings and are found abundantly in the regions inhabited by the proboscideans, their range coinciding with that of the African elephants. It is interesting to note that in the Oriental Region, another Helicopris (H. dominus) from India, Burma, Thailand, and Indochina) feeds on the dung of the Asian elephant (Annandale, 1900, cited in Balthasar, 1963:298).

In India coprophagy is extremely important, principally in connection with cattle and human excrement (see paragraph quoted from Hingston in the chapter on parasitological and economic importance). As in the Palearctic Region, the majority of deviations from this type of feeding is found in the Onthophagini (Onthophagus and Caccobius). These will be discussed primarily under Necrophagy.

In South America we find a partial displacement toward necrophagous habits which can be related to the following factors: a) the absence of large herds of herbivorous mammals, dating from the disappearance of the native forms to the introduction of cattle, sheep, and horses by the Europeans. b) the predominance of forests or other woody associations, which is greater than in any other part of the world with the sole exception of Southeast Asia. c) the scarcity of large mammals even inside the tropical American forest, in comparison with other regions, and d) the relative unimportance of other necrophagous insects, such as Silphidae, whose role in South America is played by Scarabaeinae.

In South America, which are mostly in the Canthon group, and Anisocanthus, Onthophagus, Dichotomius, and Phanaeus s. str. The majority of species of Onthophagus (especially of the subgenus of Onthophagus) are not very specific in their feeding habits and are found on dung of a wide variety of animals. On the other hand, very few species are reported from buffalo dung, as Silphidinoc. which are sometimes associated with cattle and human excrement, whereas the majority of species of Onthophagus (especially of the subgenus of Onthophagus) are not very specific in their feeding habits and are found on dung of a wide variety of animals.

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of species to the

between other Scarabaeinae species for excrement in the same way as buffalo dung. Onitis inequalis Reiche (1960), and Onitis Fabriexus Fabricius, and their allies in connection with dung have been found there is a marked possibility that other records refer to this species. In

Helicopris is a species of large size which is exploiting of regions inhabited by the African elephant Region, another species is Scarababus, Thailand, and

especially in connection with dung from Hingston (1924). As in the case of Helicopris type of feeding (stenophagy). These will

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In South America, the groups of Scarabaeinae which contain species which are mostly or entirely coprophagous are: Eucranina, Erygysternus, in the Canthonina (as far as we know): Eudinopus, Scybalophagus, Anisocanthon, Genicocanthus, and Gaphylocanthus, in the Coprini: Ontherus, Dichotomius, Ateneus, Chalcocopris, Bolbites, the subgenus Phanaeus s. str., Gromphas, Oruscatus darus (Erichson), and Enneacanthus (especially on caprine dung), and finally the majority of species of Onthophagus.

Specialization within Coprophagy

There are many species in different groups which show an affinity for excrement other than the two normally preferred ones mentioned above (bovid and human), or which have completely or partially abandoned the preferential sequence listed on p. 11. These may show a strict stenaphagy, corresponding to a very specialized ecological niche, or a lesser degree of stenaphagy, in connection with life in non-grassland biomes or in grasslands with an abundance of non-bovid mammals.

We have already discussed the feeding (indiscriminate or specialized according to the species) on various types of excrement in the African savanna. Other specializations may be observed in different parts of the world, especially in the Southern Hemisphere.

In Europe, there is a notable affinity for human excrement shown by the numerous species of the genus Scarabaeus. Heymons and von Lengerken (1929:534) indicate that on the Adriatic coast of Italy these beetles are found abundantly in inhabited areas and bathing beaches, while they are rare in the less inhabited intervening areas. One of us (Matthews) has a childhood recollection of very large numbers of Scarabaeus (probably semipunctatus Fabricius) behind the beach at Forte dei Marmi, on the Ligurian Sea. Furthermore the genus (Heymons and von Lengerken studied S. sacer Linnaeus, semipunctatus Fabricius, laticollis Linnaeus, and variolosus Fabricius) is frequent in the vicinity of many peri-Mediterranean towns, in African oases, and everywhere where human excrement abounds. According to Goggia (1926:8), Scarabaeus semipunctatus Fabricius markedly prefers, both for its own food and for the preparation of the brood ball, human excrement. As we will indicate later, the coprophagous species which preferentially utilize human excrement are those which show the greatest tendency toward occasional

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necrophagy. Hence it is not surprising that Goggio (1926:9) observed S. semipunctatus rolling a piece of chicken and that Fausek (1906) observed S. sacer rolling a small, well-decayed tortoise 6 cm long, near Ashkhabad (this was not an "error" [oshibka], as Fausek believed, but an incidence of necrophagy).

In contrast to what we have indicated for Scarabaeus, two other species abundant in the south of Europe — Sisyphus schaefferi (Linnaeus) and Gymnopleurus geometrii Füssly, although attracted to human excrement, do not consume it with facility (Prasse, 1957a:440), preferring dung of sheep or cattle.

In America, human excrement is especially attractive in forests, where cattle dung is scarce, but even in grasslands human feces are rapidly attacked by a variety of species. There are more data on the species which come to human excrement in the chapter on medical importance.

Sheep dung is especially attractive to many European and Central Asian species, among these Sisyphus schaefferi (Linnaeus) and Gymnopleurus geometrii Füssly (Prasse, 1957a:440). Scarabaeus sacer Linnaeus, S. laticollis Linnaeus, S. semipunctatus Fabricius, and S. variolosus Fabricius (Heymons and von Lengerken, 1929:533). Fabre insisted on the importance of sheep dung in the nidification of various species of Scarabaeinae in France. The present authors were able to observe how this type of dung was used preferentially in the nidification of Phanaeus palliatus Sturm, a Mexican mountain species which uses human, cattle, or sheep excrement indiscriminately as adult food. On the other hand, in mountain pastures, also in Central Mexico, Copris armatus Harold uses sheep dung (very abundant in the area) for nidification but does not show a marked preference for it over that of cattle and horses, which is also used.

Among other records of utilization of special kinds of excrement, we have Glyphaurus, a Ecectrina from the arid regions of Argentina, carrying goat dung to its nest (Martinez, in litt.).

Pig feces have yielded Glyphaurocanthus viridis championi (Bates) (Haffter), also Onthophagus antillarum Arrow on Dominica and O. batasi Howden and Cartwright on Martinique (Matthews). However, a great many unrecorded species must occur in pig dung, which appears similar to human feces. We have already mentioned the African species which come to wart hog excrement.

Rabbit pellets (Paulian, 1943: Caves) we mentioned which consume them, his studies of very attractive Rico live exclusively on indigenous mammals. not only the rat is cat excrement that the Scarabaeinae like, Canthochilum and insectivores and birds and reptiles.

A great species on the island of Borneo, Nesosiphon everts, feeds on the excrement from Borneo and Indonesia. According to 'the introduction of which were not mammals). At excriment places the cycle of one species of excrement. The dodo, but the lowland parts en excluant le trouvanc ancien de Maurice (quand petit-duc (S.) chant les hôtes pas perdre de que carnassiers que question." (Vía small excrement, larval development
observed at Fauske (1906) near 6 cm long, near Fauske believed, but Rabaeus. two other Scarabaeus, other species Schaefferi (Linnaeus), attracted to human feces (Paulian, 1943:239). preferring

Pellets are eaten in France by Onthophagus punctatus Illiger (Paulian, 1943:239), and under "Inhabitants of Vertebrate Nests and Caves" we mention a series of North American species of Onthophagus which consumes rodent and rabbit dung. Matthews (1965) found during his studies of the canthornines of Puerto Rico that fresh rodent feces are very attractive to the species of Canthochilum. The Scarabaeini of Puerto Rico live exclusively in tropical forests in which there are now no indigenous mammals (except bats) and, among the introduced forms, only the rat is abundant. Only occasionally is human, cow, horse, or cat excrement to be found in the forests, and these are also eaten by the Scarabaeini mentioned. Before the introduction of these mammals, Canthochilum and Canthonella must have fed on the excrement of native insectivores and hysticomorph rodents, and possibly also on that of birds and reptiles.

A greater problem is presented by the four species of Nesosisyphus on the island of Mauritius excellently studied by Vinson (1947, 1951). Nesosisyphus is endemic to Mauritius and is a forest genus which now feeds on the excrement of Macaca irus. However, this monkey, originally from Borneo and Sumatra, was introduced into Mauritius about 1528. According to Vinson (1951:111-112), the food of Nesosisyphus before the introduction of the monkeys must have been the excrement of birds, which were numerous on the island before colonization (there were no mammals). At present, Nesosisyphus is strongly attracted by chicken excrement placed in traps in suitable areas, and even the complete life cycle of one species (N. pygmaeus Vinson) was obtained using this type of excrement. One possibility is that Nesosisyphus was associated with the dodo, but this big bird, judging by its fossil remains, lived in the lowland parts of the island where the beetles do not occur. "Même en excluant le dronte (dodo) d'autres oiseaux d'assez taille devaient se trouver anciennement dans les forêts des montagnes, tels que le perroquet de Maurice (Lophopitacu mauritianus), l'autour (Astur alphonsi), le petit-duc (Scops commersoni), le hibou (Strix sauzaeri), etc. En recherchant les hôtes naturels possibles des Sisyphes mauriciens il ne faudrait pas perdre de vue les mollusques terrestres autochtones, tant herbivores que carnivores, qui abondent dans les zones propices aux coleoptères en question." (Vinson, 1951:112). In captivity Nesosisyphus does not refuse snail excrement, although it is not known whether this is suitable for larval development. Another possibility is the utilization of carrion, includ-
ing the dead snails themselves. It is interesting to note that in Puerto Rico snail dung also attracts some of the native Scarabaeinae (see Section 11).

In Argentina the excrement of vizcacha (*Lagostomus m. maximus* [Desmarest]) has its own fauna of Scarabaeinae which is mentioned in the section on nidicly. In the genus *Anomiaformes*, exclusively Argentine like all the Eucraniina and restricted to dry, sandy areas, two species—*A. cavifrons* (Burmeister) and *A. juriferum* (Burmeister) —have been observed on the banks of dry streams and rivers running quickly on the four hind legs, carrying recent excrement between the forelegs and depositing this in their burrows (Martínez, 1945). According to Burmeister (1861, cited in Kolbc 1905:487), another eucraniine, *Eucranius arachnoides* Brullé, carries horse dung in the same manner in sandy desert terrain. Many forest species come to deer excrement. In North America *Melanocanthus bispinus* (Robinson) and *Boreocanthon probus* (Geinart) have been collected on this type of excrement (Robinson, 1948:87), the former species also having been found in dry fungi. In the United States, various species of *Onthophagus* come to deer droppings, but not exclusively, occurring also in other types of excrement (Howden and Cartwright, 1963). In Europe it is common for many species of Scarabaeinae, especially *Onthophagus*, to go to deer droppings in the vicinity or interior of woods. On the slopes of the Himalayas (Sikkim), *Onthophagus falcifer* Harold has been collected on deer droppings (Arrow, 1931:271). Also in the Palearctic, *Copris lunaris* (Linnéus) and *C. pulch Boiss* come to deer droppings, although not exclusively (Balthasar, 1963:333-334).

Some carnivores have their own coprophagous fauna. Thus, in Java tiger excrement is sought by *Onthophagus drescherti* Paulian, according to Paulian (1943:239). In North America, *O. concinnus* Laporte comes to excrement of skunks and foxes, and only occasionally to human and cow excrement; a few have also been collected in fungi, under chicken dung, and in fermenting malt traps (Howden and Cartwright, 1963:111). Also in the United States, *O. scheffleri* Howden and Cartwright has been collected in opossum or raccoon feces, but this species also comes to other excrement and even to some decaying fruits (Howden and Cartwright, 1963:90). *O. coenobita* Herbst (a European species), when in the presence of dog and cow excrement, comes first to the latter and all others avoid it (Cacobia sos. see near Peking dog excrements, 1943). Man excrement is essentially avoided by these of man. Cats, like many forest carnivores, come to deer excrement.

Certainly herbivores and all other droppings are single Scarabaeinae, only one liter is *Concinus*, cited in Section 11. In Section 11.

In discussing the feeding habits of herbivores.

As to herbivores, in 1900, cited in Section 11. In discussing the feeding habits of herbivores.

As to herbivores, in 1900, cited in Section 11. In discussing the feeding habits of herbivores.
Note that in Puerto Rico the Scarabaeinae (see Scarabaeinae) is mentioned which is mentioned exclusively in sandy areas. This observation is based on the fact that rivers running through the forest between the mountainous regions of Sikkim. In the United States, many species of Scarabaeinae are collected in wild dog droppings. The forest Scarabaeinae is found feeding on bat dung.

In South America, birds feeding on fruit droppings (see Scarabaeinae) have been observed. In the United States, many species of Scarabaeinae are collected in wild dog droppings. The forest Scarabaeinae is found feeding on bat dung.

Caccobius sodalis Harold has been collected in wild dog excrement near Peking (Bairshans, 1963/2:139). As in the case of pig dung, dog excrement must attract many unrecorded epizoophages, as the animal is essentially an omnivore and has excrement similar to that of man. Cat feces were used successfully by Matthews in trapping forest cantharines in Puerto Rico.

Carnivore excrement is sought much less than that of herbivores and man. In many years of collecting in Mexico, where fox droppings are very abundant in some localities, we have not found a single Scarabaeinae in this type of excrement. Furthermore, there is only one literature reference to a species in fox droppings (Onthophagus concinimus, cited above).

In discussing association with caves we mention the Scarabaeinae found feeding on bat dung.

As to bird droppings, in Madagascar (according to Mocquerey, 1900, cited by Paulian, 1934:276) Epilissus feeds on bird droppings located on the leaves of trees. Janssens (1938:4) considers the genus Epilissus to be primitive within the Canthonina (the genus is fundamentally Madagascan, with three species in Australia and one in South Africa) and cites Clout des Petruces (1900), according to whom Epilissus is found on tree leaves around bird droppings, and d'Olsoufieff (1935), according to whom it is found under dung or small cadavers. According to Peronq (1900[1901], cited by Janssens, 1938-13) the South African species, E. subtilis Behman, is found in decaying vegetable matter. We also have the following additional records relating to bird droppings: In the United States, Glaophygochnesson v. viridis (Beaurev) may be found on leaves around bird droppings (O. L. Cartwright, in litt.), although this is not the only kind of excrement used by this species. Onthophagus wattmeri Martinez, from Paraguay and Argentina, has been collected only in flight or in bird excrement (Martinez, 1952-73-77). Janssens (1953:5), citing the collection data of Bechyné, indicates that in French Guinea Drepanocerus is abundant in bird droppings on trees. Janssens personally has collected only a small number of specimens of this genus in the Congo, finding them in the dung of various herbivores, living like Aphodiinae. It should be noted that neither of the two observations names the species, hence, as in the case of Epilissus, different species.
species may be involved. In the United States, Onthophagus concinnus Laporte has been collected in chicken excrement, although it is not exclusive to it (Howden and Cartwright, 1963:111). The probable importance of bird excrement to forest-inhabiting scarabaeines on tropical islands has been mentioned previously.

As for reptile excrement, Onthophagus falzonii Goidanich from Turkey and perhaps Iran lives exclusively on the excrement of the land tortoise Testudo graeca ibera Pall. (Petrovitz, 1962:108). A similar association is found in the American species of Copris and Onthophagus living in the nests of the tortoise Geophrus polyphemus (see Section 7).

A very special type of coprophagy is seen in Zonocoris gibbicollis (Harold). This curious insect has been described as a dichotomine under the name Zonocoris and as a canthonine under the name Plesiocanthon; at present the accepted opinion is that it is a dichotomine. It is found inside the shell of the land snails Balinus haematostoma and B. oblongus in Brazil and Helix sp. in Argentina, up to a dozen individuals being found in a single snail, apparently without causing harm to the latter. Most authors claim that Zonocoris feeds on the mucus and other secretory products of the snail but Martinez (1959:61) believes that it feeds on the snail's excrement, not the mucus. Other scarabaeines may also feed on snail excrement, at least in Puerto Rico and Mauritius (see Section 11).

Dung Consistency and the Microclimate

The studies made by Landin (1960) on the influence of the microclimate on the Aphodiinae inhabiting dung have not been duplicated in connection with Scarabaeinae, nor could they be, since the biology of the two groups is so different. The coprophagous Aphodiinae spend the entire life cycle inside the dung where it lies, without burying any of it. For this reason the physical conditions of the dung and its surroundings are of crucial importance. Since the Scarabaeinae practically always detach and bury a portion of the food, the microclimatic conditions at the area of original deposition are of far less importance to them. Nevertheless, these factors are still important insofar as they maintain the food in a malleable or cuttable state for more or less time.

On the whole, the Scarabaeini require firmer (less liquid) dung than the Coprini and other tribes because of the need to make it into balls. Therefore liquid to Scarabaeini on the one hand, in dry conditions exploitable for words, while Scratophagous of the biome (a) around the food, and timing, and dung.

Of equal importance is the type of the dung. Even certain types of rabbits and of snails scattered around the dung which they had. Covered with a fairly low moisture content and therefore relatively hard to provide for this reason.

No adult chewing or cutting and desiccation processes (beginning in whether this period).

Various areas of excrement, have seen that between strict biology of the some other species is common. It seems to possess a similar purpose for this purpose with which show a similar.

Fabre attests that the only is clearly preferred (1943:239) and...
although it is not particularly attractive. The probable im-
impact of the land 

Goidanich from 

A similar 

Goidanich from 

and 

B. oblonyus 

Onthophagus 

mucus and other 

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and 

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must be 

and Paulian (1943:239) claims that Scarabaeus affinis Brulle, which as an adult feeds therefore liquid dung deposited in a sunny location will become available to Scarabaeini sooner than that deposited in the shade. On the other hand, in dry climates especially, dung deposited in the shade will be exploitable for a longer time than that deposited in the sun. In other words, while Scarabaeinae are critically influenced by the climatic factors of the biome (as we will see in the next chapter), the microclimatic factors around the food deposit itself are of importance only in regard to the timing, and duration, of exploitability of the food.

Of equal or perhaps greater importance is the original consistency of the dung. Excessive hardness is probably the factor which eliminates certain types of dung as food for any kind of dung beetles. Small pellets of rabbits and goats may be thus eliminated if they are deposited in a scattered manner (not in piles), and so quickly lose what little moisture they had. Cow dung in unusually dry pastures may have very little moisture content even at the moment of deposition. Horse dung, always relatively hard because of its high straw content, is often not exploitable for this reason.

No adult Scarabaeinae are known to have mouthparts capable of chewing or cutting solid food. Hence a point is reached during the desiccation process of dung when it becomes unavailable to the beetles (beginning in the outer layers). The factors mentioned above determine whether this point will come sooner or later.

**Excrement Used for Nidification**

Various authors have pointed out that species use a narrower range of excrement types for nidification than for adult feeding. We have seen that in their adult feeding Scarabaeinae may range anywhere between strict stenophagy (usually accompanied by other factors in the biology of the animal, such as life in mammal nests or an adaptation to some other specialized niche) and broad euryphagy, the latter being more common. It seems that in the selection of excrement for nidification purposes a similar situation occurs. There are species which seem to use for this purpose whatever type of excrement is eaten by the adult, and others which show a greater specificity, using only certain kinds of excrement.

Fabre attached great importance to sheep dung, believing that it is clearly preferred for nidification by the Scarabaeinae of France. Paulian (1943:239) claims that Scarabaeus affinis Brulle, which as an adult feeds
on horse and cow dung, does not use anything other than sheep dung for nidification (in France). *Scarabaeus sacer* Linnaeus, *latillicollis* Linnaeus, *semipunctatus* Fabricius, and *variolosus* Fabricius always use sheep dung preferentially for making the brood ball, according to Heymons and von Lengerken (1929:585). However, the same authors note that it was possible to force a female to make its brood ball of cow dung, and in some areas where there are no sheep, other dung must be used; for instance, *S. puncticollis* Latreille uses camel dung, *S. semipunctatus* frequently uses human excrement (Gogio, 1926:43). It seems probable that many of the other species of *Scarabaeus* also use it for the brood ball.

Other authors after Fahre have seen that *S. sacer* uses any kind of excrement for nidification, including human. In Corsica, it makes its food balls with mule dung and its brood balls with goat dung (Gogio, 1927:43). In Turkmenia it uses cow dung (Medvedev and Medvedev, 1958:91). Siyazov (1913:119) believed that Fabre's enthusiasm for sheep dung was excessive. In Uzbekistan, according to this author, *Copris hispanus* (Linnaeus) (another species studied by Fabre) uses cow dung predominantly, and occasionally that of horses. In Dalmatia Spaney observed the construction of brood balls from cow dung by this species (von Lengerken, 1954:333), although undoubtedly sheep dung is normally used.

When analyzing the factors which determine the selection of a certain type of excrement in the preparation of the nest, it is best to discard the imaginative element which often predominates in isolated observations and to try to bring in ecological criteria. On considering the literature data summarized above, and judging from our own general experience, we can deduce that Fabre was right in stating that the species he studied used sheep dung for nidification, but that his critics were also right in affirming that other types of excrement can also be used for the same purpose. It is evident, although sometimes overlooked, that a given scarabaeine lives in a certain ecological environment (in the case of the *Scarabaeus* and *Copris* studied, the Palaeartic grasslands) which, although constant in its major characteristics, varies geographically. That is to say, the mammals of France and of Uzbekistan are not completely the same either in numbers or composition, even though the same species of *Scarabaeus* and *Copris* are found in both places, and the types of excrement will therefore not be completely comparable. We can therefore generally expect the species to vary (some species). This is supported by the results obtained by Silvani, as well as with Fabre.

Many Scarabaeidae (the most common and widespread is the Brazilian *Copris hispanus*, the Argentine *C. puncticollis* and many other habits of most of the other species of *Scarabaeidae*).

We do not confine ourselves to coprophagous habits, but also to those with one or the other, and so it may be worth noting that the scale of Coleoptera is essentially one of modern times and that, except for the habits with coprophagous habits, they are found in various places and in areas with the Old World or a little South America.
Generally expect considerable local variation in this matter (in euryphagous species). This variation is to be expected and is a poor basis for criticizing the results obtained by another author in another area (as has been done with Fabre).

2. Necrophy

Many South American Scarabaeinae are necrophagous. In the rest of the world, according to the literature data, only in India and only in one genus — Onthophagus — do we encounter numerous examples of carrion feeding. Elsewhere the incidence of necrophy is occasional and unimportant. It must be emphasized that our information contains several gaps, the most important of which concerns the biology of the Scarabaeinae of Australia and Southeast Asia.

From South America we have numerous and fairly complete data (the most complete for a tropical area), thanks largely to two investigators — the Brazilian Hermann Luederwaldt, a pioneer in these studies, and the Argentine Antonio Martínez, who in various works mentions the feeding habits of most of the species, particularly in his "Catálogo de los Scarabaeidae argentinos" (1959).

We do not believe that necrophy as a diet is basically different from coprophagy. The fact that within some genera there are species with one or the other of these diets, and that even the same species may be both coprophagous and necrophagous, even in the same locality, tends to show that the differences between the two types of feeding are not basic, but are rather the result of local or regional ecological factors, such as a scarcity of large herbivores or a reduced importance of other groups of Coleoptera which are more strictly necrophagous. Both these conditions are found in South America, as we have already noted in connection with coprophagy. Necrophy is evidently more important in the tropics, and in areas with large expanses of forest where large herbivores are few.
typically Neotropical parts of South America (that is, excluding the Chilean Subregion, which comprises Chile and the southern parts of the Andes and Tierra del Fuego) the Coleoptera which feed on cadavers are largely Scarabaeinae, not Silphidae. Even though Silphidae exist, their ecological role is of minor importance in comparison with that of the Scarabaeinae. Furthermore, as far as we know, only in the Neotropical Region (and among the Neotropical elements of North America) do the Scarabaeinae normally use carrion or other forms of animal remains for the purposes of nidification (that is, for larval food).

The following is a survey of necrophagy among South American Scarabaeinae, presented in taxonomic order.

The Eucraniina are exclusively coprophagous.

In the Eury sternina Eury sternus impressicollis Laporte is cited as a necrophage by Luederwaldt (1910 [1911]:420). However, the genus as a whole is coprophagous.

In the Canthonina, 1 a subtribe very important in numbers and variety on the American continent, there are coprophagous species, species which are predominantly coprophagous and occasionally necrophagous, species indiscriminately copro-or necrophagous, species predominantly necrophagous, and species exclusively necrophagous. This gradual variation in food preferences, which is also seen in Dichotomina and Phanaeina, is an argument in favor of our supposition that there is no basic difference between the two types of feeding, rather a local or regional response to environmental conditions.

The genus Malagoniella (the old Megathopa in part) includes species with both types of feeding. M. argentina (Gillet) is copro-necrophagous, as is M. p. puncticollis (Blanchard). On the other hand, M. bicolor (Guérin) and M. violacea (Blanchard) are exclusively coprophagous.

M. punctatostriata, according to Malagoniella, Argentine entomologist Malagoniella a. Poppe (1899: 377). M. punctatostriata is copro-necrophagous: (recent and in April. Harold, collected from the first mentioned. Harold, collected from the first from the first from the first from the first places of Buenos Aires: C. quinquemaculatus to C. curvoldilatata: C. podagrificus Harold. 26
that is, excluding the southern parts of which feed on cadavers (in Silphidae exist, their inclusion with that of the exclusively in the Neotropical area do the feeding on animal remains for which animal remains for long South American Laporte is cited as a local or regional endemic. However, the genus as a whole is not exclusive to the interior of the tropical forest. During several successive nights it came in numbers to traps baited with human excrement, without ever coming to baits of carrion or small dead animals placed in the same area under the same conditions. This is therefore an exclusively coprophagous species.

The genus Canthon is coprophagous in the United States and Mexico, although there are some occasional and exceptional citations of attraction to carrion in C. pilularius (Linnaeus) (Lindquist, 1935: 8). C. imitator Brown, and C. indigaceus chevrolatti Harold (Halfter, 1959). These incidences of necrophagy are isolated and must be weighed against thousands of specimens collected in excrement, principally that of cow and horse.

One species of Mexico and Central America, Canthon c. cyanellus Leconte (which also reaches Texas in a typical Neotropical distribution), is copro-necrophagous — exclusively necrophagous in the areas of tropical evergreen forest in the south of Mexico.

In South America necrophagy is almost as important as coprophagy in the genus Canthon (more important in the forest zones). Luederwaldt (1910 [1911]: 1916) found the following species in dead animals: C. tristis Harold, curvipes Harold, septemmaculatus Latreille, conformis Harold, podagricus Harold, rutilans Laporte, and dives Harold. C. carbonarius Harold has also been found in carrion (Kolbe, 1905). C. bipinus Germar uses both carrion and excrement to make its brood balls (Judulien, 1899: 377). Martínez (1959) cites the following Argentine species as necrophagous: C. conformis Harold, which is found on cadavers both recent and in an advanced state of decomposition, and also on excrement from the first moments of deposition to when it is almost dry; C. curvipes Harold, collected on dead fish washed up by the tides on the beaches of Buenos Aires Province, and also on excrement, preferably human; C. quinquemaculatus Laporte, frequent on cadavers soon after death; C. curvolutatus Schmidt, C. bipinus Germar, C. mutabilis Lucas, C. podagricus Harold, C. seminitens Harold, and C. velutinus Harold, all

*M. punctatostris* (Blanchard) has been found in cadavers (all data according to Martínez, 1959). One of us (Halfter), together with the Argentine entomologist Prof. Antonio Martínez, had occasion to observe *Malagoniella a. yucateca* (Harold) for various days in the extreme south of the Mexican state of Chiapas. This is a nocturnal species, exclusive to the interior of the tropical forest. During several successive nights it came in numbers to traps baited with human excrement, without ever coming to baits of carrion or small dead animals placed in the same area under the same conditions. This is therefore an exclusively coprophagous species.
found on cadavers of small animals: C. divus Harold, C. klecandai Balthasar, C. lividus (Blanchard), C. pseudoforcipatus Balthasar, and C. septemmaculatus Latreille, all copro-necrophagous, and C. ornatus Redtenbacher, very frequent on excrement but also found on cadavers. As in Malagnostra, the species of Canthon, except when specified to the contrary, were all captured on recent cadavers, during the first few hours of decay.

The genus Deltochilum is fundamentally necrophagous, even though a few species are copro-necrophagous, and one — D. (Rubrohyboma) rubripenne Gory — is coprophagous (Martínez, 1959). Furthermore, it seems that the species of the scabriusculum group are coprophagous, according to the observations of Henry F. Howden (in litt.) and G. Halffter. The species which ranges furthest to the north, entering the United States — D. gibbosum (Fabricius) — is attracted by feathers, dead animals, and hairs, and makes its brood balls out of feathers. It has only occasionally been collected on human excrement or in traps baited with decaying fungi. In South America Deltochilum has even been captured on fairly dry bones and tendons, and in garbage dumps where there are animal remains. Deltochilum, like most of the South American necrophagous Scarabaeinae, predominates in the interior of forest or other wooded areas; furthermore, as in many other necrophagous genera, most of the species are nocturnal.

There are records of necrophagy even in fundamentally coprophagous canthine genera such as Borocanthon and Glaphyrocanthon. Borocanthon lecontei (Harold) has been collected in carrion baits in the United States (Lindquist, 1935:8). Glaphyrocanthon coeruleicollis (Blanchard) on a dead fish on a bank of the River Plate, and G. simulans Martínez in a trap baited with decaying meat in Espiritu Santo, Brazil (Martínez, Halffter, and Halffter, 1964). Another canthonine, Ipselius altarengai Pereira and Martínez has been collected inside a forest (Espiritu Santo) in traps baited with dead fish and chicken entrails (Pereira and Martínez, 1963:6).

Among the American Copris, of Palaearctic origin and not penetrating extensively into the Neotropics, has been collected only a few times in carrion, according to the literature data. Lindquist (1935) cites Copris r. remotus Leconte in this connection, the species being normally a cow-dung feeder. Blatchley (1918) cites C. intermarginatus Blatchley under C. laeviceps Harold, and authors have collected D. ascensus in cadaver baits, but no coprophagous, higher.

Also of Palaeartic, captured collected on carrion or less often on excrement in shorter.

With the examples of Copris necrophagy is common in South America. Pedaridium inclinatum (Martínez, 1959). In the South American mycetophagous. Pedaridium inclinatum collected on cadavers: the author obtained C. augustus in Brazil. In one skeleton of a Canthon, Ateneus, Aurotaenius, and Dichotomius.

Two species: Ateuthus martinezi Pereira and Ateuthus brasiliensis to Luaderwaldt. Ateuthus pauperi is a coprophagous genus. The larvae of forests (Perry 1914:365-366) a species: D. ascius (Fabricius)
Harold. C. klecandai Blatchley and C. ornatus Harold, and C. ornatus Harold, were found on cadavers. except when specified to the contrary, during the first few days of decomposition.

Coprophagous, even though necrophagous, C. ornatus Harold (in litt.) and G. laticollis (Bates) — is attracted to the broad balls out of which dung is formed from human excrement (Luederwaldt 1910 [1911]:419). Furthermore, it is often necrophagous. However, it seem that in South America Deltochilum has been more restricted to cadavers, and in garbage piles, where it is likely that the maggots in the interior of the garbage will be eaten by many other necrophagous species according to Luederwaldt (loc. cit.)

Necrophagous-Pedaredrmm, Boreocorinella, and Myceto-corinella bait in the United States (Perty). C. ornatus is necrophagous—fed inside a forest (Eisenberg et al. 1988). C. ornatus Harold has been collected on carrion and in cadavers; the last-mentioned species belongs to a fundamentally coprophagous genus.

Pedicellina (formerly Pedaredrmm) is an almost exclusively coprophagous genus. Nevertheless, D. triangulariceps (Blanchard). a coprophagous species, may come to well-decomposed cadavers (Martinez 1959). D. glauces Harold has been found in cadavers in the interior of forests (Perty, cited in Kolbe, 1905:492). Luederwaldt (1910 [1911]:1914:365-366) cites the following species as occasionally necrophagous: D. ascanius (Harold), lacunosoides Luederwaldt (cited as mundus luederwaldti).
(Harold) and semiacaeus (Germar). Henry F. Howden (in litt.) found
D. amplicollis (Harold) in a dead rabbit.

In the Phanaeina. Boltites and Gromphas seem to be exclusively
coprophagous. Taurocopris mimas (Linnaeus) has been collected on fresh
human excrement. In the genus Phanaeus. there are feeding differences
among the different subgenera. Megaphanaeus includes species which
are exclusively necrophagous.\(^1\) feeding and nidificating from recent
cadavers. They are also largely nocturnal. Martinez (1959:98) has the
following to say in relation to this subgenus: 'The large species can
inter a small or medium-sized animal after one night's work. For instance.
four Phanaeus (Megaphanaeus) ensifer Germar buried the carcass
of a dog weighing 10 kg in one night.' Ph. (M.) bonarensis Gory shows
a certain preference for the cadavers of birds (Martinez, 1959).

The subgenus Coprophanaeas includes a large majority of necro-
phagous species which come to recent cadavers and which are perhaps
always nocturnal. Necrophagy has been demonstrated for Ph. (C.)
jasus (Olivier) (Ph. [C.I cyanescens Obsouiffi (Martinez, 1950:
200; Pereira and Martinez, 1956:231; Martinez, 1959), the three sub-
species of Ph. (C.) telamon Ericson: igniceterus Felsche, telamon
Ericson (Pereira and Martinez, 1956:233-234), and corvhus Harold
(authors' observations), and for Ph. (C.) phato Harold (H. F. Howden.
in litt.). The necrophagy of Ph. (C.) milon Blanchard is well known
since Fabre's time; this species uses dead birds or small mammals for
preparing the brood ball and for adult feeding.

In the subgenus Metallophanaeas. Ph. (M.) horus Waterhouse is
exclusively necrophagous, while Ph. (M.) saphirinus Sturm is exclusively
coprophagous, being attracted principally to the dung of herbivores
(as is the case with most exclusively coprophagous South American
Scarabaeinae).

In the subgenus Phanaeus s. str. the coprophagous species predomi-
nate. All the North American ones, including those of the Mexican
Plateau, are coprophagous, although Ph. triangularis Say has been
captured in carrion baits. In Central and South America there are
coprophagous species which quickly come to human excrement; cf
1961, personal observations. Like Ph. meleagris (Martinez, in litt.)
and Ph. (M.) melanocephalus (Pereira and Martínez, 1955).

The Jamaican species O. acuminata (Linnaeus) seemed to feed on cow
dung.

In the Onthophaginae, the feeding habits of the species are largely
to the recent remains of vertebrates, and of normally coprophagous
vegetable matter. Ph. (M.) Harold, a northern species (Halffter) in the
coprophagous habits of the species: O. hirsutus Harold, a norte
wald, 1910 [1915].

Feeding on carrion is common in South America. Harold on dead
conformis Harold in dead and dry
1911:424).

After South America, the most important in the Scarabaeinae are the
coprophagous Onthophagus Boucomont: in Central America only in this manner
apparent
found them to be exclusively coprophagous, having been collected on fresh cow dung. Due to feeding differences it is not always easy to elude species which are deeding from recent cadavers. The large species can come to carrion, as Howden (in litt.) found (1959:99) has the large species of the subgenus Sulcophanaeus (C. J. Howden, 1959). The majority of necrophagous species which are perhaps under-rated for Ph. (C.) magellanicus (Howden, 1959), the three subgenera Felsche, elamona and corinthus Harold (H. F. Howden, 1959) and Richard is well known for its feeding on small mammals for example Euphoria Waterhouse is an exception. Sturm is exclusively a coprophagous species predomi-
nating in South American feeding on dead arthropods is a special type of necrophagous species predominating in the Mexican region. Haris Say has been found in South America there are coprophagous species like Ph. chalcomelas Perty, a diurnal species which quickly comes to human feces in the Amazon forest (F. S. Pereira, 1961, personal communication). but there are also necrophagous species like Ph. melangris Blanchard, collected in recent cadavers of birds (Martinez, in litt.) and Ph. bispinus Bates (= Ph. digitalis Olsoufieff) (Pereira and Martinez, 1956:237).

The Jamaican species of the subgenus Sulcophanaeus (carnifex Linnaeus) seems to be exclusively coprophagous, coming abundantly to cow dung.

In the Onthophagini, we have some very satisfactory information on the species of Onthophagus of the United States and Canada, thanks to the recent revision of Howden and Cartwright (1963). When the species are extensively and carefully collected, it is found that a number of normally coprophagous species may also come to carrion and decaying vegetable matter (especially melon rinds). In Mexico, O. chevrotianus Harold, a normally coprophagous species, was collected by one of us (Halffter) in traps baited with decaying fish. In South America, necrophagous habits have been cited for only two normally coprophagous species: O. hirculus Mannerheim and O. bidentatus Drapiez (Luederwaldt, 1910 [1911]:420).

Feeding on dead arthropods is a special type of necrophagy. In South America, we have the following records of this: Canthon aberrans Harold on dead passalids (Pereira and Martinez, 1956:93); Canthon conformis Harold on a dead bee, and Deltochilum signatum (rolling a dead and dry diplopod (the last two records from Luederwaldt, 1910 [1911]:424).

After South America, India is the area where necrophagy is most important in the Scarabaeinae. Most of the records from India and Ceylon refer to Onthophagus, the rest to other Onthophagini. The following is a list of records of necrophagy, all taken from Arrow (1931): in dead lizards: Caccobius meridianalis Boucomont, C. indicus Harold, Onthophagus igneus Vigors, O. pugnax Schaller, and O. farrei Boucomont; in carrion: O. necrophagus Arrow, O. vividus Arrow (found only in this medium, according to M. J. Walhouse, 1861). O. quaeetus Sharp (also collected in a dead crab), O. amicus Gillet, and O. parvicolis

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1 Apparently not a valid name.
Arrow; under a dead bat O. lilliputianus Lansberge; and in a dead rat one specimen of O. bifasciatus Fabricius. The latter species, together with O. unifasciatus Schaller, is the principal cause of scarabasis in India (see Endoparasites of Mammals). It is interesting to note that most of the necrophagous species are from South India and Ceylon, the most tropical parts of the subcontinent.

There are also several records of Scarabaeinae attacking dead arthropods in India, again according to Arrow (1931). All records refer to the genus Onthophagus, as follows: O. bifasciatus Fabricius (already mentioned as a necrophage), O. victor Arrow, O. hindu Arrow (also a carrion eater), O. unifasciatus Schaller (cause of scarabasis and also collected in dead lizards), and O. malabarensis Boucomont. All have been found eating dead locusts.

Of particular interest is the attraction of Onthophagini for carrion-scented flowers. Coccobius diminutivus Walker and Onthophagus tarandus Fabricius have been collected in Calcutta on flowers of this type (Tiphonium tribulatum). These beetles act as pollinating agents, and their attraction to carrion-scented flowers presupposes necrophagous habits. Arrow (1931:182) quotes the description of this scarab-flower relationship given by Maude Cleghorn (Jour. Asiat. Soc. Bengal 10:421, 1914): "On examining a spathe at sundown, when the strong unpleasant odour is being given off, it will be found that the narrow constricted part is open, forming a passage down into the lower chamber. Where the pistillate and threadlike neuter flowers are concealed ... At this, the first stage, the stigmas are very sticky, and the strong carrion-like odour is off from the pistillate flowers, but the staminate flowers will be found to be still immature, with no pollen shed ... On cutting open the tube of a spathe in the second stage, when the passage is tightly closed, a number of small brown lamellicorn beetles ... will be found imprisoned inside ... It is clear that the floral mechanism of the spathe is of the nature of a trap, and by this ingenious method the plant ensures cross-pollination, for the beetles carry the pollen from one spathe to another ... The beetles remain among the pistillate flowers during their term of imprisonment in the second stage, and by the evening, when the spathe has re-opened in its third and last stage, the beetles are most anxious to make good their escape, and soon crawl up the mouth of the tube and up the lower staminate portion of the spadix, and so become covered with pollen before flying away, only to be deceived and recaptured by another spathe in the first stage of the flower, with the pollen covering the stigmas and thus ensuring reproduction.

Mecuse and calla lilies, in the United States from South Africa and according to Arrow (1931:588) to whom at one time Silphia americana (Linnaeus) was ascribed the carrion-flower habit. Arrow (1931:588) states that the female of Onthophagus celer (O. detersus Perrier) and O. herus Perrier are coprophagous and necrophagous, but necrophagous only.

In Europe, necrophagous scarabaeids are generally coprophagous. Fabris (1931:425) states that all the scarabaeids in Europe are coprophagous and necrophagous. He considers Scarabaeus sacer and Scarabaeus rufus as carrion eaters. According to whom at one time (Linnaeus) and Gmelin (1791) the latter also feeds on dead myriapods.

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In a dead rat or other species, together with the use of scarabaeis in
India and Ceylon. It is interesting to note that both India and Ceylon.

Onthophagini for carrion-

Onthophagus tarandus
flowers of this type in adults. The larvae of this scarab-flower
(Soc. Benga! 10:421).

Onthophagus praestans Péringuey has been collected on
dead myriapods found in the soil after rains (Péringuey, 1901, cited by
Kolbe. 1905:588). while another species of the genus is attracted
by dead snails (Arrow, 1931:160). According to Kolbe (1905:588)
various species of Onthophagus eat carrion in Africa. as follows: O. auriculatus Klug,
O. ditterrens Péringuey, O. ditus Péringuey, O. hagens Fabricius, and
O. heras Péringuey. It is not known what the larvae eat and whether
carrion is only occasional in the adults or not.

In Europe. necrophagy occurs occasionally in species which are nor-
mally coprophagous. Paulian (1938:226) says: "En effet les Copro-
phages européens dont les larves sont exclusivement coprophages. sont
fréquemment attirés par les cadavres. J'ai ainsi capturé en nombre
Onthophagus lucaratus, Sisyphus schaefferi, Gymnopleurus flagellatus, et
Scarabaeus sacer dans les pièges appâtés avec des cadavres de poisson
et destins à la capture de Nécrophages. ..." The observations of Paulian
do not coincide with the experiments made by Prasse (1957:a:440). according
to whom attraction to carrion was minimal for Sisyphus schaefferi
(Linnaeus) and Gymnopleurus geoffroyi Füeussly, which only approach
it after several days without any other type of food. However. Panin
(1957:62) cites Sisyphus schaefferi from both excrement and cadavers.
and according to Balthasar (1963[1]:210) Gymnopleurus mopsus Pallas.
a coprophagous species, is found occasionally on small dead reptiles and
mammals. The differences between the reports of these authors demon-
strate once again the different local modifications shown by a species in
its response to differing conditions. As is the case with the euryphagous
coprophages. which may vary in preferences according to local oppor-

spathe in the first stage. While among the pistillate flowers of the fresh
spathe the pollen with which they are covered adheres to the sticky
stigmas and thus cross-pollination is readily effected."

Meeuse and Hatch (1960) discuss pollination by beetles in arum
and calla lilies, including Dracunculus vulgaris Schott introduced to
the United States from the Mediterranean. No Scarabaeidae have been
recorded from these flowers in the United States, but the authors cite
a Swedish source who records two species of Onthophagus from Arum
dioscoridis in Lebanon. These are O. oculatus (Linnaeus) and O. sellatus
Klug.

Outside of South America and India, necrophagy is much rarer. In
South Africa. Onthophagus praestans Péringuey has been collected on
dead myriapods found in the soil after rains (Péringuey, 1901, cited by
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fréquemment attirés par les cadavres. J'ai ainsi capturé en nombre
Onthophagus lucaratus, Sisyphus schaefferi, Gymnopleurus flagellatus, et
Scarabaeus sacer dans les pièges appâtés avec des cadavres de poisson
et destins à la capture de Nécrophages. ..." The observations of Paulian
do not coincide with the experiments made by Prasse (1957:a:440). according
to whom attraction to carrion was minimal for Sisyphus schaefferi
(Linnaeus) and Gymnopleurus geoffroyi Füeussly, which only approach
it after several days without any other type of food. However. Panin
(1957:62) cites Sisyphus schaefferi from both excrement and cadavers.
and according to Balthasar (1963[1]:210) Gymnopleurus mopsus Pallas,
a coprophagous species, is found occasionally on small dead reptiles and
mammals. The differences between the reports of these authors demon-
strate once again the different local modifications shown by a species in
its response to differing conditions. As is the case with the euryphagous
coprophages. which may vary in preferences according to local oppor-

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tunities, there are euryphagous copro-necrophagous species whose presence or absence in cadavers depends on local ecological conditions.

Kolbe (1905:493) cites the two following coprophagous species as the only ones which occasionally come to cadavers: *Onthophagus oratus* (Linnaeus) (previously cited here in connection with carrion-scented flowers) and *O. coenobita* Herbst. To these species we must add the ones mentioned in the above paragraph, and another *Onthophagus*: *O. tracticornis* Preysler, which may be found in cadavers according to Panin (1957:93). Von Lengerken (1954:205) says it is not unusual to find species of *Onthophagus* near large or small cadavers, e.g. *O. tracticornis*, which has been collected in small dead animals. The carrion is not used for nidification, according to von Lengerken (loc. cit.).

Occasional adult necrophagy in the genus *Scarabaeus* has been previously discussed (p. 15-16). On the whole, it may be seen from the above that in Europe necrophagy is only occasional, though latent in many species, and limited to the adult.

3. Saprophygy

Saprophygy in the Scarabaeinae is of two different types, each of very different evolutionary significance. The most primitive type—living in decaying leaves and other vegetable detritus and probably feeding on the latter—may be seen in various groups of the family Scarabaeidae. In the Scarabaeinae the known examples are relatively scarce and their true significance is not clearly understood. They generally belong to primitive genera, usually tropical and forest inhabiting.

Much more frequently seen is the consumption of decaying fruits or other soft vegetable matter. The known examples are tropical and mostly from inside forests. This type of feeding is closely related to coprophagy, from which it appears to have been derived, since the known examples are isolated species within coprophagous or copro-necrophagous genera. The same may be said for mycetophagy, since what is normally eaten is not live fungi but more or less decayed ones. Many of the instances of mycetophagy refer to species which are normally coprophagous.

A very specialized type of saprophygy is the consumption of the debris which accumulates in the nests of *Atta* and other genera of ants. These examples will be dealt with in the section on myrmecophily.
The myrmecophilous species whose preference has been determined

...coprophagous species as can be seen from the above examples. For example, the South African species of *Epilissus* (*E. subtilis* Boheman) is found in decomposing vegetable matter, the other species of the genus being coprophagous. *Odontoloma* is also found in decaying vegetable matter (Janssens, 1938:4). Both *Epilissus* and *Odontoloma* are very small canthonines. On the island of Guadeloupe, another canthonine—*Opioanthone vittatus* (Fleutiaux and Sallé)—has been collected in humid vegetable debris (Fleutiaux and Sallé, 1889:394), but the results of the systematic collecting done by Matthews indicate that the species is coprophagous.

According to Arrow (1931:405) *Pancelus parvulum* Waterhouse is common under dead leaves in Japan. Lea (1923:361) cites three specimens of *Pancelus bidentatus* Wilson from the same habitat in Australia. Another species—*P. pisoni* Lea of Australia—is found abundantly in the damaged seeds of *Pisonia brunoniana* (Lea, 1923:361) and finally *P. tonkinensis* Paulian has been captured on rat feces (Paulian, 1945:56). We do not know for certain what is eaten by the species of *Pancelus* collected in leaf litter, just as we do not know this for the other similar examples cited in this section. It could be decaying plant debris, but it could also be small pieces of excrement, such as that of rodents and snails, or it could be carrion, as we are, as is the results obtained by Kammura, Nakane, and Kovana (1964) for *Pancelus parvulum* in Japan. It must be recalled that *Pancelus*, like the other Scarabaeidae collected in leaf litter, are among the smallest forms of the group, being only a few millimeters long.

*Haroldius perrotii* Paulian, a species belonging to a markedly myrmecophilous genus, has been collected sifting leaves (Paulian, 1945:59).

*Uroxyx virgenci* Arrow has been collected under debris near the sea, on St. Vincent (Lesser Antilles) (Arrow, 1903:510), however, the species is clearly coprophagous, according to recent collecting by Matthews. We know very little of the biology of other species of *Uroxyx*, but in general they seem to be copro-necrophagous.

In Brazil, in the humus which accumulates in the bases of bromeliads, Ohaus (1909:26) found *Bdeleyrus* sp. (cited as *Aphengium semenulum* Bates). In the Floresta de Tijuca (Rio de Janeiro), *Bdeleyrus*

Species which Live in Leaf-Litter or Other Vegetable Debris

...The carrion is not usually used by the other genera of *Onthophagus*: *O. arboreus* is found in termites. Ecíes...
lagopus Harold (probably the same species) was found in great quantity in epiphytic bromeliads, at a height of a few meters (Pereira, Vulcano, and Martínez, 1960; Pereira and Halffter, 1961:64). According to F. S. Pereira (in litt.), "In Amazonia, where bromeliads are very scarce, the genus Bdelyrus is found in quantity at the base of the petioles of the leaves of small palms, where a large quantity of decomposing organic matter accumulates." Even though the bromeliads of the South American forests form a complex biocenose, from which more than 30 species of animals have been described (mostly arthropods) and which, therefore, may provide small pieces of excrement, the species of Bdelyrus mentioned above are more likely to be truly saprophagous than any other known Scarabaeeinae.

Arrow (1931:332-333) cites Onthophagus deflexicollis Lansberge from detritus accumulated beneath the sheaths of bamboo stems in Sumatra. This citation must be included with those of species collected in leaf litter or debris — the actual food is unknown. According to Howden and Cartwright (1963:75) "Brown (1926) found Onthophagus subaeneus (carnivorus) in moist woodlands and postulated that the species might feed on decaying organic matter on the floor of woodlands. It was collected by sifting debris from the ground in moist woods. It has been taken in early spring (February) at Florence, S. C. in sifting woods trash for hibernating boll weevils. It has also been taken at fungí in carrion, under the dung of various animals, and even under chicken manure." It is not without significance that Sim (1930:141) notes that this species has always been collected under rabbit feces. Until careful studies are made we will not know whether these forest-floor species feed on humus (decomposing vegetable matter) or the excrement of small animals.

Species Collected on Fruits or Other Parts of Decaying Plants

As previously mentioned, species in this category generally belong to coprophagous genera or are themselves coprophagous. In the Neotropical Region, especially in the tropical forest, there are numerous examples of this type of saprophagy.

In Paraná, Brazil, in mature fruits of "Butia", Pereira and Martínez (1956:93) cite the presence of large numbers of Canthon lituratus (Ger-
found in great quantity in bamboo stems in the Neotropical region. According to F. S. Pereira and Martínez (1956:93), there are very scarce. the petioles of the leaves decomposing organic matter (Pereira and Halffter, 1961:63). In Brazil, Canthis has not been collected much in excrement; it is more frequent in fruits, such as those of Butia already mentioned or papaya and others (Pereira and Halffter, 1961:64).

Deltochilum sericeum Paulian and Geocanthon rubrescens (Blanchard) were collected in Bolivia, in large numbers, in recently cut "palmitos" (the tender inside part of palm shoots) (Pereira and Martínez, 1956:93). Also found in these palm shoots were Onthophagus ophion Erichson, O. digitifer Boucomont, and Canthidium cupreum Blanchard (Pereira and Halffter, 1961:64). Luederwaldt (1916:293) found Gonocanthon smaragdulas (Fabricius) (=Canthon speculifer La porte) in a fallen palm shoot; this is strictly a forest canthonine. More examples are provided by Pereira and Martínez (1956:93), who collected Peltecanthon stagi Pereira and Canthon quinquemaculatus Laporte in Brazil on a recently cut liana, the insects being attracted by a fetid odor given off by the liana. In the same liana Chalcocopris hesperus (Olivier) was also collected (Pereira and Halffter, 1961:64).

Ateuchus illaeus (Harold) was collected in St. Vincent, Grenada, and Mustique (Lesser Antilles), where it is abundant, in fallen fruits and other plant debris (Arroyo, 1903:509). However, the same species is found in cow dung in Martinique (Matthews). Dichotomius ascansus (Harold), a coprophagous and occasionally necrophagous species, sometimes feeds on decaying fruits, such as guava and pineapple (Luederwaldt, 1914:365; 1929:6). The subspecies D. a. piceus (Luederwaldt), common in dung, was found attacking coffee beans in the north of Parana, Brazil (Pereira and Halffter, 1961:63). Finally, Dichotomius glaucus (Harold), cited as a necrophage, was found several times in the pericarp of the fruits of certain Palmaeae (Luederwaldt, 1931).

Copris lugubris Boheman, a coprophagous Central American species with a Neotropical distribution, has been collected in traps baited with fermenting banana and decaying avocado (Matthews, 1961:52). In New Mexico, Phanaeus vindex McLeay, normally a coprophagous species, may have saprophagous habits: "The adults damage ripening peaches, plums,

mar). C. scrutator paraguayanus Balthasar, C. opacus Lucas, C. latipes Blanchard, C. conformis Harold, C. muticus Harold, and C. angularis Harold. In these same ripe Butia fruits the following were also found: Canthis decoratsum Perry, C. barbacenicum Preudhomme, C. splendidum Preudhomme, and C. nobilis Harold (Pereira and Halffter, 1961:63). In Brazil, Canthis has not been collected much in excrement; it is more frequent in fruits, such as those of Butia already mentioned or papaya and others (Pereira and Halffter, 1961:64).

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and other fruits and also feed on the tassels of corn" (Essig, 1926 [1952]:439).

The Scarabaeinae mentioned up to now are largely coprophagous and their presence in the succulent parts of plants is undoubtedly due to the state of fermentation of the latter. The line between this type of saprophygy and coprophagy is tenuous, and in the tropical forest of South America it is common to see a euryphagy including both these types of feeding.

In the Australian region Onthophagus and possibly Saphobius live on decaying fruits and leaves (Lea, Broun, and Montrouzier, cited in Paulian, 1934:277-278). One specimen of Monoliturgus tropicus Lea has been collected in damaged seeds of Pisonia brunoniana (Lea, 1923:360). African Gyronatus have been found in rotten fruits (Kolbe, cited in Paulian, 1934:276). Paragynoplia postica (Olivier) var. assamensis Waterhouse, of the Himalayas, has been collected in the same medium (Arrow, 1931:64).

In the genus Onthophagus there are numerous examples of saprophygy, most occurring in tropical and forested regions. In rotten papaya (fruit or stalk) various species of Onthophagus have been collected in India (Arrow, 1931), as follows: O. daparti Boucomont, O. coorgensis Arrow, and O. ramosellus Bates. In Assam, various specimens of O. fragorius Arrow have been collected in rotten fruit. (Arrow, loc. cit.). Many specimens of O. asperipennis d'Orbigny and O. garambae Frey were collected in thoroughly rotten tree trunks in the rain forest of the Garumba National Park, Congo (Frey, 1961:74).

In the United States, where the Onthophagus fauna has been carefully collected and studied by Howden and Cartwright (1963), there are records of several species found in decaying melon rinds, in the South. These Onthophagus were all also collected in human or cow excrement (they are therefore euryphagous coprophages) and also sometimes in fermenting banana and malt traps, and one species (O. pennsylvanicus Harold) in carrion. The species involved are O. medorensis Brown, O. oklahomensis Brown, O. landolti texanus Schaeffer, and O. pennsylvanicus Harold. The adults of these four species are strongly euryphagous, but for nidification they use only cow dung (in the known cases).

There are records of Onthophagus in the United States in the United States under decaying melon rinds, in Veracruz, in the interior of Veracruz, with occasional feeding on carrion.

There is a mention that there are species in the southwestern United States of saprophygy, living in the interior of the fruit, into which preserved insects are placed, such as Onthophagus in Guatemala in the United States. In the extreme north of the United States, where there are species of Onthophagus and O. coorgensis, this species in particular, is a coprophagous species in a decaying tree stump. These species are found on the surface. This is also true of a few species of Onthophagus found in its forested regions.

In the same forested regions, a few species of Onthophagus are found in the interior of tree trunks, as well as a few specimens of Onthophagus (Pereira and Montrouzier, cited in Paulian, 1934:277-278). These species were feeding on the surface of the tree stump, and could not be identified by the fact that they occurred in the interior of the tree. A few specimens of O. carpopus Harold and O. peninsularinus were collected under...
largely coprophagous is undoubtedly due to the tropical forest of the rain forest of the

There are other known instances of saprophagy in the genus Onthophagus in the Neotropical Region. Halfflter collected Onthophagus sp. under decaying Yucca (which they were eating) in the mountains of Veracruz, within the tropical forest. Onthophagus mexicanus Bates is occasionally found in rotten mangos and other fruits (Hinton, 1935).

There is a group of taxonomically related species of Onthophagus from southern Mexico and Central America in which numerous cases of saprophagy have been encountered. All these species are from the interior of the forests or from associations such as cacao plantations which preserve most of the microclimatic conditions of the tropical forest. Onthophagus belorhinus Bates belongs to this group and is found in Guatemala in fallen fruits, especially those of cacao (Bates, 1886:70). In the extreme south of Mexico, in a cacao plantation near a forest, where there were still a few trees of large size, one of us (Halfflter) and Prof. Antonio Martinez collected a large number of specimens of this species in fallen jack fruit (Artocarpus integrifolium), some slightly decayed. The beetles were feeding in the inside of the fruit and on the surface. This tree was introduced to America from Southeast Asia, where another species of Onthophagus (deflexicollis Lansberge) has been collected in its fruits (Arrow, 1931:332-333).

In the same taxonomic group as O. belorhinus Bates we have O. sharpi Harold, found in Panama in fallen fruit and resin (Bates, 1886:71), and O. carpophilus Pereira and Halfflter from the forests of southern Mexico, found abundantly feeding on the fallen fruits of zapote manev (Calocarpum zapota). The specimens of this species were found mostly in the interior of the fallen and ripe fruits, some slightly decayed, and a few specimens were collected in the soil directly underneath the fruits (Pereira and Halfflter, 1961:63). There is no doubt that the Onthophagus were feeding on the fruits and, as in the case of O. belorhinus, this could not be an accidental relationship but an habitual one, as is shown by the fact that in spite of careful collecting in the vicinity no specimen of O. carpophilus was found in excrement. (A few specimens of O. belorhinus were collected in human excrement and carrion.)

Species Collected in Funjí

A few Scarabaeinae of completely unknown biology have been collected under bark or in rotten wood. It is possible that they feed on the
mycelia of fungi growing there. The following species are involved:
Paraphytus hindu Arrow from Assam (Arrow, 1931:419), the curious phanaeine genus Dendropaemon (d'Olsoufiev, 1924:121), and two species of Onthophagus collected in the rain forest of the Congo: O. asperipennis d'Orbigny and O. garambae Frey (Frey, 1961).

In fresh or more or less decayed hymenomycetes the following have been collected: Glaphyrocanthon viridis leechi Martinez, Halfter, and Halfter, normally a coprophagous species (Halfter, 1959:170; Martinez, Halfter, and Halfter, 1964). Deltochilum tusocupreum Bates and D. granulatum Bates (F. S. Pereira, in litt.); Phanaeus daphnis Harold and Ph. endymion Harold, both normally coprophagous species (Hinton, 1935). Neocanthidium bokermanni Martinez, Halfter, and Pereira and N. kelleri Martinez, Halfter, and Pereira (Martinez, Halfter, and Pereira, 1964). Liatongus rhinocerulus (Bates), also found, though much less frequently, in dead animals (Halfter, 1964:81), and the following species of Onthophagus cited by Arrow (1931): O. dunningi Harold (also cited by Lea, 1923:367). O. agaricophilus Arrow. O. frugivorus Arrow (also collected in rotten fruit). O. germanus Gillet, and O. fasciatus Boucomont, Kolbe (1905:570) cites O. geminatus d'Orbigny, a coprophagous species, from fungi. O. s. striatulus Beauvois "is fairly distinct from other North American Onthophagus in its habits inasmuch as it prefers rotting fungi to dung as adult food. Specimens can be commonly taken under some of the toadstool fungi and have also been found by the writers on a species of Rhizopogon...Specimens less frequently are taken on rotten melons, animal droppings, or carrion." (Howden and Cartwright, 1963:45.) Ross Arnett (1960:397) mentions the mycetophagous habits of this species. Howden and Cartwright (op. cit.) obtained the life cycle of this Onthophagus using cow dung. Even though fungi were made available to the beetles they were not used for nidification, although the adults fed on them. O. striatulus floridanus Blatchley was also found in decaying fleshy fungus. O. pennsylvanicus Harold and O. tuberculifrons Harold have been taken in the same medium, but also in excrement, carrion, and decaying plants (Howden and Cartwright, 1963).

We were able to verify some of the cases of Onthophagus—fungus relationships mentioned by Howden and Cartwright thanks to the material sent us by Dr. Robert C. Graves of Flint, Michigan. This contained specimens of O. h. heca and O. h. haroldi.

Of the exceptions only O. agaricophilus (Australia) and O. h. heca (mynn) are mycetophagous. O. garambae seems to be carrion, or decaying plant feeding.

One of the Scarabaeinae is of the genus Acanthocephalum. This is the predation in Canthon diversicolor (Howden and Cartwright, 1962) and was also observed in Onthophagus. Navajas (1960) cites the same species.

In 1960 at the University of Michigan we had an opportunity to work with Prof. Eduardo Navajas. He provided us with many specimens of this species.

In the first part of his work he placed the females. According to Howden and Cartwright it is possible that the ant will concentrate on the mycelia of fungi growing there. If the ant is not able to find the contents directed toward the abdomen it will discard the broods balls for food. This is also observed by Canthon viridis. It is possible that the ant, a positive worker, will use the clypeus used in flight and the ant will then take the broods balls and discard them. If the ant is not able to find the contents directed toward the abdomen it will discard the broods balls for food. This is also observed by Canthon viridis. It is possible that the ant, a positive worker, will use the clypeus used in flight and the ant will then take the broods balls and discard them.
species are involved: (Hinton, 1931:419), the curious O. asperipennis Bates and D. daphnis Harold and the Leptidiid O. agarciphilus Arrow from India and O. dunningi Harold from Australia are exclusively mycetophagous. Other species—the Neo-canthidium, Liatongus, and Onthophagus s. striatulus—are almost exclusively mycetophagous but it is possible to collect them rarely in excrement, carrion, or decaying plant matter. The remaining cases cited seem to be euryphagous, with a wide range of food habits.

4. Predation

One of the most extraordinary feeding specializations described for Scarabaeinae is that of the Brazilian species of Canthon which attack ants of the genus Atta. The first notice of this was given by Lichti (1937) for Canthon dieres Harold. Navajas (1950) described a similar type of predation in Canthon virens Mannheimer after both field and laboratory observations carried out over several years in succession. Ritcher (1958:325) cites the same habits for Canthon deplanatus var. fastuosus Harold.

In 1960 at the Biological Institute of São Paulo one of us (Halffter) had an opportunity to discuss predation on ants by Canthon with the late Prof. Eduardo Navajas, a careful observer and first class scientist, who provided us with some hitherto unpublished data.

In the first place, the citation of C. deplanatus var. fastuosus is erroneous. According to Navajas, Ritcher obtained this name from him, but the specimens had been incorrectly determined by another specialist and were actually Canthon vires. This was the species with which Navajas worked and to which the following observations apply.

During the nuptial flight of Atta, C. vires attacks both males and females. If there are few ants, several individuals of the beetle concentrate on one ant; if there are many, each beetle attacks one ant. If the ant is a male or an unfertilized female, the Canthon eats its contents directly; if it is an ovigerous female, it makes two or three broods balls from the abdominal contents. The method of attack used by Canthon virens is the following: the beetle places itself on top of the ant, a position it achieves with more or less difficulty, and with the clypeus used as a lever, and sometimes with the aid of the dentate outer
edges of the fore tibiae, moved in an outward motion, it decapitates the ant. It then empties the body contents, burying these at a shallow depth and leaving the integument empty. It feeds on the contents or makes brood balls (if the ant is a fertile female). Each female Canthon virens deposits six or seven eggs (there is only one ovary), each in its corresponding brood ball.

Navajas reared Canthon virens in the laboratory to determine the feasibility of using it as an agent of biological control for the ant. However, it does not seem to be efficient in this respect, not killing a sufficient number of ants, which die in large numbers anyway after the nuptial flight.

Also in Brazil, Canthon pseudoforcipatus Balthasar (a copro-necrophagous species) and an undetermined species of Deltochilum may attack live diploponds (Navajas, 1950). Possibly this unidentified Deltochilum, as well as another unidentified one mentioned as attacking the diplopod Pseudonannolene tricolor (Acta Zool. Lilloana 2:418), may be Deltochilum kolbei Paulian, a species which has been observed attacking live diploponds on several occasions (Pereira and Martinez, 1956:93; Navajas, 1960, personal communication).

Luederwaldtia pseudoforcipatus (Olivier) in the Department of the Amazon recently killed collected thus, when they were attracted to the monkey oil Alouatta sp. and subhyalinus (Luederwaldtia brunneo-Wagy) obtained some encountered on the Pará, Brazil), Glaphyrocanthus (Linnaeus), the center of dispersal (Luederwaldtia 1964), where a

Also in Brazil, has been found on Costa Rica, Glaphyrocanthus in Costa Rica, host excrement has brought about especially the metasternum and tibiae are short species of the head and (litt.) found the

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zez. 1956:93; Navajas.

SPECIAL ECOLOGICAL NICHES
5. Ectocommensals of Mammals

Luederwaldt (1922:226) reports that *Glaphyrocathlon quadrijugatus* (Olivier) was found by E. Garbe (the well-known collector of the Department of Zoology in São Paulo) in Tapajós, Pará, Brazil on recently killed monkeys. About a dozen of these canthonines were collected thus. Luederwaldt notes that the monkeys soil themselves when they congregate during the night and he believes that the beetles were attracted by the odor. Pereira and Martínez (1956:92) identify the monkey on which *Glaphyrocathlon quadrijugatus* was found as *Alouatta* sp. and mention that a closely related species, *Glaphyrocathlon subhyalinus* (Harold), was collected on another monkey, *Callicebus brunneus* Wagner, in Guaporé, Brazil. The above-mentioned authors obtained some data on the frequency with which scarabaeines were encountered on monkeys captured in the Cachimbo region (southern Pará, Brazil). According to these authors also, another species of *Glaphyrocathlon*—*prosen* Martínez—is found on *Tapira terrestris* (Linnaeus), the American tapir, in Bolivia. The genus *Glaphyrocathlon* comprises coprophagous, forest-inhabiting species and has its origin and center of dispersal in the Amazon Basin (Martínez, Halffter, and Halffter, 1964), where all the above records of mammal associations come from.

Also in Neotropical America, two species of dichotomines have been found on sloths: *Uroxys gorgon* Arrow on *Bradypus griseus* (Gray) in Costa Rica and *Trichillum bradyorum* Boucomont on *Bradypus insuscatus* in Costa Rica and *Bradypus sp.* in Peru. According to Bal-rhasar (1939:15) the *Trichillum* lives near the anus on traces of the host excrement, and the association between the mammal and the beetle has brought about certain morphological changes in the latter: the body, especially the abdomen, has become shortened, with the edges of the metasternum and pygidium becoming practically contiguous; the posterior tibiae are short and stout and do not widen distally as in the other species of the genus. *Uroxys gorgon* Arrow lives deep inside the fur of the head and neck (Arrow, 1933:385-386). Antonio Martínez (in litt.) found three specimens of *Uroxys* sp. on *Bradypus* in Bolivia.

Outside America, the genus *Macropocoris* of Australia and New Guinea includes various species collected on kangaroos and wallabies.
In *Macropocupris* there definitely is a morphological modification for life on mammals: the tarsal claws are hypertrophied and deeply incised at their bases (fig. 1), serving to grip the hairs of the host.

*M. symbioticus* Arrow has been found in the cloaca of a wallaby (Lea, 1923:353). Lea (loc. cit.) also cites 11, 6, 4, and 3 specimens respectively of *M. parvus* Blanchard found around the anal region of four common wallabies (*Macropus agilis*) in Groote Eylandt (Northern Territory). The beetles were clinging to the hairs around the anus. The same species has also been collected in excrement.

What is the relationship between all these ectocommensal Scarabaeinae and their hosts? Except in the case of *Macropocupris paramelinus* Lea, which also lives in the nest of its host, we do not know where the larvae live. Halfter (1959:165-166) differs from a number of previous authors in pointing out that these beetles are not "true parasites, but phoretic commensals not causing any harm to their hosts". For the mammal the relationship may be considered neutral, neither harm nor benefit being received. For the scarab, the relationship seems to be fairly obligatory, as in the majority of cases these species have not been found elsewhere than on their mammal hosts or simply flying. They undoubtedly encounter favorable sites but are not sure. For the mammal, the question of whether the beetle is capable of collecting sufficient secretions and pheromones on the host's body surface has been searched for in the cloacal secretions and manure of the hosts. In the case of *M. parvus*, it is certain that the beetle only lives on the host, but rather within it.

Among human commensal *Scarabaeinae* accompanying breeds of the *Macropus* species, *Lophyphagus* Sharp is common, with *Zoophagus* (Iyengar) Sharp, *Scutophagus* bifasciatus (Iyengar), and *Caccobius muatans* Sharp. These specimens invariably belong to the genera *Caccobius* and *Zoophagus*, which are close relatives of the genus *Caccobius*, and which are the only genera of the *Caccobius* group in which the condition is met. The larvae of these species were egested from the hosts and have been verified and not infrequently found clinging to the excreta of the hosts, who live in underground burrows and pockmarked by night and thus are much more likely to encounter the scarabs than in the daytime. The *Zoophagus* and *Lophyphagus* have encountered the mammal.

7. In conclusion

In recent years scarabs of the genus *Caccobius* have encountered the mammal.
encounter favorable conditions on their hosts, but what these are we are not sure. For the species which live on the excrement adhering to the mammal, the question is why are they not found in this excrement independently of the mammal. It is quite possible that this is due to insufficient collecting data, since the excrement of monkeys and sloths remains on the high branches of the forest and is very difficult to search, if it has been searched at all. If the Uroxyx and Macropocopris live on the secretions and sloughings of their hosts, we have a reason for the association, but there are no data suggesting anything of the sort. In any case, it is certain that in no instance are we dealing with ectoparasites, but rather with ectocommensals or phoretic commensals.

6. ENTOPARASITES OF MAMMALS

Among human beings in India there is a recurrent intestinal illness, accompanied by bloody diarrhea, which has received the name "scarabiasis". Senior-White (1920) and Iyengar (1923-1924) report this parasitosis for the first time and state that it is common in Bengal and Ceylon. Senior-White cites as the causative agents the adults of Onthophagus bifasciatus (Fabricius) and another unidentified species of the genus. Iyengar also mentions Caccobius vulcanus (Fabricius) (as C. mutans Sharp). Arrow (1931:2), having directly examined the various specimens involved, specifies that the causative agents of "scarabiasis" are Caccobius vulcanus (as mutans). Onthophagus bifasciatus (Fabricius), and O. unifasciatus Schaller, the two species of Onthophagus, which are closely related, being the most frequent pathogens. In all cases the condition is caused by the adults. In several instances the insects were egested alive in the feces, these cases having been thoroughly verified and not open to question. Scarabiasis is found in small children who live in unsanitary conditions, and it has been suggested that the scarabs enter by the anus, which is soiled with excrement, during the night and thus enter the intestine. The two pathogenic species of Onthophagus have also been found in small dead animals.

7. INHABITANTS OF VERTEBRATE NESTS AND CAVES

In recent years there has been a great increase in the number of Scarabaeinae, mainly Onthophagus, known to occur in nests or burrows
of vertebrates. These new data, added to the few previously known, present a new picture of the relationships between Scarabaeinae and vertebrate nests.

In Argentina, the nests of the vizcacha (Lagostomus maximus Desmarest) are found in dry, sandy country. The vizcacha deposits its excrement at the entrance of the burrow, which is humid. According to a personal communication from Antonio Martínez, there is an exclusive scarabaeine fauna associated with this excrement, as follows: Tetrachaetia sanguineomandata Blanchard, Trichilium externepectatum Preudhomme, and Dichotomius bosqui Pereira. There are also the following Scarabaeinae not exclusive to this habitat: Ontherus appendiculatus Mannerheim, Ontherus digitatus Harold, and Dichotomius nobilis Waterhouse.

Outside of Argentina, where there are only three species of Onthophagus (two of them rare), in the rest of the world it is the latter genus, plus a few Copris, which represents the Scarabaeinae in vertebrate nests. The affinity of Onthophagus for nests is paralleled in various genera of Aphodinae, which are also extensively associated with this microhabitat.

The first American species cited from nests was Onthophagus polyphemus Hubbard, collected by Hubbard (1894) in the burrows of the Florida gopher tortoise, Gopherus polyphemus. In 1939, Hubbell and Goff mention O. striatulus floridanus Blanchley as an incidental guest in the burrows of Geomys in Florida. In the same year, Young and Goff published a list of the arthropods found in the nests of Gopherus polyphemus which includes Onthophagus polyphemus Hubbard "Known only from Gopher burrows and without any close allies in North America" (Young and Goff, 1939:61). In 1956, Howden, Cartwright, and Halfster list the North American species of Onthophagus associated with nests and burrows as follows: O. polyphemus Hubbard, O. orpheus Panzer, normally present in excrement of man and cow; collected in a woodchuck burrow; O. cymomysi Brown, collected in the burrows of the prairie "dog" (Cynomys ludovicianus Ord.), and O. hippopotamus Harold collected in the nests of the pocket gopher or tuza (Cratogeomys merriami [Thomas]). Howden (1960:460) mentions finding O. relatimus Horn in a nest of Neotoma albigula Hartley in Texas.

In 1963, in their revision of the genus Onthophagus of the United States and Canada, Howden and Cartwright amplify the data on the above-mentioned species and add a list of these:

O. coproidea H.F. Howden's "rodent or other"
H.F. Howden's Salto, Durango "O. rhodarensis Harold"
O. brevifrons (Neotoma)"
O. subtropicalis (Neotoma)"
O. polyphemus Carolina has been collected in the nests or burrows of O. polyphemus. Howden, Cartwright, Halfster comment concerning best accomplished by these authors in the spring it is common to find Onthophagus at the sides of nests or burrows in the deepest part of the earth, and the extreme right of the burrow may be another may probably be empty."

The complete casts of nests or burrows of Gopherus polyphemus have been occasional and found in the United States, and collected with collections of other specimens of the genus or other species.
Few previously known. Stewart and Egan (1938) suggested that the 34 species of Onthophagus microops Baird of the United States is a difficult job. Collecting even the adults is a difficult job. The best accomplished by at least partial excavation of the gopher burrow. In the spring it is often unnecessary to excavate the burrow completely. The Onthophagus being found 4 to 8 feet inside the entrance in the sand at the sides of the burrow. Excavation of the complete burrow is quite difficult because they are often 18 to 20 feet long and may reach a depth of 8 to 12 feet."

O. polyphemus sparsisetosus Howden and Cartwright has the same habits as the nominotypical subspecies. but is found in the west of Florida and the extreme south of Alabama and Mississippi. Howden and Cartwright believe that "movement of the adults from one burrow to another may possibly occur on warm cloudy days or late in the afternoon."

The complex of subspecies of O. orphicus Panzer is associated with nests or burrows of vertebrates. Specimens of O. o. orphicus Panzer have been occasionally found in cow dung or other excrement, and a few have been collected in fermenting malt traps, but the majority of specimens with collection data was found associated with nests or burrows. "One long series from Plummers Island, Md., came from a buzzard's nest; other specimens have been taken in woodchuck. Marmota monax (Lin-
naeus). burrows: still other specimens from Florida have been found in wood rat (Neotoma sp.) nests ... Inasmuch as most of the species of Onthophagus that are not general dung feeders seem to have a very restricted host preference, it seems quite likely that further investigation may show that three or four morphologically similar species with quite diversified habits are placed here under the name orpheus." (op. cit.: 50).

O. orpheus canadensis (Fabricius) is strictly associated with the woodchuck, Marmota monax (L.). Howden and Cartwright examined 336 specimens from many different localities and found none from any other type of burrow or nest, although a few were found in cow dung.

O. orpheus pseudorphus Howden and Cartwright is a prairie form, in contrast to the other two subspecies which are forest inhabiting. Of 110 specimens examined, only two were associated with nests — those of the mouse Microtus ochrogaster (Wagner).

O. cynomys Brown, a species related to orpheus, is found only in the nests of the prairie "dog". Cynomys ludovicianus (Ord.).

O. browni Howden and Cartwright has been collected in the nests of Neotoma (probably mexicana).

O. velutinus Horn is a species related to the previous one, and is apparently restricted to the nests of Neotoma albicula Hartley.

Of the 37 species and subspecies of Onthophagus from the United States and Canada studied by Howden and Cartwright, 11 are associated with nests and many of these are exclusive to this habitat; two more are very possibly associated with nests, and two have been found in caves, one of them apparently exclusive to caves.

In order to complete the picture of the relationship between American Onthophagus and nests, we will mention that we have examined a specimen of a new species of the genus, very close to coproides Horn (= cuboidalis Bates), collected at the entrance to a nest of Basarius (Procyonidae) in the mountains of Guerrero. This new species, together with the ridiculous coproides and hippopotamus, represents one more group of closely related species all apparently associated with vertebrate nests.

Outside America, Paulian (1949:1019) indicates that O. oratus (Linnaeus), which normally eats sheep dung, follows rabbits into their burrows. According to him, O. oratus was found in the burrows of Cricetus, Phodopus, and Spermophilus. He indicates that O. elasomus Fabricius is found in the nests of gerbils and pinyons, and O. choropus to Panin (1957:85). O. vitulius (Fabricius) is found in the nests of Marmota bobac Pallas, and O. vitulus Fabricius from the prairie. The latter species of Copris l. and Spermophilus.

Macropocopris pustulatus Howden and Cartwright is found taken in a nest of bank mice, and Rules, in the nests of the woodchuck.

Apart from the American Onthophagus except for the species already discussed, all other species that belong to the genus Copris are distributed in the burrows of the gerbils and pinyons in northeastern Mexico, and these burrows were found under a nest. The last species also found Copris l. in burrows in northeastern Mexico may be that of Copris luctuosa (Pallas) in the nest (Hicks, 1958). These captures in excrement.

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1 Linsley (1942:166) var. militaris Horn very close to the Yosemita National Park burrows, a feat which no times as great as 45 degrees two to six feet from the entrance to the nest it must be noted that these species in the same area.

Young and Golf (1949) the following Scarabaeinae: Forelius (cited: 1:120), Damus Oswald, and the belief that the presence of C. pupae at the entrances of the burrows.
Onthophagus have been found in most of the species of which they seem to have a very restricted distribution. Further investigation of similar species with quite similar habits is necessary. (op. cit.: 50).

Cartwright examined nests of Onthophagus and found none from any species except for the new species with quite similar habits. Cartwright is a prairie species and is found only in the United States. BEYOND LIMITED EDITION this species is found only in the United States. The latter species of Onthophagus is also found in the burrows of Cricetus and Spermophilus (Balthasar, 1963[1]:54).

Macropocopris paramelinus Lea is known from a single specimen taken in a nest of bandicoot in New South Wales (Lea, 1923:393-394).

Apart from the above-mentioned species of Onthophagini (all Onthophagus except for the Macropocopris) and the Argentine cases already discussed, all the scarabaeinae found in vertebrate nests belong to the genus Copris. Copris gopheri Hubbard lives exclusively in the burrows of the Florida gopher tortoise, Gopherus polyphemus. In northeastern Mexico, three brood balls of Copris arizonensis Schaeffer were found under a nest of Neotoma by H. F. Howden (in litt.). Howden also found Copris l. lecontei Matthews in a pack-rat nest (Neotoma) in northeastern Mexico (in litt.). A definitely accidental association must be that of Copris lunaris (Linnaeus) found in a stork nest (Hicks, 1958). This is a single isolated record among thousands of captures in excrement.

Linsley (1942:166) mentions finding Borocanthus (cited as Cantthus) simplex var. militaris Horn very abundantly in the entrances to nests of Citellus beecheyi in the Yosemite National Park (United States). "The adults were rolling dung from the burrows, a feat which necessitated rolling the balls up at a very sharp angle, sometimes as great as 45 degrees. The dung was usually buried at a distance of from two to six feet from the burrow entrance." (loc. cit.). Although these observations indicate that the Borocanthus utilizes the excrement accumulated at the entrance to the nest it must be noted that it does not live inside the latter. Furthermore, the same species in the same area is found in cow dung.

Young and Goff (1939:60-61) mention collecting in Gopherus polyphemus burrows the following Scarabaeinae (in addition to Copris gopheri and Onthophagus polyphemus): Ateuchus (cited as Chaeridium) lecontei (Harold), Phanaeus igneus floridanus Olsoufieff, and Onthophagus tuberculifrons Harold. The authors mentioned believe that the presence of these three species is incidental, all having been found at the entrances of the burrows.
As is the case with other types of ecological relationships, we have three grades of association between Scarabaeinae and nests: 1) Species which occasionally enter nests, presumably either looking for the excrement of the inhabitants or the microclimatic conditions of the nest. 2) Species found predominantly in nests, and 3) Species found exclusively in nests. These three grades represent an evolutionary sequence not only toward the nests, but also toward a de facto stenophagy restricted to the excrement of the vertebrate inhabitants of the nest. It will be noted that nests, especially those of rodents, where most nidicolous Scarabaeinae have been found, not only contain much excrement but also constant, high humidity and temperatures — factors which in a cold or dry climate may explain the scarabaeine association. The species belonging to the third category (exclusive to nests) are numerous. This fact is particularly well documented in intensively collected groups and regions, such as the Onthophagus of the United States and the mountains surrounding Mexico City, since in these cases the presence of the beetles in nests is repeatedly confirmed by frequent collecting. There can be no doubt that the scarabaeine fauna associated with nests is much more extensive, since only Europe, parts of the United States, and the montane region around Mexico City have been methodically explored in search of these beetles.

What has been said concerning association with nests applies equally well to association with caves. The Scarabaeinae presumably seek constant, high humidity and temperature conditions and the accumulated excrement (guano). The following examples of cavernicolous Scarabaeinae are known.

Two specimens of Aulacopris reichi White, the largest Australian scarabaeine and a very rare species, were collected in one of the Yessabah caves on the McLeay River. They were found together with 16 balls of bat dung, of the size of nuts, each containing a larva or pupa, and in one case an egg (Lea, 1923:362).

The first apparently truly cavernicolous scarabaeine to be recorded is Onthophagus vesperullo Howden, Cartwright, and Halfter, described from Acuitlapan cave, Guerrero (Howden, Cartwright, and Halfter, 1956). This is also the first recorded cavernicolous Scarabaeidae after Trox cosilatus Wiedemann. This Onthophagus seems to be extraordinarily localized, being known only from a single mound of guano. It has not been found outside, nor has it or any other scarabaeine been encountered in other caves of the region to be extremely endangered, located has been the subject of various investigators. O. vespertilo and other collected species have been found in every mound of guano, as well as any other Scarabaeinae species. There is a danger of extinction, mainly for use as fertilizer.

O. vespertilo is one of the species previously mentioned as a United States species (O. brevifrons, O. suborbitalis, and O. vespertilo), and O. vespertilo bear biological data which the Texas and Missouri.

There is a third species, Onthophagus: O. vespertilo. which eight specimens have been collected. They are probably attracted by the excrement in cow dung and other

There is a good chance that beetles which live in ant nests is rather casual for ants' nests.

One specimen of O. vespertilo was collected in Madras in a nest of Acromyrmex, and the nests of Acromyrmex in Buenos Aires Province, Argentina, by Hinton and Ancona, in scabriuscalim Bates in Temascaltepec, Mexico.
In other caves of the region or of Mexico generally, *O. vespertilio* appears to be extremely endemic, since the region where Acuitlapan cave is located has been the subject of detailed bio-speleological explorations by various investigators, especially Dr. Federico Bonet and G. Halffter in 1956 and on other occasions. These investigators methodically examined every mound of guano without finding other populations of *O. vespertilio* or any other Scarabaeinae. If it really is this restricted, the species is in danger of extinction, since the guano of Acuitlapan cave is being mined as fertilizer.

*O. vespertilio* is closely related to *O. brevifrons* Horn, a nidicolous species previously mentioned. Howden and Cartwright (1963) described a United States species, *O. cavernicollis*, which is also closely related to *O. brevifrons*, *O. subtropicus* Howden and Cartwright (both nidicolous species), and *O. vespertilio*. The eight specimens of *O. cavernicollis* which bear biological data were collected in bat dung inside caves in Arkansas, Texas, and Missouri.

There is a third known (non-exclusive) cavernicolous species of *Onthophagus*: *O. o. orphicus* (Panzer), previously cited from nests, of which eight specimens have been collected in a cave in Tennessee, possibly attracted by the bat guano. This species has also been taken outside in cow dung and other excrement.

**8. Myrmecophily**

There is a good representation of Scarabaeinae among the numerous beetles which live in ants’ nests. In some cases the association with the ants is rather casual, in others the species have been collected only in ants’ nests.

One specimen of *Sisyphus longipes* (Olivier) was collected in Madras in a nest of *Pheidole rhombinoda*, under a stone (Arrow, 1931: 73). This seems to be a casual association.

Among the Canthonina, *Pseudophilus lunatus* (Schmidt) lives in the nests of *Acromyrmex ambiguus* Forel in the southwestern part of Buenos Aires Province, Argentina (Pereira and Martinez, 1956:93). Hinton and Ancona (1935:308) collected 22 specimens of *Deltochilum scabriusculum* Bates in the debris deposits of *Atta sexdens* (Linnaeus) in Temascaltepec, Mexico. These authors add that "although we carried
out a detailed search in cow dung and human excrement, we did not find a single specimen there. However, other authors, including the present ones, have collected D. scabriusculum in human excrement.

Janssens (1949:26) created a subtribe Alloscelina of Scarabaeini which includes part of Arrow’s Panelini. This subtribe has many examples of myrmecophily and from the few data which we have all members of the subtribe seem to be associated with ants or to have been collected in plant debris and other decaying organic matter. The following have been found associated with ants: Ponerotrogus annandali Silvestri in a nest of Ponera tesserinoda1 (Arrow, 1931:12), Haroldius heimi Wasmann in nests of Pheidole lateritosa (Wasmann, 1918:2, cited in Paulian, 1945:59; Arrow, 1931:415), Haroldius philippinensis Pereira in a nest of the ant genus Diacamma (Pereira, 1954), Allo(3)paradoxus Boucomont in nests of Dorylus and frequently in the marching columns of this ant (Collart, 1934:240; Janssens, 1939:9), and Megaponerophilus sp. in a nest of an undetermined species of ant (Balthasar, 1963[1]:61).

Among the Dichotomina, Balthasar (1963[1]:61) cites the genus Paraphytus Harold from a nest of an undetermined ant. Luederwaldt (1931) mentions finding colonies of 20 or 30 individuals of Ontherus zikani Luederwaldt in nests of Acromyrmex, and Ontherus cephalotes Harold in the decomposing “aboborais” (mounds of vegetable debris) and in the fungi cultivated on them by the ants. According to a personal communication from F. S. Pereira, O. zikani has also been found in nests of Acromyrmex octospinosus. Uroxyx dilaticollis (Blanchard) and Onthocaris bonariensis (Bruch) were collected in nests of Acromyrmex landii (Pereira and Martinez, 1956:93; Martinez, 1959:65-66). One specimen of O. bonariensis was collected under excrement.

We have examined four specimens of Dichotomius centralis (Harold) (a species commonly found in dung) collected once by J. Hendrichs in an Atta mexicana nest in Ajijic, Jalisco. However, careful collecting in these same nests on other occasions by Hendrichs, C. Bolivar, P. Reyes, and G. Halffter failed to reveal any more specimens of this Dichotomius.

Von Lengerken (1954: 183, citing Eidmann, 1937) indicates that Ateuchus granigerum (Harold) nidificates under the old debris chambers of Atta nests, forming more or less vertical burrows which are filled with the ant debris. Ven Lengerken (1954: 183, citing Eidmann, 1937) also indicates that Ateuchus granigerum (Harold) nidificates under the old debris chambers of Atta nests, forming more or less vertical burrows which are filled with the ant debris. Ven Lengerken (1954: 183, citing Eidmann, 1937) also indicates that Ateuchus granigerum (Harold) nidificates under the old debris chambers of Atta nests, forming more or less vertical burrows which are filled with

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1 New Bothroponera sulcata (Frauenfeld) (Pereira, 1954:6).

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rement, we did not find any species of Scarabaeinae, including the present one, among the excrement.

Scelina of Scarabaeini (Cremen t.) has many examples of ants consuming old debris, as we have all members of the group that have been collected, including those collected by Balthasar. The following have been collected:

- Ateuchus myrmecophilus (Boucomont) and A. viridis (Boucomont) from nests of Acromyrmex lobicornis.
- Scatimus ovatus Harold from the nest of the harvest ant Pheidologeton diversus.
- Anoctus myrmecophilus Arrow was found in the nest of the harvest ant Pheidologeton diversus, in the debris accumulated near the entrance of the nest (Arrow, 1931:138). Arrow believes it likely that this species reproduces in the nest. Anoctus siamensis Balthasar is cited from nests of Acromyrmex (Balthasar, 1963[1]:61). Anoctus laevis Sharp is cited by Balthasar (loc. cit.) from the nest of an unidentified ant.

In nests of Atta mexicana Smith from Ajijic, Jalisco, P. Reyes collected a specimen of Scutinus ovatus Harold. These nests, to which we have already referred, have been carefully examined by G. Halffter and P. Reyes on numerous occasions and described by Hendrichs and Reyes (1963) in connection with the passalids which occur there. They are rich in Scarabaeinae and have an Onthophagus and a Liatongus in addition to the species previously mentioned. All live in the debris chambers, which are superficial in this case, with excess material overflowing to the outside. This debris, which the ants are continuously ejecting, is made up of bits of twigs and leaves not over 3 mm in length, reddish or dark brown in color, and of pieces of ants and other insects. The mounds in which the debris is decomposing may reach a depth of 30 cm or more. They are usually quite damp, especially in the lower layers where decomposition forms a type of humus. This debris supports, together with the Scarabaeinae, a rich fauna of cetonines, passalids, tenebrionids, staphylinids, etc.

In the Onthophagini the genus Anoctus contains three species inhabiting ants' nests. A. myrmecophilus Arrow was found in the nest of the harvest ant Pheidologeton diversus, in the debris accumulated near the entrance of the nest (Arrow, 1931:138). Arrow believes it likely that this species reproduces in the nest. Anoctus siamensis Balthasar is cited from nests of Acromyrmex (Balthasar, 1963[1]:61). Anoctus laevis Sharp is cited by Balthasar (loc. cit.) from the nest of an unidentified ant.

Caccobius megaponerae Brauns is regularly found in the nests and sometimes in the columns of Megaponera foetens (Collart, 1934:240). Hinton and Ancona (1935:308) collected large series of Onthophagus rufescens Bates in the debris mounds of Atta sexdens (Linnaeus) and Atta jervis Say. The same authors collected some specimens in dung and one at the entrance of an ants' nest, where the ants passed it by without molesting it. Howden, Cartwright, and Halfter (1956:12) provide more evidence of the association of this species with ants' nests.

1 Determined by Dr. Walter Kempf of Sao Paulo.
Subsequently, G. Halffter and Violeta Halffter collected *O. rufescens* in *Atta mexicana* nests in several localities in the upper Balsas valley in central Mexico—the same region collected by Hinton and Ancona. In this area, which includes the state of Morelos and parts of Puebla, México, and Guerrero, the climate is hot and dry and the vegetation sparse and xerophytic. The *Onthophagus* have always been collected in the debris which overflows from the *Atta* nests, a few centimeters down.

G. Halffter collected this same species in Ajijic, Jalisco. Later P. Reyes found a large number of adults, pupae, and larvae in the debris of nests of *Atta mexicana* in this locality. The adults had dug vertical tunnels beneath the mass of debris and were found about 10 cm. below fresh debris. P. Reyes and G. Halffter found this *Onthophagus* is several other localities in the Balsas basin or the southern edge of the Mexican Plateau, always in association with the debris of *Atta mexicana* nests.

In Chilapa, Guerrero, G. Halffter collected one specimen of *Onthophagus mexicanus* Bates (a species common in excrement) in *Atta* debris.

Another species found in the debris of *Atta mexicana* is *Liatongus monstrosus* (Bates), apparently exclusive to this microhabitat and to Ajijic, Jalisco. It should be pointed out that this large species is not closely similar to other American *Liatongus* and should perhaps be considered a separate genus. Bates (1889:391), citing Flohr, is the first to indicate that *L. monstrosus* is found in ants’ nests. Halffter (1964:81) confirms the presence of larvae and adults in the nests of *Atta mexicana*, living in the debris. Both adults (males and females) and larvae are found in the mounds of debris (which as we have mentioned overflow to the surface) at shallow depths (5 to 35 cm) in the mass. No specimen has been found outside the debris. In the same locality at a later date P. Reyes observed larvae inside tunnels which run through the debris, and adults in oblique tunnels 10-14 cm deep. Other adults and larvae were loose (that is, not in distinct tunnels) in the mass of debris.

We will attempt to make a preliminary analysis of the relationship between Scarabaeinae and ants. In the Neotropical Region, where most of the examples occur and where these are best known, the Scarabaeinae are found in the debris of fungus-cultivating ants (Attini) of the genera *Atta* and *Acromyrmex*. The relationship between the scarabs and the ants corresponds in Wasmann's classification, followed by Wheeler (1910), to that of tolerated guests or neutral synoeketes. The scarabs live without direct contact with the ants, presumably without any feeding relationship; the relationship is neutral, in that they are tolerated by the ants directly. Feeding is on the refuse and not the fungus cultivation of the ants. Only in Thailand has a fungus-cultivating species been collected.

The list of Scarabaeinae associated with fungus-cultivating ants includes *Pseudopilissus luna*, *Liroxys dilator*, *Anocetus sién*, three species of *Atocetus*, *Anoctus simillimus* and *Liatongus monstrosus* Bates, 1889.


Of the above examples, two have been found exclusively American, these are normally collected in large numbers. In Mexico, the genus *Anocetus* was found in all stages of development in the larval food is the waste products from the nidification behavior. The larval food is not seen in coprophagy, but in the refuse and conditions of the nest.

There is a considerable number of philous Scarabaeinae, however, unfortunately we know little of these. The *Sisyphus phillos* is found in the nests of *Pheidole* species, a fungus-feeding ant. Although not found in the entrance of the nest.

But what about the larvae of the phagous ponerines?
collected *O. rufescens* in the upper Balsas valley in Ajijic, Jalisco. Later P. and Ancona. In this area of Puebla, México, the vegetation sparse and collected in the debris meters down.

Onthophagus is several on edge of the Mexican *Atta mexicana* nests.

One specimen of *Onthophagus* in *Atta* debris.

*Atta mexicana* is *Liatongus* microhabitat and to its large species is not should perhaps be considered. Flohr, is the first to Balthasar (1963:61) is clearly in error in citing the Oriental species *Anoctus siamensis* Balthasar as coming from a nest of *Acromyrmex* in Thailand. since this genus of ants is exclusively American (see Wheeler, 1910; Gonçalves, 1961) and even the Attini as a whole are exclusively American (Wheeler, 1910).

Of the above list of myrmecophilous Scarabaeinae, some species have been found only in very small numbers in ants' nests and some of these are normally coprophagous. The Deltochilum and *Onthophagus* were collected in large numbers inside the ant debris, and *Ateuchus granigerum*, *Onthophagus rufescens*, and *Liatongus monstrosus* have been found in all stages of development. In these latter species the proven larval food is the debris of the nests, which is also eaten by the adults.

Nidification behavior in most cases seems to be the same as the normal one seen in coprophagous species of the same genera, but adapted to the conditions of the debris deposits.

There is a different scarab-ant relationship among the myrmecophilous Scarabaeinae of areas outside the Neotropical Region, and unfortunately we do not know what the beetles eat in even a single instance. The *Sisyphus* and *Haroldius heimi* seem to be associated with nests of *Pheidole*, a genus which includes harvesting as well as entomophagous ants. *Anoctus myrmecophilus* lives in the debris accumulated at the entrance of the harvest ant *Pheidologeton*.

But what about the Scarabaeinae associated with highly entomophagous ponerines such as *Ponera* and *Diacamma* (*Ponerotrogus*, *Haroldius philippinensis*, and most probably *Megaponerophilus*), or the Allos-
celus found in the nests and marching columns of the voraciously carnivorous Dorylus? One may suppose that these scarabaeines, all Alloscelina, feed on the remains of insects and other animals left by the ants. In this case there must be a closer relationship between the beetle and the ant. While still being synoeketes, they must have some sort of protection (odor mimicry, agreeable exudation, "armor" to fend off attacks by the ants, or the like) which permits the survival of these beetles in association with highly predatory ants. Indeed, the alloscelines are morphologically more modified than the New World myrmecophiles, being somewhat globose and very short-legged.

9. Termitophily

According to Balthasar (1963[1]:62) the alloseline Afroharoldius enearthrhus Janssens from the Congo has been collected in small termite nests.

Caccobius megaponerae Braun, a myrmecophilous species, has been found in a termite nest in Katanga (Doutrelepont, cited in Collart, 1934:240-241). However, as Collart points out, the normal ant host of this beetle (Megaponera foetens) is an exclusive predator of termites and could well have brought the synoekete with it into the termite nest.

The literature dealing with the beetle and the biome in which it has been found has there been an article which influence the beetle and the manner in which it has been found.

Kolbe, at the beginning of this aspect of the natural history available at his time in national and regional studies of the western Europe and later in Rumania, Yugoslavia, and other parts of the former Austro-Hungarian Empire, fairly detailed indications of the relationships of the European myrmecophiles to Europe cannot be found. However, there continues to be a problem.

We are not proxemics, but only proxemics, of each aspect of each biome about which there are proxemics, demonstrate the influence of the areas in which there are proxemics, and proxemics and evolution of the biology.

Goljan (1953): "The phagacous beetle depending on the sort of excrement in this conclusion concerning the microclimatic factors, especially in other parts of the world, in which there appear to be may well be the best."

We do not have a biome. The food, edaphic, and veg...
RELATIONS TO THE BIOME

The literature dealing with the relationships between Scarabaeinae and the biome in which they live is very sparse. On only a few occasions has there been an attempt to determine the factors, other than food, which influence the distribution and biology of this group of insects, and the manner in which these factors operate.

Kolbe, at the beginning of this century, showed great interest in this aspect of the natural history of the Scarabaeinae, but the information available at his time did not permit him to go very far. In the works on national and regional faunas published in various countries of Western Europe and lately in various Socialist countries (Czechoslovakia, Rumania, Yugoslavia, etc.), in volumes dealing with the Scarabaeidae, fairly detailed indications are given as to the biotopes inhabited by each species. As a result, we have a fairly exact idea of the ecological relationships of the European fauna. However, the conclusions applicable to Europe cannot be indiscriminately extended to other regions where there continues to be a great dearth of information.

We are not presuming to write a chapter on biogeographical ecology, but will only mention a few cases and examples of species characteristic of each biome in different regions. We will analyze certain areas about which we have more complete information in order to demonstrate the influence of the environment on the distribution of Scarabaeinae, and examine the influence of different factors on the biology and evolution of these beetles.

Gélian (1953) maintains that "The occurrence of a given coprophagous beetle depends strictly on an adequate biotope, regardless of the sort of excrement to be found in this area". We do not believe that this conclusion can be regarded as a general law. Under certain conditions, especially in the temperate zones of Eurasia, it appears that the microclimatic factors are decisive. However, we have examples from other parts of the world (see the preceding sections on food relationships) in which there appears to be a strict stenophagy, and where the food may well be the limiting factor in distribution.

We do not wish to separate the food from other factors of the biome. The food is one more factor, strictly related to microclimatic, edaphic, and vegetational factors and in no way separable from them.
If it has been treated separately this has been only with a view to facilitating presentation. We believe this stipulation to be very important. It is our opinion that in studying Scarabaeinae, for instance in grassland biomes, all ecological factors must be considered together—factors such as insolation, temperature, herbaceous cover, abundance of mammals, abundance of excrement, feeding preferences, behavior, etc.—all of which are dependent on each other. In certain circumstances a factor may be determining, but it will never act in isolation and we must always remember that the greater or lesser importance of other factors is the result of selective forces which vary in different environments.

This long preamble was necessary to explain our criticism—explicit or implicit—of those authors who either speak only of food, or who dismiss its importance in general and a priori, in their notes or studies on the ecology of Scarabaeinae.

10. Grassland Biomes

It has already been pointed out in this work that at the present time the Scarabaeinae are especially important (in community dynamics) and numerous in the various types of grassland biomes. Several factors may account for this phenomenon. We have mentioned that we believe abundant pasturage in grasslands—and the consequent numerous herbivorous mammals and abundant excrement—led to the development and dominance of coprophagy among the Scarabaeinae. Historical circumstances enabled the Scarabaeinae to meet the opportunities of the grassland biome and adapt to it both trophically and behaviorally, with the result not only that grassland adaptations became basic and dominant in the subfamily, but also that the subfamily became one of the dominant elements in grassland biomes.

There is an accumulation of evidence to suppose that the development and dominance of coprophagy in the subfamily occurred in a biome of the grassland type. Aside from the numbers and importance of Scarabaeinae in grassland formations, other types of evidence support this contention, as follows: 1) The almost complete absence of saprophagous and necrophagous forms in grasslands. The known cases of sapro- and necrophy is isolated and do not represent stenophagous specializations, in contrast to what we see in the tropical forest; 2) the rolling behavior characteristic of Scarabaeini, the appearance and development of which cannot be tied with few roots and predominant in other circumstances. The larva avoids the winter or dry season, and nighttime temperatures.

However, it is arising especially in the different plant associations in different regions of the Central saprophages and omnivores were

The various graminaceous plants—all inhabited by grasslands and the results in humidity and continue to govern insolation and humidity.

Nowhere is this so clearly evident if not all. Scarabaeinae in desert ecotones, European region (1963). 1

1 It should be noted, especially on the basis of the Central Asia and the Oriental arid zones, many climes mountains in genera such as tropical areas of Asia are exclusively fossil.
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The various types of grassland formations — savanna, steppe, prairie, 
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Nowhere is the relationship to the grasslands and their desert eco-
tones so clearly seen as in the Palaearctic and Ethiopian regions (we 
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However, it is not the insolation that is crucial, but rather the insolation arising especially in the Mediterranean regions where grasslands exist in different phytoclimatic regions. The Mediterranean grasslands are characterized by the presence of a large number of saprophagous and necrophagous forms, which from the present study can be considered as a result of the insolation and humidity conditions.

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ively on the basis of his conclusions derived from the species of Europe, Asia Minor, and Central Asia. In these areas all the Scarabaeinae (except a few Onthophagus) are from grasslands or strongly isolated cleared areas. But even though in East Asia and the Oriental Region the Scarabaeinae continue to be abundant in grasslands and arid zones, many species are found in or are even exclusive to tropical forests or mountainous which are covered with tropical or temperate forests. This is seen in genera such as Gymnopleurus, Sisyphus, and Onitis which in Europe or Central Asia are exclusive to grasslands. It is evidently risky to generalize by extending to tropical areas observations made in Europe, North Africa or the Middle East.
In Europe, the species of Gymnopleurus, Scarabaeus, Sisyphus, etc., which penetrate northward, do so following open areas — insolated pastures and steppes. In woods the species of Scarabaeinae are very few (some Onthophagus), and the Geotrupini predominate.

In order to present an idea of the importance of herbaceous biomes in Africa, we will summarize the data from Frey (1961) and Ferreira (1962:49-58) on the Scarabaeinae other than Oniticellini of the Garamba National Park (Congo).

In the different types of gallery forests we find: Anachalcus cupreus (Fabricius), Catharsius polynices Kolbe, Copris carmelita Fabricius, Copris interioris Kolhe, Copris jacundus Gillet, Litocopris muticus (Bohemian), Pedaria cribicrima Waterhouse, and Pedaria taylori Waterhouse. These are eurytopic species, as none is exclusive to the forests, all being also found in savannas. Of the 91 species of Onthophagini known from this region, the following have been collected in the gallery forests: Onthophagus latestriatuus d’Orbigny, O. picturatus d’Orbigny, O. asperipennis d’Orbigny, O. garambae Frey, O. interstitios d’Orbigny, O. curtulus Frey, O. insignis astrosplendens Frey, O. denticularis d’Orbigny, Diastellopalpus condoms d’Orbigny, and Milichius pictivollis Gerstaecker. Some of these Onthophagini seem to be true forest species, including those found inside rotten tree trunks: O. asperipennis and O. garambae.

In the various types of mixed forest-savannas, with sparse to moderately dense woody vegetation not over five or six meters high, we find: Garreta 1 sp., Allogymnopleurus 1 sp., Anachalcus 2 spp., Copris 6 spp., Litocopris 1 sp., Heliocopris 3 spp., Catharsius 3 spp., Metacatharsius 1 sp., and Pedaria 2 spp. Nearly all the species are the same ones found in the predominantly grassland savanna, but several from the latter biome are missing. Among the Onthophagini there are 16 species in the forest-savanna plus 28 common also to the grassland savanna.

In the true savanna with a predominance of various graminaceous plants, with the same trees as in the forest-savanna but more sparsely distributed, we find a surprising wealth of Scarabaeinae: Scarabaeus 1 sp., Kheper 1 sp., Gymnopleurus 1 sp., Allogymnopleurus 1 sp., Anachalcus 2 spp., Copris 11 spp., Litocopris 2 spp., Heliocopris 7 spp., Catharsius 9 spp., Metacatharsius 1 sp., Pedaria 4 spp., and Onitis 1 sp.
There are in addition 33 species of Onthophagini, plus the 28 held in common with the forest-savanna.

It is obvious that in Africa Scarabaeinae predominate in the savanna. The forest-inhabiting species are few, and in the case of the gallery forests which cross the savanna, most of the species inhabiting them are eurytopic.

In other parts of the world, we continue to find a close association between Scarabaeinae and grasslands. However, this relationship is neither a general rule as it is in the Palaearctic region, nor are there as many species living in the grasslands as there are in the Ethiopian Region. In America and in the Oriental Region there are still many grassland species, but those living in forests are also abundant, especially in tropical areas. We can no longer talk about the complete predominance of the relationship between scarabaeine abundance, coprophagy, and grasslands. There are definite tendencies in many groups toward life inside forests and toward necrophagy.

We will now analyze some examples of distributions in the American grasslands. It should be noted again that we have no data on the ecological distribution of Scarabaeinae in Australia.

The Case of Mexico and Guatemala

The distributional differences between grassland and forest species are more accentuated in Mexico and Guatemala because of the contact there between two faunas which are very different in origin and in present characteristics—the Neotropical and Nearctic faunas.

The Alpine taiga and temperate deciduous forests (located at high altitudes in a country of the latitude of Mexico) have a Nearctic or Palaeoamerican entomofauna. The Plateau, covered with grasslands which become transformed into desert or semidesert in the north, has its own entomofauna (partly shared with the southern and especially southeastern United States) of Neotropical origin, but evolved in situ. The subtropical and tropical forests, as well the tropical savannas, have

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7 We are following the terminology proposed by Halfter in 1962 and 1964. For a detailed study of the distribution of some insects in Mexico see the latter paper.
what Halfter (1962: 1964) has called the typical Neotropical entomofauna. It may be seen that in the Plateau and the mountains, ecological separation is accompanied by faunistic diversity, and in fact it is the former which continues to maintain and reinforce the latter.

There are no Scarabaeinae among the insects of Nearctic origin or distribution which occupy the coniferous and mixed coniferous-deciduous forests of montane Mexico and Guatemala. The Geotrupinae predominate in this faunal complex. Some Scarabaeinae penetrate these montane forests, but they belong to genera of Palaeoamerican distribution — usually eurytopic or ubiquitous species which are found both inside the forest and in the Alpine prairies, such that the biome does not seem to be a determining factor in their distribution. We have in this category some species of Coptis and Onthophagus, genera of northern origin but of very ancient penetration in Central and South America (Palaeoamerican groups). Among these are Coptis armatus Harold and Onthophagus chevrolati Harold, found both in the Alpine prairie and in the mixed forest such as the pine (Pinus) forest, attacking horse, cow, or less often sheep dung, and strictly limited in altitude to 2,800-3,100 meters.

On the Mexican Plateau there is a predominance of characteristic species of South American genera (the Plateau distribution pattern). These species are found in grasslands or in ecotones tending toward the desert (the types of formation which predominate on the Plateau), and they only penetrate forests in a very superficial and marginal manner. The characteristics of microclimate and vegetation appear to play a very important role in their distribution. Among these are Phanaeus quadridens Say, Coptis humectus Say, Onthophagus mexicanus Bates. all coprophagous species.

Some of the species with the Plateau distribution climb the slopes of the mountains and partially penetrate the temperate deciduous forests (usually above 2,000 m): these include Phanaeus palliatus Sturm, Phanaeus damocles Harold, and in some areas Phanaeus adonis Harold. However, as a whole the Plateau species, all coprophagous, are inhabitants of the prairie or grassland formations, is a relationship with the determining factors governing climatic barriers. Dichotomius carolinus, cleared of forest and nail rate, horse excrement. Watering holes, and other open forest conditions for the expansion at the expense of the
Neotropical entomofaunas of montane and coastal plains and in fact it is the latter.

Elements of Nearctic origin or coniferous-deciduous Geotrupinae preclude these montane distributions — usually both inside the forest and in this category some of them seem to be a northern origin but of Neotropical (Palaeoamerican Onthophagus and Onthophagus Burmeister in the mixed forest areas, or less often sheep and deer eaters."

The presence of characteristic distribution pattern. Temperature does not seem to be a determining factor in its distribution in the sense that it is found both in temperate regions, such as the United States and Mexico, and in hot and humid tropical regions. It is always associated with grassy or other open formations throughout its range and penetrates forests only occasionally and for a few meters only, nearly always following paths or other cleared areas. It is never found in the interior of the forests.

In 1964 the authors placed traps baited with cow dung, human excrement, and small dead animals in the forests located between Lake Catemaco and the sea (Dos Amates and Sontecomapan) in the southern part of the state of Veracruz, Mexico. D. carolinus was collected in the traps placed in open areas and along paths, never in the overgrown forest areas. Collecting under dung gave the same results.

It is significant that a species, so clearly associated with grassland formations, is strictly coprophagous and prefers cattle dung. This relationship with the biome and with cow dung is one of the determining factors governing its distribution, which jumps geographical and climatic barriers. D. carolinus extends throughout all areas which are cleared of forest and where there is cow dung, or at least human and horse excrement. With the destruction of the forest, the grasslands and other open formations (cultivated or abandoned land, pasture land, roadsides, etc.) have greatly increased their area, creating suitable conditions for the expansion of D. carolinus and other open-land species at the expense of forest species.
Within grassland formations, especially in temperate climates, *insolation* is a very important factor. The Scarabaeinae of the temperate zones are thermophilous and often display certain tendencies toward xerophily, hence insolation and temperature are very important factors in their distribution. It is quite possible that low insolation and consequently low diurnal temperatures, plus a deficiency of large mammal dung, are the factors which almost completely bar European Scarabaeinae from entering forests. This is a phenomenon which becomes more evident as we go northward, where it just about becomes a general rule (see Landin, 1957, for the fauna of Sweden).

There are a few studies which demonstrate how insolation and temperature influence the Scarabaeinae of grasslands. In *Sisyphus schaefferi* (Linnaeus) and *Gymnopleurus geoffroyi* Füessly, temperature acts as a direct stimulus for ball-rolling activities (Prasse, 1957b:592). These activities begin at 20°C and reach their peak between 25 and 30°C. The effect of insolation may be appreciated from the fact that activity becomes rapidly reduced when the sun is blocked by clouds. Humidity, and especially rain, has a negative effect; the beetles bury themselves when rainfall begins, abandoning the ball. Normal winds have no appreciable effect, but strong winds reduce activity considerably. The response of *Gymnopleurus mopsus* Pallas to insolation and heat are very similar to those just described (Prasse, 1958:715). In *Scarabaeus sacer* (Linnaeus), *S. semipunctatus* Fabricius, *S. laticolus* Linnaeus, and *S. variolosus* Fabricius, Heymons and von Lengerken (1929:543) found that the optimum temperatures are between 22 and 30°C; when the sun is covered by clouds activity begins at 25°C.

In North America we have been able to observe that various species of *Canthon* (pilularius Linnaeus, indigaceus chevrolati Harold, humectus Say, and others) are active in summer, especially during the hours of maximum insolation. The activity of these species of *Canthon* is directly related to rains, and in this respect they differ from the Scarabaeini of the temperate zones of Europe, since in the American species the period of maximum activity corresponds with the rainy season or with rainy spells, which in Mexico coincide with the hottest times of year (from the end of spring to the beginning of autumn), and often the greatest activity is seen just after rains.

In Sardinia Scarabaeinae of the humid (rainy) season group as a whole, are very dry (it does not rain), thus we see the Scarabaeinae is synchroous with temperature, which becomes the determining factor. In areas with great or winter rains, temperature, appearance or activity is a determining factor.

Another important factor is the type of soil. Activity is not as important as the presence of the European species (except *O. coenobia* L.) in areas, while *Copris* is not. However, according to van Lengerken (1957), *O. coccothamnus* is found in hard soils in Mexico (Linnaeus) var. *mediterraneus* G. O. (Geljan, 1953).

Loose soils, including Palaeartic Scarabaeinae, which require sandy soil is accented, and easier rolling and mobility.

The important point is that many of its species are rare in desert proper. In the case of *S. punctatus* Fabricius and other species are able...
Formations

Temperate climates. In the temperate climates some tendencies toward certain factors are very important factors in the distribution of large mammal dung beetles. The European Scarabaeinae becomes more evident in general a rule (see Krausse, 1905, 1907). Thus we see the same thing that we see in Mexico, and probably in all temperate or warm climates with well-defined rainy seasons which coincide with the warm months of the year: the activity period of adult Scarabaeinae is synchronized with the duration of rains. Rain now becomes the determining factor governing the activity of the imagos, the temperature being uniformly high throughout the season.

In areas with greater general humidity, or more spread-out rains, or winter rains, temperature becomes the determining factor in the appearance or activity of the adults.

Soil

Another important factor governing distribution in grasslands is the type of soil. According to Bunte (1930), soil factors are as important as the presence of excrement in determining the distribution of the European species of Onthophagus, which prefer sandy areas (except O. coenobita Herbst, which inhabits clay soils). According to von Lengerken (1952), Copris lamaris (Linnaeus) is found in sandy areas, while Copris hispanus (Linnaeus) lives in very hard, clay soils. However, according to Whacher and Allen (1948) C. lamaris is also found in hard soils in southern England. In Poland, Onthophagus vasa (Linnaeus) var. medius Kugel is directly linked to clay areas of pastures, while O. taurus Schreber selects sandy areas with sparse vegetation (Goljan, 1953).

Loose soils, including even pure sand, seem to be preferred by the Palaearctic Scarabaeinae. Under the conditions prevailing in this region, sandy soil is accompanied by greater insolation, higher temperatures, and easier rolling and burial — all consequences of the sparser vegetation.

The important genus Scarabaeus is xerophilous and thermophilous, many of its species being even psammophilous, although none enter the desert proper. In the Mediterranean, S. sacer Linnaeus and S. semipunctatus Fabricius abound in the dunes of the marine littoral, while other species are absent or very rare in the littoral dunes, such as S.
Sardinia. *S. affinis* Brullé is found in non-sandy terrain, in the interior of the island, while in Italy it occurs in areas of alluvial sand. When *sacer* and *affinis* coexist in the same area, it is the first species which occupies the sandy zones (Ronchetti, 1949).

Among the North American species of Scarabaeinae we have various examples which demonstrate the importance of edaphic factors. *Onthophagus oklahomensis* Brown is a species closely related to *O. pennsylvanicus* Harold and both may be found in the same localities, but the former species is restricted to sandy areas (Howden and Cartwright, 1963:82). Another North American species of sandy soils (shaded in this case) is *O. medorensis* Brown (Howden and Cartwright, 1963:115). Another example in which soil may act as an isolating factor between two closely related species is the case of *Canthon imitator* Brown and *C. pilularius* (Linnaeus). Both species coexist in Oklahoma and Texas, but the former is restricted to sandy areas where it replaces *pilularius* (Brown, 1946). However, it should be noted that in areas where *imitator* does not occur, such as Georgia and parts of Florida, *pilularius* is typical of sandy areas (Matthews, 1963a:78-79).

In the Antilles, the Jamaican *Phanaeus* (*Sulcophanaeus*) *varniflex* (Linnaeus) is largely restricted to the red laterite or bauxitic soils of the island, although a few individuals may be encountered elsewhere. In Martinique, and possibly other islands of the Lesser Antilles, *Atrechus illaeus* (Harold) is restricted to sandy, xeric grazing lands.

Some species, while preferring a certain type of soil, are capable of nidificating in very different types, although with differences in the depth of the nest. Thus we have, for instance, *Scarabaeus sacer* Linnaeus in Central Asia nesting 40 cm down in loose soil and 7-20 cm in more compact or stony soil (clay in all cases) (Medvedev and Medvedev, 1958:913).

Colonization of Arid Areas

Colonization of xeric biotopes by Scarabaeinae is preceded by three types of adaptations: affinity for areas which are strongly isolated and have elevated daytime temperatures, preference for sandy soils, and coprophagy. Some species which enter the deserts do so by following

---

the camel caravan route, as far as we know, and others by their natural migration routes.

In the Palaearctic region, species such as *Onthophagus* are found in the edaphic desert. In North American steppes and deserts the sandy soils are adapted to extreme conditions (see Section 20) and there may be found on the borders of the deserts or on sandy spots.

Inhabiting very dry areas is *Canthon*, which, while not exclusive to the desert ecotones, is largely adapted to extreme conditions.

*Canthonoidia* are mainly found in the sandy beds of dry areas, far from any kind of uniform vegetation. In the subtribe *Eucrania*, the southern part of Brazil extends to the south of São Paulo with less than 800 mm. The characteristic of the

---

The distribution of certain species tends to be more or less randomly distributed, being characterized by the fact that they are not exploited to the point of extinction. In the edaphic desert of *Onthophagus*, a typical example of adaptation is finding two dozen *Onthophagus laevis* (cited as *laevis* D.), but this is not significant; on some occasions 600 individuals
in terrain, in the interior of alluvial sand. When the first species which we have various xerophilous factors. Onthophagus related to O. pennsylvaniae are related to the same localities, but the sandy soils (shaded, in Cartwright, 1963:115), as well as the factor between imitator Brown and Cartwright, 1963:115), replacing pilularius in areas where imitator is typical

Scaphophanaeus carnifex lives in sandy or bauxitic soils of the Lesser Antilles. Ateuchus inhabiting arid lands.

...of soil. are capable with differences in the two taxa, Scaphophanaeus sacer Linneaeus and 7-20 cm in more Balthasar and Medvedev.

...is preceded by three strongly insolated months for sandy soils, and do so by following the camel caravan routes (Heymons and von Lengerken, 1929:533) and, as far as we know, all the species of arid regions are coprophagous.

In the Palaearctic there are numerous psammophilous species which are found in the ecotones of the prairie or steppe merging with the desert. In North Africa, the genus Babas lives in the driest sandy steppes. Under the same conditions we find Synapsis tmolus (Fischer) in the semi-desert steppes of Central Asia, a good example of a species adapted to extreme temperature changes and little rain. Its deep nest (see Section 20) is a response to these environmental conditions. On the borders of the Sahara Desert, Mennatium and Mnematidium are found on dunes with sparse vegetation (Balthasar, 1963[1]:139, 144).

Inhabiting very arid places in North America is the genus Borecanthos, which, while not being truly a desert form, penetrates deeply into desert ecotones.

Canthonidia rubromaculata (Blanchard) in Argentina lives in the sandy beds of dry streams, or those which are dry most of the year, far from any kind of vegetation and never occurring in places with abundant vegetation (Martinez, in litt.). A truly xerophilous group is the subtribe Eucraniina, exclusive to Argentina, which occurs from the southern part of Buenos Aires, Rio Negro, and Neuquen provinces to the south of Salta, in sandy zones with an annual rainfall of less than 800 mm. The canthonine Syncalophus patagonicus Martinez is characteristic of the cold deserts of Patagonia (Martinez, 1959).

Aggregation

The distribution of Scarabaeinae in grasslands and other open formations tends to be clumped. Not only is the excrement unequally distributed, being concentrated in certain spots, but also many mounds are not exploited while others harbor dozens of individual beetles. We have been able to observe this sort of aggregation in various species of Onthophagus, Ateuchus, Canthon, etc. Lindquist (1935:6-7) mentions finding two dozen or more individuals of Canthon pilularius (Linneaeus) (cited as laevis Drury) attacking a mass of cow dung and destroying it completely; on hot days in Texas there may be 50 to 100, exceptionally 600, individuals in a single cow pat. Balthasar (1963[1]:64)
mentions similar cases, citing a mound of cow dung 35 cm in diameter with 400 to 450 individuals of various species of *Gymnopleurus* in it.

11. Forests

The different types of forest have very different scarabaeine faunas
with regard to both composition and abundance. In the taiga and other
forests with a predominance of coniferous trees in the Northern Hemi-
sphere, Scarabaeinae are very rare, their place being occupied by Geo-
trapini. In the temperate deciduous forests there are a few species, but
it is in the tropical forest that Scarabaeinae achieve a position of major
importance in the forest biome.

**Scarabaeinae in the Tropical Evergreen Forest**

*The case of Mexico and Guatemala.*—The tropical evergreen forest
in Mexico and Guatemala is found within the limits of the Neotropical
Region and has a typical scarabaeine fauna restricted to this biome.
The Scarabaeinae of open areas do not enter the forest, not even such
species as *Canthon indigaceus* *chiapas* Rehmsen, which inhabits the
clearings inside the wooded regions of southern Mexico and may be
found on the edges of the forest but never in the interior, or *Dichotomius
carolinus* (Linnaeus), a widespread species with great adaptive capa-

cities.

The following species of Scarabaeinae are exclusive to the tropical
forest of southern Mexico and Guatemala: *Uroxyx boneti* Pereira and
Halffter, various subspecies of *Glyptotrichium viridiz* (Beauvois), Geo-
canthus femoralis Chevron, *Malagonella astyanax* *guateaca* (Harold),
all the species of *Eurysternus*, and most of the species of *Deltochilum*
and *Dichotomius*, as well as many *Phanaeus*, such as *melampus* Harold,
*amorphus* (Harold), *chrysemis* Harold, and *endymion* Harold.

All the genera mentioned are South American, and with the excep-
tion of *Phanaeus* and *Dichotomius* their penetration into Mexico is
restricted almost entirely or entirely to the tropical forest. *Phanaeus*
and *Dichotomius* advance further northward and, both in the tropical
zones and in the Plateau, have grassland species which are different
from those which inhabit the tropical forest.

The following are the Scarabaeinae of Mexico and Guatemala:

<table>
<thead>
<tr>
<th>Daytime</th>
<th>Nighttime</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Canthon c. capinii</em></td>
<td><em>Canthon c. capinii</em></td>
</tr>
<tr>
<td><em>Onthophagus batesi</em></td>
<td><em>Onthophagus batesi</em></td>
</tr>
<tr>
<td><em>Deltochilum (D.)</em></td>
<td><em>Deltochilum (T.)</em></td>
</tr>
<tr>
<td><em>Deltochilum (T.)</em></td>
<td><em>Phanaeus (Cephalonia)</em></td>
</tr>
<tr>
<td><em>Deltochilum (D.)</em></td>
<td><em>Phanaeus (Cephalonia)</em></td>
</tr>
<tr>
<td><em>Ateuchus</em> sp.</td>
<td><em>Onthophagus (Bonettii)</em></td>
</tr>
<tr>
<td><em>Onthophagus (Bonettii)</em></td>
<td><em>Onthophagus (Bonettii)</em></td>
</tr>
</tbody>
</table>

Under the same traps, and not more than 100 meters away, the follow-
ing necrophagous species were collected: *Copris laevis* (Hbst.), *Copris
discolor* (Bopp.), *Copris laevis* (Hbst.), *Copris laevis* (Hbst.),
and *Copris laevis* (Hbst.).

The terms "rare" are relative, and do not apply to the common species.
The following analysis of collection data from certain forested areas of Mexico and Guatemala helps us to understand the role of the Scarabaeinae in this biome.

Table 1

| Scarabaeinae collected in Sentecomapan, Veracruz, Mexico, on 26 and 27-IX-1964 by E. G. Matthews and G. Halffter. |
| Daytime — Necrophagous species |
| Canthon c. cyanellus Lecente (very abundant) |
| Daytime — Coprophagous species |
| Onthophagus batesi Hewden and Cartwright (at dusk, not abundant) |
| Nighttime — Necrophagous species |
| Deltochilum (D.) pseudoparile Paulian (very abundant) |
| Deltochilum (T.) gibbosum var. sablaeae Bates (abundant) |
| Phanaeus (Coprophanacus) telamon corvus Harold (very abundant) |
| Nighttime — Coprophagous species |
| Deltochilum (T.) gibbosum (Fabricius) (very rare) |
| Deltochilum (D.) pseudoparile Paulian (rare) |
| Phanaeus (Phanacus) chryseicollis Harold (very rare) |
| Areuchus sp. (abundant) |
| Dictymius sp. (very rare) |
| Onthophagus batesi Hewden and Cartwright (very abundant) |

Under horse dung, but not in the traps baited with human feces. Copris laeviceps Harold was collected, Areuchus sp. (the same species as in the traps) and numerus Onthophagus batesi Howden and Cartwright were also collected under horse dung.

1 We collected with traps baited with fish in the early stages of decay (for necrophagous species) and human excrement (for coprophagous species). All traps were set inside the forest. The horse dung was on a road crossing the forest. The forest was of the tropical evergreen type, very humid, with an undergrowth of arums, and very near the sea at an altitude of about 50 m.

The terms “rare” and “abundant” refer to the number of beetles that fell into the traps, and are not meant to be an estimate of numbers present in the area.
Table 2

| Scarabaeinae collected in Dos Amates (Catemaco), Veracruz, Mexico, on 24-26-IX-1964 by G. Halffter and E. G. Matthews.¹ |

Daytime
No really diurnal species were collected

<table>
<thead>
<tr>
<th>Nighttime — Necrophagous species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deltochilum (D.) pseudoparicle Paulian (abundant)</td>
</tr>
<tr>
<td>Phanaeus (Coprophanaeus) telamon corinthus Harold (abundant)</td>
</tr>
<tr>
<td>Hroxyx boneti Pereira and Halffter (abundant)</td>
</tr>
<tr>
<td>Neocanthidium sp. nov. (not abundant)</td>
</tr>
<tr>
<td>Copris laeviceps Harold (abundant)</td>
</tr>
</tbody>
</table>

Nighttime — Coprophagous species

| Phanaeus (Phanaeus) endymion Harold (not abundant) |
| Hroxyx boneti Pereira and Halffter (very rare) |
| Onthophagus batesi Howden and Cartwright (not abundant) |

In horse and cow dung located along a footpath which crosses the forest the following were collected (buried at shallow depth under the dung): Onthophagus batesi Howden and Cartwright, Copris laeviceps Harold, and Ateuchus sp. One specimen of Euryternus magus Laporte was collected beside some horse dung.

¹ We collected with traps baited with small dead mammals, birds, and reptiles (for necrophagous species) and human excrement (for coprophagous species), also directly under cow and horse dung. All collecting was done inside the forest, which was of the tropical evergreen type, very humid, at an altitude of about 100 m and fairly near the sea (not as near as in Sonetecomapan). Between this locality and that of Table 1 there is a distance of about 15 km.

The terms "rare" and "abundant" refer to the number of beetles which fell into the traps, and are not meant to be an estimate of numbers present in the area.

Several conclusions can be drawn from Tables 1 and 2 on the role of the Scarabaeinae. In the first place, all the coprophagous groups (or even species) do not penetrate the forests to northern Sonetecomapan.

In the second place, we found outside the traps a complete exclusion of the necrophagous Scarabaeinae. There is no doubt that the large group of D. lugubris Boheman (scarabaeid) and its allies and relatives did not penetrate the dense forest area where we worked. They are nocturnal, hence their penetration inside the forest is dependent on humidity. The beetles which we collected are what maintain the human excrement (coprophagous species) and penetrate by way of the footpath.

During their course of exploration, we observed many times the circular exclusion of green vegetation. The two preceding tables show that the footpath set the same nights and at the same hours as those at Sonetecomapan and the surrounding area. This includes, apart from the fact that the species of Phanaeus and Copris are abundant in the area, the same species are abundant in the area inside the forest. It is most likely that the exclusion of the footpath is maintained by all Scarabaeinae.

The third conclusion is that there are two distinct faunas of Scarabaeinae, and only Onthophagus and halffteri are seen flying at dusk in the area of Sonetecomapan, whereas most of the Scarabaeinae are not.
which crosses the depth under the light. Copris laevicaps laporte

Several conclusions may be drawn from the data presented in Tables 1 and 2 on the role of Scarabaeinae in the Mexican tropical forest. In the first place, all the species are strictly Neotropical. They belong to groups (or even species) which extend throughout the Central American forests to northern South America.

In the second place, all are strictly stenotopic species they are not found outside the tropical forest and, at the same time, there is a complete exclusion of the forms which inhabit open areas. There can be no doubt that the large trees and the roof of vegetation that they create play a very important role in governing the distribution of Mexican Scarabaeinae. For example, Dichotomius carolinus (Linnaeus) and Copris lagabris Boheman (species of cleared areas) reach the edge of the forest and penetrate by way of paths and clearings, but are never found inside the dense forest itself. This is all the more remarkable as both species are nocturnal, hence shade by itself cannot be the factor which impedes their penetration into the forest. Some delicate microclimatic mechanisms dependent on humidity, temperature, and possibly foliage density must be what maintain the ecological separation; however we do not know what they are or how they operate.

During their collecting experience the authors have been able to observe many times the importance and precision of this ecological separation. The two previously mentioned species were collected in traps at the very edge of the forest, while they did not fall into identical traps set the same nights 50 or 100 m inside the forest itself. In Dos Amates and Sontecomapan there is a rich scarabaeine fauna of open terrain which includes, apart from the two species previously mentioned, two species of Phanaeus and Canthon indigacus chiapas Robinson. These five species are abundant in the clearings and pastures, but not one was collected inside the forest. It is noteworthy that these five species of cleared areas are all coprophagous.

The third conclusion we can draw from the data is that there are two distinct faunas inside the forest — the nocturnal and the diurnal (only Onthophagus batesi is not well defined in this respect; it was seen flying at dusk and in the early hours of the night). In open areas most of the Scarabaeinae are diurnal, while in the forest the great
majority is nocturnal. Only Canthon c. cyanellus Leconte is diurnal and numerically important in the forest.

It has been said many times that life in tropical rain forests is primarily nocturnal, and the Scarabaeinae seem to support this contention. Further on we will emphasize this point again, with other examples.

Finally, we have a fact of great ecological and evolutionary significance in the Scarabaeinae: the deviation toward necrophagy. In open land, a few meters from the areas collected and tabulated in Tables 1 and 2, the Scarabaeinae are all coprophagous. Inside the forest we have, in Sontecomapan, three strictly necrophagous taxa, two primarily necrophagous taxa (Deltochilum pseudoparile and D. gibbosum), one coprop-necrophagous taxon (Copris laeviceps, which, while not coming to the human feces, was collected in numbers under horse dung, and in Dos Amates came to cadavers), and only four strictly coprophagous taxa. Apparently coprophagy and necrophagy have the same value in numbers of species, but in numbers of individuals the necrophagous forms are more abundant.

In Dos Amates the importance of necrophagy was even greater. There were instances in which no scarabaeines came to the traps baited with human excrement, and intact horse droppings were found inside the forest. In numbers of species, there were two strictly necrophagous ones here and two almost exclusively necrophagous, but with a slight affinity for excrement (this includes Deltochilum pseudoparile which, although not found in excrement at Dos Amates, came in very small numbers to it at Sontecomapan). In addition, there was one copro-necrophagous taxon and four strictly coprophagous ones. Once again, the necrophagous forms were more abundant in numbers of individuals. A good example of the situation here is provided by a human fecal trap to which there came only one specimen of Uroxyx boneti during the whole night, while in a nearby dead rabbit trap there were six Copris laeviceps, two Necanthidium n. sp., and five Uroxyx boneti. In spite of the fact that at some time during the night the bait was removed by some predatory animal.

Sciarabaeinae collected 25 km from

Inside the forest:

Uroxyx boneti Per. & Hald.
Copris laeviceps Hald.
Phanaeus (Copro- in flight)
Onthophagus carpinus Hald.
Onthophagus acer
Onthophagus cicla
Onthophagus cornutus

In a clearing:

Copris incertus Say
Onthophagus bellicosus
Onthophagus thoracicus
Onthophagus manillae

Table 3 shows dominance of necrophagy, not a single species.

Collection data:

Dos Amates, in May:

Tropical evergreenforest
Pereira and Haldór

No collecting
excrement unless otherwise noted.
Leconte is diurnal and tropical rain forests is to support this contention, with other examples, and evolutionary signif-
icient and necrophagy. In open
summary tabulated in Tables 1 and 2 the forest we have.
the two primarily necrophagous
coprophagous, one copro-
ible not coming to the
in these dung, and in Dol
ne coprophagous taxa.
ance value in numbers coprophagous forms are
was even greater.
utes to the traps baited
coprophagous ones with a slight affinity
able which, although
very small numbers
coprophagous forms in the necrophagous
coprophagous taxa. A good example
trap to which there
whole night, while
Cephus, two Neocan-
the fact that at some
 predatory animal.

Table 3

<table>
<thead>
<tr>
<th>Scarabaeinae collected in Finca San Carlos, on the Coatzacoalcos River. 25 km ESE of Palomares, Oaxaca, Mexico in May, 1959, by G. and V. Halffter.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inside the forest 2</td>
</tr>
<tr>
<td><em>Eurysternus mexicanus</em> Harold (nocturnal)</td>
</tr>
<tr>
<td><em>Uroxyx boroni</em> Pereira and Halffter (nocturnal)</td>
</tr>
<tr>
<td><em>Copris carneiceps</em> Harold (nocturnal)</td>
</tr>
<tr>
<td><em>Phanaeus (Coprophanaeus) telamon eurythus</em> Harold (nocturnal, taken in flight)</td>
</tr>
<tr>
<td><em>Onthophagus carpophilus</em> Pereira and Halffter (diurnal, feeding on fruits of <em>zapote mamey</em> (<em>Calocarpum zapota</em>))</td>
</tr>
<tr>
<td><em>Onthophagus acuminatus</em> Harold (nocturnal)</td>
</tr>
<tr>
<td><em>Onthophagus cyclographus</em> Bates (nocturnal)</td>
</tr>
<tr>
<td><em>Onthophagus corrosus</em> Bates (nocturnal)</td>
</tr>
<tr>
<td><em>Onthophagus marginicollis</em> Harold</td>
</tr>
</tbody>
</table>

In a clearing in the forest

*Cephus incertus* Say

*Onthophagus belothinum* Bates

*Onthophagus rhinolopus* Harold

*Onthophagus marginicollis* Harold

Table 3 shows, once again, the stenotopic character and the predominance of nocturnal forms in the Scarabaeinae of the tropical forest; not a single species is shared between the two types of terrain indicated.

Collection data obtained in Rosario Izapa, Chiapas, and Retalhuleu, Guatemala, in May, 1963, by Antonio Martinez and Gonzalo Halffter.

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1 Tropical evergreen forest at 150 m altitude. These data were first published by Pereira and Halffter (1961).
2 No collecting was done with carrion baits. All species were collected in excreta unless otherwise indicated.

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confirm many of the observations made from the previous data. In both places collecting was done in tropical evergreen forest (up to 500 m above sea level) or in cacao plantations which have replaced this type of forest but which have an interior microclimate fairly similar to that of the original biome. However, it should be noted that this collecting was done on the edges of the forest and so turned up some species of open terrain which came in from the outside. In the carrion traps in the daytime Gaphyrocanthon viridis championi (Bates) (previously Canthon championi Bates) was collected. This canthonine came in large numbers to the traps in the morning, while none was collected in the afternoon. In the afternoon and evening numerous Onthophagus belorhinus Bates were collected, as well as a very few Onthophagus batesi Howden and Cartwright and a few Phanaeus (Coprophanes) telamon corithus Harold (a predominantly nocturnal species, but one which may be caught at dusk).

In the excrement traps in the daytime a few Gaphyrocanthon w. championi (Bates) were collected (a euryphagous species, but one showing a preference for necrophagy), as well numerous Onthophagus batesi Howden and Cartwright, collected in the afternoon.

At night the fauna is more abundant, both in numbers of species and of individuals. The carrion traps yielded Phanaeus (C.) telamon corithus and Phanaeus endymion Harold, both represented by only a few specimens. The human fecal traps yielded large numbers of Mala­goniella astyanax guateca (Harold) (previously Megathopa yucateca Harold). This canthonine began arriving at dusk and kept coming until 22:00 hrs. In the same traps at dusk numerous Onthophagus batesi Howden and Cartwright began coming and continued until about 22:00 hrs. when they ceased activity completely (this shows that activity in this species is limited to dusk and the early hours of the night). From 22:00 hrs on Copris lugubris Boheman began to arrive. One specimen of Deltochilum scabriusculum Bates was also captured. In some cases where the traps were set near the edge of the forest, Dichotomius carolinus (Linnaeus) was also collected: this species is very abundant in the adjacent open land.

In Rozario Izapa, in rotten “jack fruit” (Artocarpus integrifolium, an introduced tree), a large number of Onthophagus belorhinus Bates was collected during the night.

Other areas.—We confirm the decisive importance of Scarabaeinae in the vegetation of South American forests and restricted to the tropical evergreen forest biome, which has replaced this type of forest but which has an interior microclimate fairly similar to that of the original biome. In both places collecting was done on the edges of the forest and so turned up some species of open terrain which came in from the outside. In spite of this, the decisive importance of Scarabaeinae must be acknowledged, and confirmed by the data of the present work, with the exception of the region around the Sierra de la Ventana, which is characterized by xerophytic vegetation.

All the above-inhabiting in the brood of the investigated individuals emerging from the litter collected comprising 27 species of tropical evergreen forest. D. carolinus (Linne) is the most typically forest scarab associated with many of the species mentioned above.

Conclusions on the tropical evergreen forest.—In spite of this, the data of the present work, with the exception of the region around the Sierra de la Ventana, which is characterized by xerophytic vegetation.
Other areas.—We have a few data from South America which confirm the decisive importance of the biome in governing the distribution of Scarabeinae. Among the species which are more strictly stenotopic and restricted to the tropical evergreen forest, are those which feed on decaying vegetable matter (see Section 3). The Scarabeinae of the South American forests include both coprophagous species and numerous necrophagous ones, in many instances definitely stenophagous.

A case of forest adaptation within a genus is provided by Glaphyroncanthon (see also Martínez, Halffter, and Halffter, 1964). The probable origin of this genus is to be found in the forests of the Amazon Basin, from which we have drawn four phyletic lines, all associated with forests. The species which extends furthest north, G. viridis (Beauvois), includes a subspecies, G. v. viridis, which exceeds the limits of the tropical forest and extends through northeastern Mexico to the central and eastern United States, but even this species seems to be found principally in the temperate deciduous forests of the region, continuing to be linked to forest biomes. Another subspecies, G. v. leechi Martínez, Halffter, and Halffter, is collected in Mexico both in tropical forest and in cleared land. A third subspecies, G. v. corporali Balbisar is characteristic of the Balsas Valley in Mexico, a region of mesophytic and xerophytic vegetation. Among the other species, G. pilluliformis (Blanchard) and G. coeruleicolor (Blanchard) follow the subtropical gallery forest down to the level of Buenos Aires in Argentina. G. coerulescens (Schmidt) is found in this habitat, but in southern Brazil and in the Sierra de la Ventana and Sierra de Córdoba in Argentina — areas with xerophytic vegetation. This is the southernmost species.

All the above-mentioned species may be considered to be forest-inhabiting in the broad sense (only G. v. viridis and G. v. leechi partly emerge from the forests). Except for these two species, the remainder, comprising 27 species, all lives strictly within the confines of the tropical evergreen forest of South and Central America and represents some of the most typically forest-inhabiting Scarabeinae, including some species associated with mammals (Section 5).

Conclusions on the natural history of Scarabeinae in the tropical forest.—In spite of the notable absence of ecological information available from the literature, we can come to the following tentative conclusions concerning the role of Scarabeinae in the tropical evergreen forest.
1. Most of, in some localities, all the species of Scarabaeinae inhabiting the tropical evergreen forest are stenotopic and strictly limited to this biome.

2. In Central America (including southern Mexico) and South America there are many necrophagous species, about equal in number to the coprophagous ones. Although several of these species are euryphagous, some (both necro- and coprophagous) are strictly stenophagous and others show a strong preference for one trophism or the other.

3. Inside the forest, the Scarabaeinae are much more numerous, both in numbers of species and of individuals, during the night hours, In grasslands and other open terrain most of the species are diurnal.

4. The instances of saprophagy and ectoparasitism are relatively numerous (see Sections 3 and 5) and almost exclusive to tropical or other types of forest (except for these saprophagous species associated with ants).

Of particular importance to the Scarabaeinae of tropical forests is the influence that man is exerting on this type of biome. In recent years the destruction of the tropical evergreen forest has reached alarming speed and proportion. This is a general phenomenon, but is especially serious in numerous regions of the Americas. In southern Mexico the destruction of the tropical forest, either by clearing for pasture lands and corn fields, or by profoundly altering it for coffee or cacao cultivation, is strikingly influencing the distribution of the flora and fauna, including the Scarabaeinae. We have seen that the tropical forest species are stenotropic, so that when their habitat is destroyed or altered, they disappear or become reduced to small populations.

Furthermore, the mere presence of man, even when he does not completely destroy the biome, leads to a brutal extermination of the large mammals and birds, which evidently must also affect the Scarabaeinae living on their excrement.

The open areas, which are often at a disclimax stage of dense bushes, are expanding. This in turn brings about an expansion of the Scarabaeinae adapted to these conditions, the most conspicuous and aggressive of which is Dictyotomas carolinus (Linnaeus), a very heterogeneous species, possibly with several subspecies, which is rapidly expanding in conjunction with the clearing activities and the cattle industry.

The destruction of the tropical forests of which far exceeds what the latter (usually considered) serves then if properly subject to conservation measures, and is almost exclusive to tropical or other types of forest (except for those saprophagous species associated with ants).

Puerto Rico.—Only a mesophytic forest exists on the southwest coasts. Today there are surviving to a considerable extent, scarce species of Puerto Rican Scarabaeinae of one of us (Matthews, 1965).

The Scarabaeinae genera: Canthodiscus, of which five species, oakleyi Chapin and erroneously in Matthew, is Dichotomius carolinus Harald. We will refer to (nutt. nec Harold), in well-shaded, humid areas, cases dense thicket, trees, shrubs, etc., the septic woods and swamps, both genera are the dominant biome of the Caribbean made open biomes of the Scarabaeinae.

Altitude is the determining factor. One eurytopic species lives in almost any type of forest up to 4,000 ft. This wide distribution is a clinal nature acet...
The destruction of the tropical forest is at a pace and on a scale which far exceeds what is happening to temperate or boreal forests. The latter (usually coniferous) are being exploited commercially, which preserves them if proper forestry practices are employed, and the former are subject to conservation measures in many countries and are thus partly spared from destruction.

**Insular Forests**

*Puerto Rico.*—Originally, Puerto Rico was covered with tropical mesophytic forest except for a xerophytic band along the south and southwest coasts. Today this forest has been largely destroyed, although there are surviving pockets scattered throughout the island, some of considerable extent, such as the Luquillo Experimental Forest. The Scarabaeinae of Puerto Rico were collected intensively and systematically by one of us (Matthews) and a detailed work on this subject is in press (Matthews, 1965).

The Scarabaeinae of the island are grouped into two canthonine genera: *Canthonella*, with one species, *C. parva* Chapin, and *Canthochilum*, with five species: *C. andij Chapin, C. hispidum* Chapin, *C. oakleyi* Chapin, and two new ones. One of the new ones is referred to erroneously in Matthews (1965) and previous literature as *histroides*. We will refer to it in the present work simply as "*histroides*" (untt. nev Harold). Both genera are found in the mesophytic forest or in well-shaded, humid areas covered with arboreal disclimaxes or in some cases dense thickets. They are absent from the halophytic forests (mangroves, etc.), the seaside forests growing in alluvial sand, and the xerophytic woods and scrub in the southwest part of the island. In other words, both genera are found in the remnants of what used to be the dominant biome of the island; they are completely absent from the man-made open biomes or "culture-steppe" (pastures, etc.), which are devoid of Scarabaeinae.

*Altitude* is the determining factor in the distribution of these canthonines. One eurytopic species — *Canthochilum "histroides"* — is found in almost any type of forest at almost any altitude, from sea level to 4,000 ft. This wide distribution is accompanied by geographical variation of a clinal nature according to altitude.
The remaining five species of canthonines are all limited to three distinct altitude belts, the lowest one occupied by *Canthochilum* n. sp. and one subspecies of *Canthonella parva* Chapin, the middle one occupied by *Canthochilum oakleyi* Chapin, and the other subspecies of *Canthonella parva*, and the highest one occupied by *Canthochilum hispidum* Chapin (the only wingless species). The exact altitude limits of these belts vary according to the longitude, being low in the east (the Luquillo Range) and high in the west (the Central Range). Thus in the Luquillo Range the limits of the three distribution belts are approximately 0-1,000 ft, 1,500-3,000 ft, while at the level of Cerro de Punta, in the Central Range, the limits are approximately 0-2,000 ft, 2,000-3,300 ft, and 3,300-4,000 ft. Since *C. hispidum*, the only species occupying the highest belt, is "pushed" upward in the west, its range there has become fragmented on mountain peaks. This has resulted in the formation of at least two distinct subspecies in the center and west, and only one (different one) in the eastern half of its range. One species, *Canthonella parva*, has two subspecies which occupy each a different belt: in the center and west the lowest one, in the east the middle one, apparently without any direct contact. The isolation of these subspecies is therefore maintained by ecological factors.

There is very little overlap between these distribution belts and therefore a minimum of contact between species, although in certain spots, such as 1,500 ft in Luquillo, up to four species may coincide. Where there is complete coincidence throughout a belt, for instance in the case of *Canthonella parva* and one or more species of *Canthochilum*, mutual contact may be minimized by other factors, in this case by the fact that *Canthonella* is fully diurnal and the species of *Canthochilum* are fully nocturnal. We thus see the same division into diurnal and nocturnal forms, with a predominance of the latter, that we saw in the Mexican forests.

The eurytopic *Canthochilum "histeroides"* is evidently, by its distribution, tolerant of a wide fluctuation in environmental factors. We would expect it to be able best to withstand human interference and intrusion, and in fact it is the only species to be found in small patches of woods, such as wooded hilltops above cow pastures, lightly wooded stream-sides in agricultural country, and in coffee plantations.

The factors which control the distribution of the stenotopic species are obviously the temperature and humidity conditions of the microcli-
There are all limited to three species of Canthochilum n. sp. The middle one occupied 3,000 ft. while at the limits are approxi- mately 3,000 ft. Since C. hispidum, "pushed" upward in the mountain peaks. This is a distinct subspecies in the eastern half of the island. and the other two subspecies which represent the lowest one, in direct contact. The distribution belts and distribution belts and may coincide. Where for instance in the case of Canthochilum, mutual interference and interactions may coincide. Where for the species of Canthochilum are fully of the lowland, nocturnal and nocturnal "pushed" upward in the Puerto Rican canthonines have been observed to feed on snail and bird excrement, including a regurgitated owl pellet.

Other Antillean islands.—Among the canthonines of the Antilles, the pattern of ecological distribution seen in Puerto Rico is repeated. The species are restricted to natural forests, and distributed according to altitude. In the genus Pseudocanthon, for instance, there is one lowland (0—50 ft) and one highland (±1,500 ft) subspecies in Jamaica. One lowland (0—550 ft) and one highland (1,400—2,800 ft) species in Dominica. and one species in Guadeloupe found only below 1,000 ft. In Santo Domingo there is one lowland (±500 ft) and one highland (±6,000 ft) species of Canthonella, similarly found only in forests. One canthonine found on the latter island, Nesocanthon violaceus (Olivier), appears not to be a forest inhabitant, being found abundantly in low-altitude cow pastures, but a trap set well inside a xerophytic forest near Bani, Dominican Republic, yielded no less than 72 individuals of this species, indicating that this is really a xerophytic forest species which has been able to adapt to pasture conditions. In Cuba, of the eight species.

- mate, which in turn are controlled by the effects of altitude and prevailing winds. The exactness with which these distribution belts may be delineated, and the almost geometric precision with which they rise westward (see Matthews, 1965), are due to the almost constant direction and intensity of the winds affecting the island, and the consequent relatively constant year-around climate.

The Puerto Rican canthonines are general coprophages and may be trapped in large numbers with cow or human excrement. Multiple-choice bait trapping in the Luquillo forest has revealed a strong preference for human excrement in all studied species, followed, in preferential order, by rat, cow, cat, and snail excrement. It is curious that the most preferred excrement in this series is one that did not occur naturally before the advent of man. This is, however, not too surprising, as we may expect that in a general (euryphagous) coprophage there will be an adaptation to choose whatever excrement is most nutritious, a maximum flexibility in this respect being of selective advantage. Before the advent of man (believed to be about 2,000 years ago), these beetles fed on the excrement of the insectivores and hystricomorph rodents present on the island. Their excrement must have been similar to that of Rattus which now abounds in the forests and is now in the No. 2 position of preference.

Under natural (non-trap) conditions the Puerto Rican canthonines have been observed to feed on snail and bird excrement, including a regurgitated owl pellet.
of *Canthochilum* known (but mostly undescribed). Three are widely distributed in the lowlands, but the remaining ones are extraordinarily localized, usually known from only a single mountain in the interior (Zayas and Matthews, 1966).

The other (non-canthenine) groups of Antillean Scarabaeinae are apparently not forest dwellers and respond much less to altitude factors, with the exception of a newly discovered *Drepanocerus* and two known species of *Uroxys*, all of which are forest species. Among the open-land groups, we have for instance *Onthophagus antillarum* Arrow found in Dominica and Martinique in cow pastures at nearly all altitudes (up to 2,400 ft on Mt. Pelé). *Ateuchus illaeus* Harold on Martinique is restricted to the highly xeric, sandy grazing lands in the rain shadow of Mt. Pelé, between St. Pierre and Précheur.

*Phanaeus (Sulcophanacus) curtifex* (Linnaeus) in Jamaica is largely restricted to the red laterite soils (Eauxite) of the central part of the island, at all altitudes. The latter two cases are clear examples of distribution according to edaphic factors, relatively independent of altitude. In Jamaica also, *Oniticellus antillensis* Laporte is abundant in all pastures and roadsides from sea level to at least 2,000 ft. An extremely wide altitude distribution is shown by *Onthophagus albicornis* Beautuis, which is found at all altitudes from 0 to 4,500 ft in Santo Domingo, in cow pastures or woodlands, including the high altitude pine forests which are now largely destroyed. In all of these species, in contrast to the canthenines, *Drepanocerus*, and *Uroxys*, response to altitudinal factors is minimal and this seems to accompany an adaptation to the open-terrain types of biomes, in the same way that altitude sensitivity seems to accompany an adaptation to forests.

As natural cleared areas are greatly restricted in the Antilles (their original locations probably being indicated by such names as "Savane", "Grande Savane", "Sabana Alta", etc., persisting as place-names), these non-canthenine species may all have been originally xerophytic scrub inhabitants, and the creation of extensive cow pastures by European man must have greatly favored these species, at the expense of the mesophytic forest dwelling canthenines (except *Nesocanthon violaceus*). *Uroxys*, and *Drepanocerus*.

As far as we know, all Antillean Scarabaeinae, even the forest species, are coprophagous; carrion-baited traps collect very few of the known species. This is somewhat unexpected and inexplicable at the moment.

Mauritius — The island is well isolated in the Indian Ocean, and the forest species here are extremely sensitive to altitude and humidity. Like the Peninsular Indian forests, but unlike the canthenines species here do not seem to form a patchwork of partial altitudinal distributions, but rather as a result of the extreme differences in rainfall, as given by Vinson being 114 acres, *N. reynardi* Vinson (winged) 100 acres. The first species occurs on the southeastern plateau of Mauritius, while other species occurs on the western plateau of Mt. Ory the three species *N. rotundatus* occurring together, or in the north of Mt. Ory, only *N. le Pouce* only *N. reynardi*. An extraordinary rest

It is difficult to determine which species, the forest species, the governors of Puerto Rico and the Barbados. It may be, as perhaps the shift in humidity on Mauritius, which has led to an extraordinary rest

At present, the American monkeys (Macaca nemestrina) have invaded the eastern coast of Mauritius and have led to the extinction of several species.
are extraordinarily sensitive to altitude factors. Two known species of the genus Nesosisyphus, N. vicinus and N. reynardi, are restricted to the open-land forests on Martinique and on Mauritius. The former can be found at all altitudes (up to 900 ft) on their side of Martinique, and on Mauritius they are restricted to the rain-shadow of the island, which is therefore referred to as the red lateritic plateau. The latter, however, is known only at low altitudes. The distribution of Nesosisyphus according to edaphic, according to the Antilles (their French place-names as “Savane”), and according to the Antilles (their French place-names as “Savane”), these species have a partially overlapping distribution at moderate altitudes. On the south slope of Mt. Ory the three species more or less coincide at 1,250–1,500 ft (N. rotundatus occurring only here), but elsewhere only two species may be found together, or a single one alone. For instance, on the north slope of Mt. Ory, only N. pygmaeus occurs (1,650–1,850 ft), and on Mt. Le Pouce only N. reynardi occurs (1,450–2,400 ft). Finally, there are a number of mountains on which none of these species occurs.

Mauritius.—The island of Mauritius, in the Mascarene Archipelago, well isolated in the Indian Ocean, has a very interesting endemic genus, Nesosisyphus, which is well known thanks to the excellent and thorough investigations of Jean Vinson. The data which follow are taken principally from his 1951 paper.

The four species which make up this genus are strictly xerophilous and extremely sensitive to the conditions of the microclimate, especially humidity. Like the Puerto Rican canthonines they are restricted to natural forests, but unlike these they do not occur in the lowest altitudes. Also, they do not seem to occupy definite altitude belts, but rather occur in a patchwork of partially overlapping populations, often disjunct (partly as a result of the extensive deforestation). The major distributional differences reside in the actual area occupied by the species, the figures given by Vinson being as follows: N. vicinus Vinson (winged) — 25,000 acres, N. reynardi (Alauaud) (flightless) — 400 acres, N. pygmaeus Vinson (winged) — 12 acres, and N. rotundatus Vinson (flightless) — 8 acres. The first species occurs discontinuously on the island’s high southeastern plateau, at altitudes of 1,700–2,400 ft, where none of the other species occurs. The remaining three species have a partially overlapping distribution at moderate altitudes. On the south slope of Mt. Ory the three species more or less coincide at 1,250–1,500 ft (N. rotundatus occurring only here), but elsewhere only two species may be found together, or a single one alone. For instance, on the north slope of Mt. Ory, only N. pygmaeus occurs (1,650–1,850 ft), and on Mt. Le Pouce only N. reynardi occurs (1,450–2,400 ft). Finally, there are a number of mountains on which none of these species occurs.

It is difficult to detect a clear pattern in the distribution of these species, the governing factors evidently being more complex than those of Puerto Rico and being more like those of Cuba. A complex topography and, perhaps, shifting winds may reduce the areas of high year-around humidity on Mauritius to just a few pockets, and this may explain the extraordinarily restricted ranges of some of these species.

At present, the principal food of Nesosisyphus is the excrement of monkeys (Macaca irus) introduced by the Portuguese around 1528. Vinson believes that before the introduction of these monkeys into Mauritius (where there are no native mammals other than bats) the beetles must have fed on the excrement of birds, which were very numerous before
colonization (see passage quoted from Vinson on p. 19 of the present work). He was able to demonstrate a strong attraction among the beetles for chicken excrement, and one species was reared in the laboratory in this medium.

It is also possible that *Nesosisyphus* used mollusc excrement, as snails abound in the area. The beetles fed on the excrement of the snail *Pachystyla inversicolor* in the laboratory.

**Temperate and Boreal Forests**

We have very little information on the Scarabaeinae of temperate and boreal forests. As is usually the case with literature data concerning relations to the biome, there are very few of them and they are of little significance. As far as we know, no one has carried out systematic collecting in this type of forest, with different types of baits and at different times of the day and night, as has been done in the tropical forest. Nevertheless, we can present some data on the Scarabaeinae inhabiting these forests in Mexico.

**Mexico.**—Scarabaeinae are very rare in the boreal type of forest, composed of fir (*Abies*), or some species of *Pinus* or *Pinus-Juniperus*, occupying the highest zones of the Mexican mountains. In these forests the entomofauna is typically Nearctic, and in the richest type—the pine forest—the Geotrupini are the dominant laparosticts. The Scarabaeinae are almost completely absent from the fir and juniper-pine forests.

In some areas of the Transverse Volcanic Range in central Mexico *Onthophagus chevrollati* Harold and *Copris armatus* Harold enter the boreal forests—especially the pine forest, but occasionally also the edges of the juniper-pine and fir forests. These are coprophagous and eurytopic species which are more abundant in the adjacent pastures.

At lesser altitudes, lower than 2,500 m, in the complex association which Leopold (1950) unites under the general term “oak-pine forest” (*Pinus-Quercus*), there is a richer laparostict fauna composed in part of some strictly forest elements. *Geotrupes* and especially *Ceratotrupes* continue to be the dominant elements, but the Scarabaeinae begin to be well represented, for instance by the majority of the Mexican species of *Copris*, which live in the two Sierras Madre and the Transverse Volcanic Range in this type of forest.

**Other areas.**—In the following species: *Boreocanthon proboscidium gibbosum* is very common in the mountains of Madre del Sur. None of these species (with the possible exception of the woods they attack) are characteristically montane tropical in origin.

On the edges of the cloud forest, on the highest slopes of the mountains, the montane species *Ph. damocholes* Harold.

Also in this type of forest, *Liatornis rhinocerulus* Harold, taking higher fungi and mycetophagous, etc.

The cloud forest is an environment of Neotropical origin, in the same way as the oak-pine grass associations. The scarabaeine species collected in *C. satanas* [Harold]) is a species of these species are still found. Some species are strictly forest inhabitants but others move to the montane tropical forest.

1 This type of forest includes those areas of Madre del Sur, and Sierra Madre del Sur. The snow line is at 1,650 m and up to about 2,000 m, characteristic of temperate taxa such as *Fagus, Nyssa, Tilia*, and epiphytes.
...p. 19 of the present investigation among the beetles reared in the laboratory in mollusc excrement, as excrement of the snail

The scarabaeinae of temperate data concerning and they are of little conducted out systematic col­
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...scarabaeinae of Neotropical species are partly eurytopic (such as the Copris), but most are strictly forest inhabiting and similar to, or the same as, those found in the montane tropical forest.

On the edges of these forests (oak-pine) there are some elements of Neotropical origin, which evolved on the Mexican Plateau and the slopes of the mountain systems, such as Phanaeus palliatus Sturm and Ph. damocles Harold. All the species mentioned so far are coprophagous.

Also in this type of forest, in the Transverse Volcanic Range, Latongus rhinocerulus (Bates) has been collected in large numbers attacking higher fungi and, rarely, carrion.

The cloud forests, are invaded by Scarabaeinae of Neotropical origin, in the same way that they are penetrated by tropical thicket and grass associations. These elements contrast with the Nearctic ones (such as Ceratotrupes) and comprise a few species of Dichotomius (including saranas [Harold]), some Onthophagus, Copris incertus Say, etc. Some of these species are partly eurytopic (such as the Copris), but most are strictly forest inhabiting and similar to, or the same as, those found in the montane tropical forest.

Other areas.—In the United States, one of us (Matthews) collected the following species in the open forests of the Eastern lowlands: Boreocanthon probus (Germar), Canthon chalcites Haldeman, and Deltochilum gibbosum (Fabricius). Phanaeus igneus floridanus Olufsfieff is very common in the pine woodlands of the sandy areas of Florida. None of these species can be considered to be strictly a forest form (with the possible exception of D. gibbosum) because of the nature of the weeds they inhabit — generally open, with much inselation of the substrate — and because they are also found outside the forests. Woodland-inhabiting species of Onthophagus (generally saprophagous, mycetophagous, er nidicolous forms) have been previously mentioned.

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1 This type of forest is found in the mountains (Sierra Madre Oriental, Sierra Madre del Sur, and Sierra Madre de Chiapas) in very humid areas, generally above 1,650 m and up to about 2,200 m. It is a forest with two distinct elements: 1) trees characteristic of temperate forests, especially the Appalachian flora such as Liquidambar, Fagus, Nyssa, Tilia, Cornus, etc. and 2) tropical low trees, thicket, herbs, vines, and epiphytes.
in the chapter on food relationships, and Ritcher (1945) cites *Ateuchus histeroides* Weber as a woodland species.

12. Colonization of High Mountains

In previous pages, when talking about the forests of Mexico, the Antilles, and Mauritius, some reference was made to Scarabaeinae with very restricted altitude distribution, in contrast to other species which are distributed almost independently of altitude. With regard to the influence of altitude we find, as we do in food habits and to a much lesser extent in biome preference, two ecological extremes among the Scarabaeinae: a strict stenotopy on the one hand and a broad eurytopy on the other. Between these two marked, or in some cases exaggerated, extremes we find numerous intermediate stages more or less inclined to one extreme or the other.

Kolbe (1905:554-562) made a preliminary analysis of the distribution of laparosticts in certain mountains of Europe. According to his analysis, the following species are found in the low hills and plains of Switzerland at altitudes of 100-800 m: most of the species of *Onthophagus*, *Onthoceras falcatus* (Goeze), *Copris lunaris* (Linnaeus), *Gymnopleurus mopsus* (Pallas), *Sisyphus sturni* MacLeay, and *Scarabaeus laticollis* Linnaeus. In addition, *Sisyphus schaefferi* (Linnaeus) climbs to 1,000 m and *Caccobius schaefferi* (Linnaeus) to 1,600 m (the subalpine zone).

No Scarabaeinae reach the alpine zone (1,800 m and higher) but Geotrupinae and Aphodiinae do, and a few species of aphodines even reach the sub-snow zone (2,300 to 2,800 m). Kolbe notes that it is also the Aphodiinae which extend furthest north in Europe, reaching approximately the 70th parallel.

In the southern Tyrolean Alps, *Onthophagus fracticornis* Preysler, *O. nuchicornis* (Linnaeus), and *O. ovatus* (Linnaeus) enter the alpine and sub-snow zones and thus reach a much higher relative altitude than in Switzerland.

Kolbe (*loc. cit.: 558*) also notes that of these 34 high altitude species of Geotrupinae, Aphodiinae, and Scarabaeinae, 20 also occur in the Norwegian Arctic and Lapland, including *O. nuchicornis* and *O. fracticornis*. A boreo-alpine type of distribution thus seems to be the rule. In the Caucasus they reach the sub-snow zone.

In Japan, on the island Caccobius collected from the Japan Alps (Mt. Jô (3041 m), below the sub-snow zone) in Europe.

It is interesting to compare the Geotrupinae and eurytopy of the Scarabaeinae with the stenotopy of Geotrupinae and Aphodinae which is limited to the Northern Hemisphere and is not found in the Southern Hemisphere. The Scarabaeinae are more widely distributed and are not restricted to the boreal forest zone.

The following species of Scarabaeinae known from different parts of the world show a boreo-alpine type of distribution:

- In Africa, the genus *Geotrupes*, the genus *Caccobius*, and *Sisyphus* from much lower altitudes and in other places their distribution is limited to the sub-snow zone.
- In South America, including species such as *Sisyphus maderaspatae* Fabricius

In South America, *Sisyphus maderaspatae* is found at elevations of 4,000 m (Martín) and 4,500 m. The highest point of elevation in the high mountain range in Central America is the peak of Cerro del Quemado (5,200 m) at the northern border of Costa Rica. In the high mountain range of the Andes in the north of Peru, *Sisyphus maderaspatae* is found at 4,500 m. The highest point of elevation in the high mountain range in Central America is the peak of Cerro del Quemado (5,200 m) at the northern border of Costa Rica.
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The following is an account, necessarily incomplete, of the species of Scarabaeinae known to live at an altitude of 3,000 m or higher in different parts of the world.

In Africa, three species of Onitis, adelphus Kolbe, subcrenatus Kolbe, and sulcipennis Felsche, reach 3,000 m. Most of the species of the genus are lowland forms and even the three species mentioned extend from much lower altitudes, altitude not being a determining factor in their distribution (Janssens. 1938b:12-13). Catharsius sesostris Waterhouse is present at almost any altitude between 925 and 3,000 m in the Albert National Park (Congo). On the other hand, altitude is usually an important factor in the distribution of other Coprini in this area. For instance, the Western or Guinean fauna predominates at lower elevations, including species such as Litocoris muticus Bohemian, Heliocoris ha
madryas Fabricius, and H. haroldi Kolbe (Janssens. 1939).

In South America, Scybalophagus rugosus (Blanchard) is always found at elevations above 1,000 m and is very common on the Andean Plateau of Argentina, Bolivia, and Peru at altitudes between 3,500 and 4,000 m (Martinez, 1959). Gutiérrez (1950:54-55) cites this species from a locality in northern Chile (Parinacota) at an elevation of 4,400 m, the highest point reached by a Scarabaeinae in America and, except

rule. In the Caucasus, O. fracticornis and Aphodiinae are found in the sub-snow zone, in the highest areas reached by the nomad herdsmen.

In Japan, on the other hand, the species of Onthophagus and Caccobius collected by Kamimura, Nakane, and Koyama (1964) in the Japan Alps (Mt. Jônen) do not extend beyond the montane zone (1,300 m), below the subalpine zone, and thus climb much less high than in Europe.

It is interesting to note that in the Northern Hemisphere the Geotrupinae and especially the Aphodiinae go higher both in altitude and latitude than the Scarabaeinae. This phenomenon is clearly seen both in Europe and in North America, and is not satisfactorily explained only in terms of nidification or duration of life cycle. To a certain extent it is an indication that the center of evolution of the Scarabaeinae in the Northern Hemisphere has been the warm-temperate grasslands and not the boreal forests nor the high mountains. In the Northern Hemisphere, the Scarabaeinae which go highest in altitude and possibly in latitude are in the genus Onthophagus.

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The following is an account, necessarily incomplete, of the species of Scarabaeinae known to live at an altitude of 3,000 m or higher in different parts of the world.

In Africa, three species of Onitis, adelphus Kolbe, subcrenatus Kolbe, and sulcipennis Felsche, reach 3,000 m. Most of the species of the genus are lowland forms and even the three species mentioned extend from much lower altitudes, altitude not being a determining factor in their distribution (Janssens. 1938b:12-13). Catharsius sesostris Waterhouse is present at almost any altitude between 925 and 3,000 m in the Albert National Park (Congo). On the other hand, altitude is usually an important factor in the distribution of other Coprini in this area. For instance, the Western or Guinean fauna predominates at lower elevations, including species such as Litocoris muticus Bohemian, Heliocoris ha
madryas Fabricius, and H. haroldi Kolbe (Janssens. 1939).

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for one *Onthophagus*, in the whole world, *Phanaeus* (*Ph.*) *batesi* Harold is also found here higher than 3,000 m.

In Mexico, various species of *Copris* and *Onthophagus* climb to considerable heights in the Sierras Madre and the Transverse Volcanic Range. The following may exceed 3,000 m: *Copris armatus* Harold, *Onthophagus chevrolati* Harold, and *O. hippopotamus* Harold. Nevertheless, as we have indicated in discussing temperate and boreal forests, the Geotrupinae predominate in the high mountains of Mexico (especially inside the forests) and it is the Aphodiinae which reach the highest elevations — 4,050 m on the volcano Popocatepetl, very near the limit of perpetual snow.

It is from the Himalayas that the greatest number of high mountain Scarabaeinae has been reported. Various species of *Copris* climb these mountains, and *C. saccontala* Redtenbacher, common between 2,000 and 2,500 m, has been collected at 3,200 m. *Caccobius himalayanus* Jekel has been collected several times at 3,000 m, and *C. denticollis* Harold at 3,800 m. *Onthophagus tibetanus* Arrow lives between 3,000 and 4,200 m. In Sikkim and Tibet, *O. cupreiceps* Arrow has not yet been collected below 4,000 m. The highest locality known for this species (and the highest recorded for any Scarabaeinae) is at 5,200 m. *O. amicus* Gillet reaches 3,000 m; *O. falcofer* Harold is found (in deer dung) between 1,650 and 3,300 m; *O. hingstoni* Arrow is another high-mountain Himalayan species. All the foregoing data on the Himalayas are taken from Arrow (1931) and Balthasar (1963).

In the previous chapter we discussed the ecological aspect of Scarabaeinae. In the following section we will consider their life history.

It is evident from what we have said that olfaction is the dominant factor as a means of locating and image perception and as a general orientation. Sound-producing mechanisms, on the other hand, also seem to be important to Scarabaeinae, and the ability to maintain a preferred temperature is often crucial. In some cases it is important to be able to manipulate the image of the adult beetle or even to separate the treatment of the adult from that of the larva.

In general, the period after emergence from the puparium which do most of the work appears to be an important stage in the life history of Scarabaeinae. It seems to be necessary for the development and for this reason it is called the Reifungssfrass period. This period is no suitable Enright (1931) used here throughout his study of *Sisyphus* studied for 22-3 months.
FEEDING BEHAVIOR

In the previous sections of this work we have considered primarily the ecological aspects of the natural history of scarabaeine dung beetles. In the following sections we will be concerned primarily with behavior.

It is evident from the observations of numerous investigators that olfaction is the dominant sense of scarabaeines. Vision is poorly developed and image perception apparently nil. Light is important only for orientation and as a general stimulus to initiate activity (in diurnal forms). Sound-producing mechanisms are present in some genera, but auditory stimuli also seem to be unimportant in general. On the other hand, tactile perception appears to be highly developed, at least in ball-rolling beetles, and the ability to manipulate plastic masses is often remarkable. Ambient temperature is often critical for most species, and activity normally takes place within rather narrow (and high) temperature limits. In other words, it is important to bear in mind, when reading the following pages, that scarabaeine beetles live in a world of smell and touch almost exclusively, and that a suitable ambient temperature is the first requisite for activity.

In this chapter we will consider all known behavior related to the manipulation of the food material. The food may be for feeding either the adult beetle or the future larva, as it is not possible in many cases to separate the treatment of the food according to its ultimate purpose.

13. Duration of Adult Feeding

In general, the adult undergoes a fairly lengthy period of feeding after emergence from the nest. This contrasts with many other insects which do most of their feeding in the larval stage. In Scarabaeinae, it appears that there is just enough food accumulated for the larva to carry it through metamorphosis. Thereafter, copious and prolonged feeding seems to be necessary for the full development of the gonads and eggs, and for this reason the German investigators have called this adult feeding period the Reifungsfrass-period, or period of maturation-feeding. As there is no suitable English equivalent for this word, Reifungsfrass will be used here throughout in reference to feeding before nidification. The Reifungsfrass period is 3-3½ months in the species of Gymnopleurus and Sisyphus studied by Prasse (1957a). Phanaeus quadridentis Say undergoes 3½-4 months of Reifungsfrass (Halffter), and even in the minuscule
Nesosisyphus pygmaeus Vinson on Mauritius the female will not begin egg-laying until she has fed a whole month after emergence (Vinson, 1947:27) — to select but a few examples.

In temperate climates the beetles nidificate in the late spring to early summer. As soon as the new adults emerge (middle to late summer), they undergo the Reifungsfass period which is carried over through the early part of the following spring. Overwintering is consequently in the adult stage, in deep burrows. In tropical climates the life cycle may be very different, and is always governed by the incidence of rains. Thus in central Mexico the new adults appear at the beginning of the rainy season in May and feed throughout the following months, many species not initiating nidification until September, the end of the rainy season. It appears that the adults do not survive the ensuing dry winter (with the known exception of some species of Copris), which is passed by the next generation in some immature stage. In areas of continuous rainfall, such as parts of Puerto Rico, there may be no evident seasonality. The small canthionines occurring in the forests there are found in more or less equal abundance throughout the year. At the opposite extreme, in Continental climates such as that of Central Asia, scarabaeines seem to have a very prolonged life cycle — over two or three years (Siyazov, 1913) — accompanied by prolonged adult longevity (Balthasar, 1963:42).

14. Flight, Detection of Food, and Approach Behavior

We know little about food-search behavior in the Scarabaeinae, other than that it is carried out on the wing, as a rule. Such aspects as the pattern of search flight, territory covered by a single beetle, altitude of flight, distances at which the smell of food is first perceived, etc., are nearly unknown.

Experiments by Comignan (1928b) and Warnke (1934), and the observations of numerous investigators, indicate that the antennae are the principal organs of chemoreception over long distances, and the maxillary palpi at close range (Prasse, 1957a:440). Warnke (1934) showed that the chemoreceptors on the antennae are the so-called sensilla basiconica — thin-walled cones which project through pores in the chitin. These are found over all surfaces of the club segments, interspersed with very numerous short, curved hairs (sensilla trichodea), which give the club its tomentose appearance. The inner surfaces of the club lamellae (those apposed when the club is outstretched, hence maximum chemoreception) have a thin spread. As long as the antennae smell normally, but as the outer surfaces were made principal, Copris and Copris have a smell. It is interesting to note that pleurosticts, have an inner sensilla placodea.

There does not necessarily follow from the frequent tendency to flying. The present state of the nines.

At least some species show a (range) search flight, owls. and the sqving tendency, occurring in the forests, such as parts of Puerto Rico, there may be no apparent seasonality. The small canthionines occurring in the forests there are found in more or less equal abundance throughout the year. At the opposite extreme, in Continental climates such as that of Central Asia, scarabaeines seem to have a very prolonged life cycle — over two or three years (Siyazov, 1913) — accompanied by prolonged adult longevity (Balthasar, 1963:42).
female will not begin emergence (Vinson, 1948).

Emergence typically occurs from late spring to early fall, depending on species (Vinson, 1948). Emergence is consequently dependent on the availability of rains during the emergence season. Thus, the beginning of the rainy season, typically late May to late summer, marks the beginning of the rainy season. Many species emerge during one or more months. Some species may emerge over a long period of the rainy season.

During the dry winter (with low rainfall), species which are passed by the rainy season have lost evidence of rains. Thus, the beginning of the rainy season, which is generally mid-winter, marks the beginning of the rainy season. Many species emerge during mid-winter, and some species emerge during the rainy season.

The rainy season is consequently dependent on the season of the rainy season. The rainy season is initiated in more or less continuous rainfall. A relatively seasonable season is one in which the season is not continuous rainfall, but is seasonally intermittent. The seasonality of the rainy season is initiated in more or less intermittent rainfall. However, it is in the opposite extreme, in which the rainy season has more or less continuous rainfall, that the scarabaeines seem to be more abundant. It is interesting to note that the melolonthines, and presumably other pleurostics, have entirely different antennal chemoreceptors, called sensilla placodea.

There does not seem to be any visual perception of the food. Heymons and von Lengerken (1929:535) note that this is demonstrated by the frequent tendency of Scaraeaeus to "overshoot" the dung when flying. The present authors have noted the same thing in some canthorines.

At least some tropical forest species do not execute cruising (long-range) search flights, but sit on leaves and branches, with the antennae outstretched, apparently waiting for odor currents to lead them to food. Ohaus (1909:102) describes this behavior in Delotochilum tesselatum Bates, which thus supposedly detects the odor of tapir and "Wasserschwein" (capybara) excrement in eastern Ecuador. The same author reports this behavior to be very common in forest-inhabiting small canthorines and "Copris" (this must refer to some small dichotomines such as Canthidium) in eastern Ecuador and central Brazil. "and one is then astonished to find dung beetles on the sheet after beating [vegetation]" (Ohaus, 1900:222; 1909:72). Halffter has collected Onthophagus carpophilus Pereira and Halffter (1961:63) and Geocanthon femoralis (Chevrolat) on leaves in the tropical forest. This behavior, evidently common in forest species, must be an adaptation to forest conditions and may replace, at least partially, the cruising flight behavior of open-land species in search of food. When odor currents are detected, the beetles presumably take to the wing and execute short-range search flight patterns.

Prasse (1960) made a special study of flight behavior in Sisyphus schaefferi (Linnaeus). This species is very prone to take to the wing, providing the air temperature is at least 22°C and there is sufficient light. When searching for food, this species flies 1.5-3 m high in open country, principally in an upwind direction. The distances flown in each
uninterrupted flight are small (40-60 m), after which the beetle temporarily alights on the ground or vegetation. Prasse estimates that the maximum air speed in full flight is 3-6 m/sec, the wings beating at a rate of 109 beats per second. *Gymnopleurus geoffroyi* Füessly has a wing beat of 105/sec and *Onthophagus fracticornis* Preyssler 114/sec. These wing movements are faster than those commonly attributed to Coleoptera in standard physiology texts.

The beetle passes through a sequence of preparatory movements before taking flight. These are 1) pumping the abdomen 3-10 times, with a slight lifting of the elytra, 2) lifting of the middle legs so that the tarsi are held aloft, 3) further lifting of the elytra into flight position (without opening them), and 4) spreading the wings. Not counting the pumping movements, the preparatories take an average of 0.39 sec in *Sisyphus schaefferi* and 0.31 sec in *Gymnopleurus geoffroyi*.

There seems to be some controversy about the significance of the position of the middle tarsi (common to perhaps all beetles in flight). Without being able to discuss the matter fully here, we may say only that Prasse concludes that the middle tarsi, which are held high during flight, act as air-speed and turn indicators for the beetle, as their positions relative to the tibiae, and relative to each other, vary according to speed of flight and degree of turning in flight. They are not gyroscopic organs equivalent to the halteres of Diptera, nor do they vibrate fast enough to act as "stimulators for buzzing flight", as claimed by von Lengerken (1934, cited in Prasse, 1960).

Flight is effected by maintaining the elytra lifted but closed or almost so while the wings beat (this appears true of all Scarabaeinae). Prasse demonstrated with high-speed photography that the elytra open and close very slightly in coordination with the wing beat. In the genus *Gymnopleurus* the elytra are excised along the anterior outside edges, permitting the hind wings to be unfolded rapidly with a minimum of lifting of the elytra.

Our observations indicate that many scarabaeines approach the food flying very low (down to one or two feet) above the ground surface, and in a flight pattern representing a zig-zag or oscillation in the horizontal plane, of wide amplitude and often recrossing the path in a figure-8. Rarely beetles may be observed making a direct flight to the food, but our opinion is that the direct straight-line flight is the normal long-distance cruising flight, only if it happens to approach abruptly, probably in an emergency. Normally the food source is located by the beetle then switching to the method of close-range searching.

The method of approach on the food in different genera, *C. h. hamectus* and *C. h. hamectus* Preyssler, involves the beetle holding some distance away from the food, then walk the rest of the distance to the food. In the species *Sisyphus schaefferi* (1957a), the beetle flies immediately to the food. A flying posture is first perceived, and the beetle then holds the head up and moves jerkily toward the food in flight. At very short range may be detected. Some observers ([Heymons and von Lengerken, 1957] may circle it a few feet, almost to a hover. In contrast to *Copris*, *Phanaeus* has a short-range rapid activity and so the
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only if it happens to be right in the line of flight. It will then land
abruptly, probably in response to the sudden intensity of olfactory stimuli.
Normally the food is detected at a certain (unknown) distance, and
the beetle then switches from straight-line flight to the zig-zag pattern
of close-range search.

The method of final approach to the food source seems to differ
in different genera. Our observations on Canthon pilularius (Linnaeus)
and C. h. humectus Say indicate a relatively poor aim. The beetles often
land some distance away from the food (3-80 cm in C. pilularius) and
then walk the rest of the distance, usually in a straight line, to the
food. In the species of Sisyphus and Gymnopleurus studied by Prasse
(1957a), the beetles likewise almost never make the final approach on
the wing. A flying beetle drops to the ground as soon as the food odor
is first perceived, apparently 1-1.5 m from the dung. It then proceeds
to search on foot “with great agitation”. A beetle searching on foot
holds the head up and the antennal lamellae fully spread, and walks
jerkily toward the food source, with increasing rapidity as the food is
approached. At very close range the movement of the maxillary palpi
may be detected. Similar behavior was reported for Scarabaeus sp. by
Heymons and von Lengerken (1929). This imprecision in locating the
food in flight would therefore seem to be a general characteristic of
Scarabaeini, but at least one forest species — Malagoniella astyanax
yucateca (Harold) — observed by Halffter in Chiapas, flies in a straight
line rapidly and directly to human feces as soon as these are deposited.
Other observers (for instance Ohaus, 1900:222) have noted the rapidity
with which tropical-forest scarabaeines come to dung or other bait.

In contrast to most Scarabaeini, which do not make the final
approach on the wing, five species of Phanaeus which we have been able
to observe (mexicanus Harold, nimrod Harold, quadrident Say, damon
Laporte, and vindex McLeay) display a remarkably controlled flight
behavior. The beetles approach the food in the usual zig-zag pattern,
may circle it a few times, and then, gradually slowing down the flight
almost to a hover, land directly on it. Thus in spite of their clumsy
appearance Phanaeus are excellent fliers. Other common genera, such
as Copris, Dichotomius, Deltochilum, and others, are nocturnal in their
activity and so their flight behavior has not been clearly observed. We
have not carefully observed the approach in any species of *Onthophagus*, but believe it involves direct flight right up to the food.

Once they have actually arrived at the food source, the beetles exhibit a behavior which, once again, varies according to the genus. *Canthon* will either burrow directly into or under the dung mass, perhaps after briefly wandering over its surface, or it will immediately begin to carve out a ball. Which of these two types of behavior it shows depends almost certainly on the ambient temperature, the former behavior occurring during low temperatures when balls are not made (see Section 18). The species of *Phanaeus* observed by us will either burrow immediately beneath the dung mass, or it will immediately begin to push away a portion of it, depending on the sex of the beetle, the type of terrain, and the type of dung (see Section 17). *Onthophagus* will burrow under the edge of the dung mass immediately and will not be seen again. *Onthophagus* burrows are dug directly beneath the dung, as a rule, and provisioned with material removed from below. A piece or mass of excrement attacked by *Onthophagus* will eventually be reduced to a hollow shell consisting of only the dried outer crust, and may offer to the observer few outward signs of exploitation, other than some loose soil around the edges. Most of the soil brought up to the surface in digging the burrows replaces the dung removed from under the crust. However, in the four European species observed by Burmeister (1930), which make extensive and complex underground galleries, the soil will be piled up beside the dung (if the dung was soft and could be attacked from the side) or on top of it (if a hard crust had been formed). Species of other common digging genera, such as *Copris*, *Dichotomius*, and *Onthrus*, dig their tunnels to one side of the dung mass, accumulating a large pile of loose soil to one side of the dung.

While we are on the subject of the method of attack on the food material, we should mention this aspect in necrophagous species. Unfortunately we have no direct observations of attacks on cadavers by necrophagous Scarabaeinae. We know that the huge individuals of the subgenus *Megaphanaeus*, for instance, can inter the fresh carcase of a medium-sized dog (in pieces) in a single night (see section on necrophagy). One of us (Haffter) placed a dead tcad on a path inside a forest in Palenque, Chiapas, and found it the next morning buried in the same spot in several large pieces, together with two *Phanaeus* (C.) *telamon corcythus* Harold. The same thing happened to a dead bird on another occasion. Even the beetles, but we cannot see the tibiae, moved sideways with the aid of the edeal and *P. virens* Mannerheim in one of our European species, movements are probably possible, and there is no indication of changes in behavior.

The degree of the beetle's behavior toward it is usually dependent on how the surface of the dung mass has become quickly dried (see Section 18). The requirements of keeping *Onthophagus* to excrement immediately beneath the surface, fact that *Scarabaeus* will not attack in *situ* without a little water, liquid excrements a while from the latter has acquired (cf. 1929:537). *Canthon* (Haffter), seems to prefer hard crusts, when the surface is dug. Species of partially dried dung do not carve balls or extensive galleries. *Phanaeus* vinae., however, come to semi-liquid excrements and utilize it in that state.

In the case of *Onthophagus*, we have observed the nest burrowed by the tarsi, the opening of the nest and feeding on the excrements.

The only Scarabaeinae observed in the present study that may be important part of the process of feeding of the larvae of the species is *Phanaeus*.*
species of Onthophagus, food.

A source, the beetles according to the genus, the dung mass, perhaps will immediately begin of behavior it shows the former behavior not made (see Section this will either burrow im­ plement will start to push the beetle, the type of Onthophagus will burrow again not be seen again. the dung, as a rule. A piece or mass of material be reduced to a ball, and may offer to a beetle other than some loose mixture,擤 to the surface in some under the crust. Burmeister (1930). galleries, the soil will could be attacked if (as had been formed). Copris, Dichotonius, dung mass, accumula­ dung.

on attack on the food necrophagous species. Unpar­ racks or cadavers by the individuals of the fresh carcass of a situation on necro­ on a path inside a morning buried in two Phanaeus (C.) come to a dead bird on another occasion. Evidently, firm flesh can be torn into small pieces by the beetles, but we do not know how they do it. Probably the fore tibiae, moved sideways in a slicing motion, can accomplish the task with the aid of the edge of the head. A similar motion is used by Canthon virens Mannerheim in decapitating ants (see section on predation). The movements are probably the same as those used in handling excrement, and there is no indication that necrophagous habits involve any important changes in behavior regarding the manipulation of the food.

The degree of plasticity of the excrement food, which in turn is usually dependent on its humidity, is a very important factor affecting behavior toward it. Thus, Onthophagus nuchicornis (Linnaeus) when stockpiling its nest does not utilize isolated pellets of sheep dung, which become quickly dried out (von Lengerken, 1954:206). It may be that the requirements of plasticity explain the fact that some species come to excrement immediately as it is deposited and others only when it has lost some of its liquid content and is in a more pasty state. The fact that Scarabaeus and other Scarabaeini often do not eat the excre­ in situ without first forming a ball and rolling it, means that very liquid excrements are not exploited immediately. Scarabaeus may drink a while from the liquid excrement, but the ball is not begun until the latter has acquired a pasty consistency (Heymons and von Lengerken, 1929:537). Canthon pilularius (Linnaeus), observed in Florida (Matthews), seems to prefer cow dung with more than a day of exposure, when the surface is hardened although the interior is plastic. This sort of partially dried dung can still be exploited by Scarabaeinae, which carve balls or extract portions from the interior, underneath the crust.

Phanaeus vindix McLeay, and probably most other Coprini, will come to semi-liquid cow dung immediately and appear to be able to utilize it in that state, since in this group balls are not made.

In the case of human excrement, which is generally more pasty, we have observed many species coming a few minutes after deposition of the feces and beginning ball-making and rolling immediately.

The only Scarabaeinae known to come habitually to really dry excrement are the Eucraniina (Martinez, in litt.), and this is evidently an important part of their adaptation to semi-desert conditions.

Once the beetle has arrived at and attacked the food material, it proceeds either to feed on it directly, to bury it, or to transport it overland. These matters will now concern us in the following sections.
15. Feeding Without Burial

The adult Scarabaeinae and Geotrupinae are distinguished behaviorally from Aphodiinae (and nearly all other Scarabaeidae) primarily by the fact that they nearly always bury the food, both for themselves and for the larvae. However, in the tribe Scarabaeini especially, there are observations of feeding directly at the food source for just about every species observed. This occurs either before or during the ball-making process, but in the genus Gymnopleurus, nearly all the species observed feed exclusively at the surface, without making a food ball. In the other tribes, direct observation is difficult because of the largely underground and often nocturnal activity of the beetles.

16. Burial Without Overland Transportation

The members of all tribes except Scarabaeini bury the food, both for the adult and for the larva, directly beneath or beside the food source, with a few known exceptions. A few Scarabaeini also do this (see Aberrant Nidification Behavior in Section 20). Conversely, some or most species of Phanaeus (tribe Coprini) may transport the food over considerable distances overland (see following section).

In all tribes except Scarabaeini, the burrow which is to receive the food is always dug out completely before the food is brought in. If two beetles are involved, both digging and subsequent provisioning seem to be cooperative (see section on Sexual Relationships). The digging process, which is probably similar in all tribes other than Scarabaeini, is best described by Rommel (1961:328-330) for Copris hispanus (Linnaeus). The soil is loosened with powerful movements of the head and forelegs away from each other. With the forelegs soil is pushed backward between the middle and hind legs; thus loose soil accumulates behind the beetle as it moves down into the earth. When a certain amount is accumulated, the beetle turns around and pushes the soil to the surface with the head, walking forward. In Onthophagus ramosellus Bates (cited as O. capella Hope), Hingston (1923:215) noted that to push soil to the surface the insect does not turn around but walks backward, pushing the soil out of the burrow with its "plug-like rear end." This has not been observed in any other species.

With the burrow dug, the beetle (or beetles) begin(s) to bring down the food. In all observed species of all tribes except Scarabaeini, burial of the food is at the burrow entrance. A portion of the food is placed between head and foreleg (if a large one) below the beetle presumably to be fed to the larvae. Some experiments by Bates were made but the beetles cannot dig the tunnels necessary to have no difficulty further that the mass laid on the surface and to it, and that this process is not necessary. The beetles can once the tunnel is open at both ends, excavate food to freedom. We must as the branched nests and tunnels.

In the tribe Scarabaeini, different from those of this tribe as is the digging of the previously dug, but the digging of food and piece of food and the digging of the burrow. very probable that it is the chilum which do not scurce. burial is stored mostly by the finding of such that these continue in the same manner (personal contact with the other two genera).

17. Overland Transportation

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burial of the food is always accomplished by the beetle backing into the burrow entrance (Onthophagus, Dichotomius, Copris, Phanaeus). A portion of the food is detached from the main mass and is held between head and forelegs and is carried (if a small piece) or dragged (if a large one) backwards into the burrow. Inside the burrow the beetle presumably turns around to pack the food into the end, then turns around again to walk out forwards.

Some experiments on the digging ability of Onthophagus ramosellus Bates were made by Hingston (1923:214-226). He found that the beetles cannot dig through a fine net, roots, or paper (larger genera seem to have no difficulty tearing through grass roots). Hingston found further that if the Onthophagus are in the soil, the "pressure" of a mass laid on the surface will induce them to dig their way upward to it, and that this pressure is more important than the smell of the food. The beetles can only dig vertically; when they are placed in a tube open at both ends, laid horizontally, they often cannot dig their way to freedom. We must accept these results with some caution, however, as the branched nests of European Onthophagus often contain horizontal tunnels.

In the tribe Scarabaeini, the digging and burial processes are quite different from those described in the foregoing, and as are characteristic of this tribe as is the ball-making and rolling behavior. A burrow is not previously dug, but rather the soil is pushed away from under the hall or piece of food and the latter is thus buried intact simultaneously with the digging of the burrow. Precise observations are lacking, but it seems very probable that in those species of Canthon, Canthonixia, and Canthocophilum which do not roll balls, but bury the food directly below the source, burial is still in the manner of Scarabaeini. This is indicated mostly by the finding of intact large pieces of dung buried in the soil, such that these could not have been carried down in a piece-by-piece manner (personal observations on Canthocophilum by the authors and on the other two genera by Martinez, in litt.).

17. OVERLAND TRANSPORTATION WITHOUT FORMATION OF BALL

Three confirmed methods of overland transportation of the food, other than ball rolling, have been observed in the subfamily, and one or two others may exist.
In the first method the beetle grasps a portion of the food with the forelegs and with the remaining legs walks backwards toward the burrow, carrying or dragging the food. This behavior is not sharply distinguishable from that used in provisioning the burrow, as discussed in the previous section, since as they use up the food supply on the surface the beetles must have to go out further from the burrow entrance to get more. Genera which have been observed to transport in this manner are Onthophagus, Copris, Dichotomius, Phanaeus (many observers) and Phalops divius Wiedemann (Hingston, 1923:232). Exact data are scarce on how far a beetle may thus transport food, walking backwards. Rommel (1561:335) observed the male partner of a nesting pair of Copris hispanus (Linnaeus) thus carrying dung to the waiting female for a distance of 25 cm.

In the second method pieces of the food material, not formed into a ball, are rolled away from the food source by the beetle walking forward and pushing against the piece with its head and forelegs. This “butting” technique is frequently to be observed in Phanaeus vindex McLeay, Ph. nimrod Harold, Ph. mexicanus Harold, and was once observed in Ph. quadridens Say (authors’ observations). It is apparently very common in Ph. (S.) carnifex (Linnaeus) in Jamaica and has earned this species the name “tumble-bug” among the natives (according to a Jamaican source).

In Phanaeus vindex McLeay, one individual was observed by Matthews in Florida to roll a piece of human excrement 1.5 m in this butting manner before starting to bury it. Burial of the dung is by the usual method, that is, small pieces are detached from the large piece (that was rolled) and held with the forelegs while the beetle backs into the burrow which had been previously dug near the large piece. Dung was never observed to be pushed into the hole with the head. The butting technique enables very large pieces of food to be transported over considerable distances. It is not likely that pieces can thus be transported repeatedly over the same route from supply to burrow. One apparent attempt to bring a second piece to the same burrow, observed by Matthews in Georgia, resulted in the beetle missing its burrow entrance by 20 cm, and consequently abandoning the first burrow.

In Phanaeus nimrod Harold, observed by the authors in Ixtapan, State of Mexico, in September, butting is very common and is always performed by the female. Both the head and forelegs are used to roll
of the food with the toward the burrow, not distinguishable at the previous surface the beetles once to get more. a manner are Onvers) and Phalops are scarce on how backwards. Rommel air of Copris hismale for a distance, not formed into the walking foward. This "butting" index McLeay, Ph. observed in Ph. very common armed this species to a Jamaican observed by Mat­

m in this butting is by the usual piece (that was into the burrow. Dung was never butting technique over considerable ported repeatedly parent attempt to Matthews in Geor­
e by 20 cm. and authors in Ixtapan. on and is always are used to roll

Fig. 2. Female Phanæus mexicanus Harold rolling a piece of horse dung. Head is placed under edge of dung.
Fig. 3. Beetle has lifted edge of piece with head and is pushing it over with fore legs. (Drawn from photographs taken by the authors)
the piece of excrement (usually horse dung). The head is used to lift up the edge of the piece and the forelegs give it the push which sends it tumbling. Butting was most commonly seen on a country road, the dung being pushed downhill, but it was also observed once on a pasture. There was some evidence that less butting occurs in pastures, as there the great majority of earth mounds dug up by this species and Ph. mexicanus Harold was directly beside the pile of excrement. Females only were observed butting, often alone but sometimes closely followed by a male. Three total rolled distances measured were 1.30, 2.60, and 18.60 m, practically in straight lines (this is from initiation of rolling to final burial). One female was actually observed detaching and forming a hall from the edge of a mass of cow dung. The movements used were astonishingly similar to those employed by Canthon, etc., in forming a ball. When completed, this ball (oval in shape) was rolled away by butting. Thus cow dung may occasionally be transported in this manner, although this behavior seems to be usually directed toward horse dung and (at least in Ph. vindex) human stools.

For Phanaeus mexicanus Harold, also observed in Ixtapan, our observations are similar. Only females were seen rolling, using the head and forelegs (figs. 2 and 3), and two measured distances rolled were 1.84 and 11.30 m. Speed of rolling was between 30 and 50 cm per minute, on a road. In both this species and Ph. nimrod, rolling activity was seen only in the hottest hours of the day, between about 10:30 and 17:00, when the air temperature was 25°C or higher.

All these observations indicate that overland transportation is highly developed in Phanaeus (note that more than 18 meters can be covered) and that in this respect they rival the Scarabaeini. The quantity of food transported can be far larger, in relation to the size of the beetle, than in the Scarabaeini (see fig. 3). There is even some ability to make a sort of a hall. However, the method used for transport is always butting, not rolling backwards with the legs as in Scarabaeini, and there are no morphological modifications for this habit. Males are not seen butting (at least in Ph. nimrod and mexicanus), and it is possible that the long cephalic horn in this sex would make this habit difficult to perform. We would not be surprised if careful observations reveal this transporting ability in many species of Phanaeus, at least under certain circumstances.

The same method of transportation was observed in an individual of Dichotozonius nits (Olivier) by Luederwaldt (1914:369-370) in Brazil.
The beetle was rolling a piece of horse dung measuring 3 x 3.5 cm on a footpath, using the head and pronotum to push the piece. Luederwaldt notes that the "obvious purpose" of the manoeuvre was to transport the dung to a safer place, although the beetle did not consistently maintain a given direction and so did not succeed. According to Daniel (1940), Oxysternon conspicillatum Weber also rolls dung over the surface in Colombia, presumably by butting (the exact process was not described). Butting has not been observed in other genera and species of Scarabaeinae, although it is also known in Geotrupes (von Lengerken, 1954: 189).

In the third method of overland transport without ball making, the beetle grasps the food with the forelegs and head and, elevating the forebody and food, runs rapidly forward on the remaining four legs. This extraordinary method of transport is known only in the Argentine subtribe Eucraniina, presently classified in the tribe Scarabaeini. It was first recorded by H. C. C. Burmeister in 1861 (as reported by Kolbe, 1905:489) for Eucranium arachnoides Brullé and was confirmed by the personal observations of Antonio Martinez (in litt.) for species of Glyphoderus and Anomiopsoides as well. The beetles scuttle spider-like back and forth over the hot desert sand in the full sun. rapidly provisioning their burrows, which are situated in slopes and have semi-circular entrances (Martinez, 1959:18). The pieces of dung thus carried tend to be dry. The beetles are morphologically modified for this behavior by possessing short, spiny forelegs, a spiny head, and middle and hind legs provided with long hair fringes (fig. 4).

The position of the subtribe Eucraniina in the tribe Scarabaeini is based on the form of the legs, however, the very different method of food transport indicates a separate evolution for this group, the similarity of leg structure possibly being convergent (as pointed out by Kolbe, 1905:488-489).

Additional methods of overland transport, other than ball rolling, have been mentioned in the literature but have not been confirmed by subsequent observers. Ohaus (1909:72) claims that South American Eurysternus carry dung on their flattened back: "The latter [Eurysternus] loads dung on its back as on a wagon, using its large, bent middle legs and holds it if need be with the middle legs, while it walks around with the fore and hind legs; as the upper surface, the thorax and especially the elytra, are completely flat in contrast to the strongly
rounded underside, it is able to transport a fair quantity of food." No one seems to have observed ball rolling in *Eurysternus* and related genera, and the position of the subtribe Eurysternina, like that of the Eucraniina, in the Scarabaeini is therefore open to question.

Fig. 4. *Anomiaopsides pereira* Martínez of the tribe Eucraniina, showing spiny fore legs and head used for carrying dung, and fringed middle and hind tarsi adapted for running on sand. (From Martínez, 1945:278.)

Finally, Arrow (1931:68) claims that the hooked dorsal hairs of some species of *Sisyphus* in India serve to hold a layer of excrement on the beetle and that this may be a method of transporting the food, which can later be cleaned off with the long hind legs. It remains to be proved that this is not merely a device to hold a layer of soil on the beetle, something seen in several Scarabaeinae, such as *Drepanocerus* and *Canthochilum hispidum* Chapin.

18. OVERLAND TRANSPORTATION WITH FORMATION OF BALL

To this behavioral category belong all the members of the tribe Scarabaeini, with four groups of exceptions: 1) The subtribe Alloscelina (mostly myrmecophagous), 2) Eurysternina (another myrmecophilous category), 3) Eucraniina, which have secondarily lost the mark-making behavior of the Eurysternina, and 4) *Eurysternus*, which is a large genus with a broad range of habits. In the vast majority of the Scarabaeini, the marking of the dung ball is a distinct behavior in which the individual leaves a characteristic mark on the ball before moving it to the place where it is to be buried.

In the vast majority of the Scarabaeini, the marking of the dung ball is a distinct behavior in which the individual leaves a characteristic mark on the ball before moving it to the place where it is to be buried. This behavior is usually associated with the formation of a ball or ball-rolling, which is a common method of transportation in the Scarabaeini. The balls serve as a protective covering for the larva (brood ball), and can also be used for transportation of dung. In some cases, the beetles roll the ball to a sheltered spot, where it is then buried intact. In other cases, the ball is transported by a male beetle or a male-female pair. In still other cases, the ball is transported by the female alone. A number of factors contribute to the success of ball-rolling, including the presence of predators, the need to find a sheltered spot, and the need to transport the ball over long distances.

The purpose of ball-rolling is probably not that of transportation, as suggested by some authors. Instead, it is likely that ball-rolling is a way of marking the territory of the beetles, which helps to prevent competition between individuals. Ball-rolling behavior is also associated with the formation of brood balls, which are used to store the dung and protect the larvae. The brood balls are usually formed near the nest, and are then transported to a sheltered spot where they are buried.

In addition, there are times between spells of ball-rolling when the beetles are not engaged in any particular activity, but are simply resting or engaging in other behaviors. This period of inactivity is likely to be necessary for the beetles to conserve energy and to allow them to rest before the next spell of ball-rolling.

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2) Eucraniina and 3) Eurysternina (discussed under the pre-
vious category), and 4) the scattered members of other subtribes which 
have secondarily lost ball-making behavior (see Aberrant Nidification 
Behavior in Section 20).

In the vast majority of the tribe Scarabaeini, ball-making and 
rolling techniques seem to be highly developed and have received some 
detailed study in various parts of the world. The careful studies of 
Fabre (Souv. V:1-92), Goggio (1926), and Heymons and von Len-
gerken (1929) on Scarabaeus served as a basis for subsequent studies.

The balls serve to feed either the adult beetles (food balls) or the 
larva (brood balls). In either case, the ball is made at the food source 
on the surface, rolled a certain distance over the ground, and then 
buried intact. Only after its burial (or, in some cases, its placement in 
a sheltered spot) is it consumed or is an egg laid in it. Either a single 
beetle or a male-female pair may make and roll a ball. In the former 
case the ball is usually a food ball, in the latter case usually a brood 
ball. A number of exceptions to these generalities may be seen. In 
addition, there are many differences in detail between genera and some-
times between species.

The Biological Advantage of Ball Rolling

The purpose of transporting the food long distances overland is 
probably not that of selecting a more suitable burial spot, as is claimed 
by some authors. It is rather the dispersal of the food material to avoid 
congestion at the source. The need for maximum dispersal would explain 
the beetles' often tenacious adherence to a more or less straight line 
in rolling and their apparent use of environmental factors (terrain, wind, 
sun position) to maintain this course (see section on directions below). 
Ball-rolling behavior must have arisen in savanna-type biomes, not only 
because rolling is effective primarily in open terrain, but also because 
in the savanna the available excrement tends to be that of large 
herbivores, which deposit concentrated masses of dung. The ability to 
carry the dung a certain distance away would bestow an advantage 
on these beetles in competition with other groups (Coprini, Onthophagini, 
etc.) struggling for burial space beneath or beside the dung mass. Of 
course, this does not mean that ball-rolling beetles could not have
subsequently invaded forest habitats, as many species have. Furthermore, the ability to disperse the food is of equal advantage in dealing with the concentrated mass represented by a vertebrate carcass, in any biome.

**The Behavioral Origin of Ball Rolling**

The observations of Prasse (1957b:599) on *Sisyphus schaefferi* (Linnaeus) provide us with a clue as to how ball-rolling behavior could have originated. One of the rolling positions, for either a single beetle or one of a pair, is head downward on the side of a ball, with fore and hind legs on the ball (fig. 9, right hand beetle). The beetle then simply walks down, pushing against the ground with its head, thus rolling the ball. Nothing more than normal walking movements are required for this procedure. If applied against dung pellets which were already more or less spherical, such as those of rodents, lagomorphs, and caprines, this behavior could have preceded the ability to actually make a ball.

**Ball-Making Behavior**

The ball is always made in situ, at the food source, before it is rolled. The behavior employed in making a ball from a large mass of food does not seem to differ in any known species. It has best been described by Comignan (1928b) in *Scarabaeus semipunctatus* Fabricius. The beetle places itself on top of the dung, bends the forebody down so that head and fore tibiae cut into the mass, and then proceeds to execute three simultaneous movements: a bending and unbending of the fore body in relation to the hind body, a back-and-forth movement of the fore tibiae toward and away from the head, and a rotation of the whole body about the vertical axis. In this way the beetle pivots about in a circle and rapidly builds up a mass of dung beneath itself. Apparently the middle and hind legs serve to gauge the size of the mass. As the dung builds up, the beetle moves around the sides of the now-large mass, executing the cutting movements in an ever decreasing radius, eventually severing the mass at the base. This first phase of ball making was termed the "cutting phase" by Matthews (1963a). This is then followed by the shaping phase, in which the crude ball is converted to a more or less perfect sphere by repeated patting of its surface with the antennae. New material may be added if the ball is too small; otherwise, it will take more than half an hour (Matthews, 1963a). Ball making has been studied in *Gymnopleurus* and *Scarabaeus*.

The stimuli which have been investigated by Malysheva (1956), for two combinations of olfactory temperature is advantageous. Movements until a ball is of suitable malleable pulp, thus separable from a ball being made, are made to the antennae; this is found that malleable pulp.

Puzanova-Méndez, by Fabre and H.-J. (1956), *Scarabaeus sacer* be readily accepted or not perfectly suited. A flat disk of dung with its edges. A narrow pointer is presented with suitable material, but always horizontal pointer, and the halves still of the weight of a lead weight with pieces put back to it and a lead weight without pieces put back to it. it will apparently
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The beetle then

The stimuli which induce a beetle to initiate ball-making movements have been investigated by Comignan (1928b) and Puzanova-Malyshova (1956) for two different species of Scarabaeus. Both indicate that a combination of olfactory and tactile stimuli are needed, once the ambient temperature is at a suitable level. A beetle will not start ball-making movements until the proper intensity of olfaction is achieved and a suitable malleable material is touched. This was shown by Comignan by suspending a piece of excrement out of reach above a non-nutritive pulp, thus separating the olfactory and tactile stimuli. This resulted in a ball being made of the pulp (although ammonia had to be applied to the antennae; this seems to cause exaggerated movements). Puzanova-Malyshova offered material containing dung in various proportions. She found that material must be at least 50% dung to be made into a ball.

Puzanova-Malyshova (op. cit.) elaborated on the experiments made by Fabre and Hingston (1923:253-272). Some of her results with Scarabaeus sacer Linnaeus as as follows. A man-made dung ball will be readily accepted, but trimmed to proper size and shape if too large or not perfectly spherical. New material will be added if it is too small. A flat disk of dung will be made into a ball by pulling up on all the edges. A narrow cylindrical piece will be rolled into a ball shape. When presented with scattered small pellets, the beetle will hold on to one with its hind legs and reach out to grasp others, pressing them to the first one to make a larger ball. A forming ball is never left to get more material, but always dragged along. A ball impaled on a vertical or horizontal pointer is freed (after some hesitation) by being cut in two and the halves stuck back together. The beetles also have an awareness of the weight of a ball. An artificial ball of the proper size but containing a lead weight will be torn apart, the weight removed, and the dung pieces put back together again. However, if the weight is less than 20 gm it will apparently not be detected. We thus see that the beetles have an acute awareness of the exact shape, size, and weight of the masses
they are handling, and an ability to cope with a wide variety of situations regarding the ball, including some which must very seldom be encountered under natural conditions.

Hingston (1923:253) found that removal of one hind leg of Gymnopleurus miliaris Fabricius results in the loss of the ability to make a perfect sphere, supporting the contention of Fabre and other observers that the hind legs act as calipers to measure the ball.

The species of Gymnopleurus and Sisyphus observed appear to be as adept as Scarabaeus at ball making. In particular, both genera can make a ball from smaller pellets (Prasse, 1957b:597). This ability has not been observed in any species of Canthonina as yet, although Deltochilium gibbosum (Fabricius) uses very similar movements in making a feather ball (see below). Frequently balls will not be as perfectly shaped as is implied by the observers mentioned above. Thus Goggie (1956) notes that the "balls" of Scarabaeus semipunctatus Fabricius in Rimini are seldom spherical and that the beetles will often not bother to shape a piece of excrement before rolling it off. Matthews (1963a) noted that only the brood balls of Canthon pilularius (Linnaeus) are perfectly spherical, the food balls being irregular, Halffter (1961:293) also observed regular and irregular balls in Canthon indigaceus chevrolati Harold.

The temperature factor influences ball making, as it does all other activity. In Scarabaeus, Comignan (1928b) indicates that balls will be made at temperatures up to 30°C, but in ever reduced sizes as the temperature increases. Above this temperature the beetles will burrow directly into the food without making a ball. The lower temperature limit for ball making in Scarabaeus semipunctatus Fabricius was set at 21°C in Italy by Heymons and von Lengerken (1929:543), the optimal range being 25-30°C.

The present authors observed that in Cuernavaca, Morelos, Canthon indigaceus chevrolati Harold is governed primarily by substrate or dung temperature, rather than air temperature, in its ball-making behavior. On the partially cloudy day on which the observations were made, the air temperature remained at a steady 28°C throughout, but the beetles did not initiate ball-making activity in the piles of cow dung, which were subjected to intermittent sunshine, reached 34°C in the outer layers (this happened to be at 13:30 hrs). Before this, the beetles remained quiescent inside the cow dung, having been flying to the dung...
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flying to the dung and penetrating it throughout the morning. Canthon
h. humectus Say in the Valley of Mexico was similarly observed to
remain quiescent (feeding?) inside cow dung until the full heat of the
day began.

Balls may, of course, be made from any malleable food material
whatsoever, according to the preferences of the species or the exigencies
of the moment. Carrion is a frequent food material in South America,
as we have seen (Section 2). Perhaps one of the most unlikely of raw
materials for ball making are the chicken feathers used by Deltochilum
gibbosum (Fabricius) for its brood ball (Cartwright, 1949; Howden
and Ritcher, 1952). Presumably this species normally feeds on bird
cadavers and mixes the feathers with skin, flesh, etc. to make a ball
in the normal manner. With chicken feathers alone the beetle appears
to have considerable difficulty. One specimen was observed by Matthews
attending to make such a ball one night in Florida in April. It came
to the feather pile at 21:00 hrs and began handling the feathers with
the same movements used by Scarabaeus in making a ball out of smaller
pellets. That is, it reached out and grasped a few feathers from the
nearest portion of the mass, transferred these to the middle and hind
legs, reached out for more, and simply tried to press these to the first
batch, as if they were malleable material. This procedure was observed
over and over again for the next two and three-quarter hours. At the
end of that time a very small, very irregular mass of feathers had been
built up from the accidental intertwining of the feather shafts. The
beetle showed no ability to cut the feathers, and no unusual dexterity
in intertwining the loose ends, the observer lost patience at that point
and removed the ball, which by comparison with a fully-formed feather
ball found on another occasion, proved to be about half made. This
means it would have needed about 5½ hours for its completion! Lueder-
waldt (1910[1911]:431) notes likewise that in the necrophagous species
of Canthon in Brazil, ball making from carrion, which normally takes
a few minutes, may last for "hours" if the beetle is struggling with a
tendon. He observes in that case that the beetles do not abandon the
task to make a ball from an easier portion.

There is a close correlation between the size of the beetle and
the ball it makes, as might be expected. The accompanying graph (fig.
5) shows this correlation in representatives of all four subtribes under
consideration. The data on Canthonina are taken from our own pub-
lished and unpublished information, those on *Sisyphus* and *Gymnopleurus* from Prasse (1957b:598), and those on *Scarabaeus* from Heymons and von Lengerken (1929:591). In most cases it was not possible to correlate ball size with the size of the individual beetle actually making it; therefore most curves were obtained simply by plotting the extremes and averages of ball sizes and of *Scarabaeus*). The curve is more in the case of one species than in another, for differently situated slopes seem to result in variation in relation of the New Jersey individual considerably less in the South Carolina individual.

A case of the observed by Harold. In one other of two different types of shape and 10-11 mm, and of irregular possible that the relatively, as Math. *Canthon pilularius* and *Canthon imitator* more carefully than than the food ball and *Scarabaeus* and *Sisyphus* consistence between a single beetle (1923:240).

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of ball sizes and beetle sizes (the averages only in the case of Scarabaeus). The curves are thus based on at least three points, several more in the case of the canthonines. It may be seen that the members of one species tend to fall along a remarkably straight line, which is differently situated from the lines of the other species, although the slopes seem to remain fairly constant. The graph also shows geographical variation in relative ball size in Canthon chalcites Haldeman. New Jersey individuals (from the Pine Barrens area), while averaging considerably less in size, tend to make proportionately larger balls than South Carolina individuals.

A case of variation in ball size within a single population was observed by Halfpier (1961:293) in Canthon indigaceus chevrolati Harold. In one location in Yucatan individuals were rolling balls of two different types: some smooth, of finely selected dung, regular in shape and 10-11 mm in diameter, and some rough, containing straws, and of irregular shape varying from 12 to 17 mm in diameter. It is possible that these corresponded to brood balls and food balls respectively, as Matthews (1963a) made a similar observation in regard to Canthon pilularius (Linnaeus). In this species, the brood balls are much more carefully made, more regularly spherical, and smoother surfaced than the food balls. Observers of the European Gymnopleurus, Sisyphus, and Scaraebaeus have not noted any difference in size, shape, or consistency between food balls and brood balls, or between balls made by a single beetle (usually food balls) or two beetles (usually brood balls).

The species of Gymnopleurus studied by Prasse (1957a,b:1958a) (G. Geoffroyi Fuesly and G. mopsus Pallas) are unique in the tribe, as far as is known, in that they never make food balls. The adults always eat directly from the dung source above ground. This is frequently seen in all other genera and species studied, but there it is not the only method of feeding. On the other hand, Gymnopleurus millari Fabricius will bury and eat a food ball, as in the other genera (Hingston, 1923:240). In Sisyphus scharfii (Linnaeus) food balls are made principally during the feeding season, feeding often being at the source at other times (Prasse, 1957a:441).

Few data are available on the number of balls made by individuals in a lifetime. Teichert (1959) brings together all known data on this, mostly from the works of Prasse and Heymons and von Lengerken. During the Reifungsfrass period, Sisyphus scharfii (Linnaeus) makes
about 20 food balls and Scarabaeus spp. probably an equal number. During the breeding period, S. schaefferi pairs make about 10 brood balls (i.e., 10 eggs are laid), Gymnopleurus mopsus Pallas and G. geoffroyi Fuessly make about 5, and the three species of Scarabaeus studied make 3-6. These small numbers indicate a very high survival rate for the offspring.

**Initiation of Ball Rolling**

At the end of the shaping phase the ball is fully formed and rolling movements begin. If a beetle encounters a ready-made ball of food material, it shows no hesitation in accepting it and rolling it off. It will be recalled that in order for a substance to be made into a ball, it must be at least 50% dung, according to Puzanova-Malysheva's (1956) experiments on Scarabaeus sacer Linnaeus. In order to be rolled off, a ball need be far less than 50% food; it is sufficient that a small portion of the surface be smeared with dung (Heymons and von Lengerken, 1929:557), the remainder being some non-nutritive material. Comignan (1928b) found that the ball may be entirely non-nutritive and be accepted if actually placed between the legs of Scarabaeus, providing the temperature is high (27°C).

In the same way that the olfactory stimuli need be less strong to initiate ball rolling, as opposed to ball making, so also the ambient temperature need be less high. Whereas Scarabaeus semipunctatus Fabricius in Italy will not begin to make balls until the air temperature reaches 21°C, it will roll ready-made balls at 19°C (Heymons and von Lengerken, 1929:543). The rapidity and "skill" of rolling increase as the temperature increases, the optimum range being 25-30°C. Almost identical results were found by Prasse (1957b:592) for Sisyphus schaefferi (Linnaeus) and Gymnopleurus geoffroyi Fuessly in Germany. Paulian (1943:163) ascribes the rarity of rolling behavior in the scarabs of the Ile d'Yeu to the low temperatures prevailing there.

**Ball-Rolling Positions**

The usual rolling position for a single beetle is head downward behind the ball, the forelegs applied to the ground and the other legs on the ball, with the middle legs occasionally touching the ground. This position is the exclusive one for Canthon and Scarabaeus rolling alone.
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the other legs

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and the usual one for Gymnopleurus. In Sisyphus (schefferi Linnaeus

being the only species studied), the position behind the ball is quite dif-

different. The beetle maintains its fore and hind legs in constant contact

with the ball, its middle legs in the air, and its head only pushing against

the ground (fig. 9, right-hand beetle). In Gymnopleurus and Sisyphus

a lone beetle (usually a male) may pull the ball instead of pushing it.

In this case, the beetle walks backward, head up, in front of the ball, the

fore and middle legs pulling the upper surface of the ball toward the

beetle, the hind legs walking backward along the ground (fig. 8, left-hand

beetle). This position was found by Matthews (1965) to be the usual

e one for Canthonella parva Chapin in Puerto Rico when rolling alone.

Lone beetles will never use this position in studied Scarabaeus and Can-

thon, and very seldom even when in pairs. Henceforth, the head-up posi-

tion before the ball will be referred to as the "pulling" position and the

head-down one behind the ball as the "pushing" position. Prasse (1957b:

599) called these positions I and II respectively.

When one ball is being rolled by two beetles (practically always of

opposite sexes), the positions assumed differ somewhat in the different

genera studied. In Sisyphus, one beetle (usually a female) assumes the

pushing position and the other the pulling position (fig. 9). The same

is nearly always true of Gymnopleurus (fig. 8), however, in the species

studied the beetle in the pulling position may occasionally climb on the

ball and balance on it (fig. 7). In both these cases rolling is clearly

cooperative; this fact emerges particularly when an obstacle has to be

overcome. In that case, the pulling beetle will actively aid the pusher in

carrying the ball over the obstacle (Prasse, 1957b:603). In Canthon

pilularius (Linnaeus), C. i. chevroleti Harold, and C. h. humectus Say

c one beetle (the male) is in the normal pushing position, but the other

always balances on top of the ball while it is being rolled (fig. 6), never

assuming the pulling position and never aiding in rolling, except possibly

to pull on grass stems from the balancing position (authors' observations).

This also seems to be true of Malagoniella violacea (Blanchard) (Mar-

tinez, 1950) and all other canthonines briefly observed by the authors

except Canthonella parva Chapin, in which the pushing-and-pulling posi-

tions are assumed (Matthews, 1965).

An interesting variation in the position of the female on the ball was

noted in C. h. humectus Say by the authors in the Valley of Mexico.

When a male was rolling on terrain heavily covered with grass, the
Fig. 6-11. Positions of some Scarabaeini when rolling in pairs. Arrow indicates direction in which ball is being rolled. Fig. 6. Canthon pilularius (Linnaeus) (from Matthews, 1963a, originally from photograph); fig. 7. Gymnopleurus geoffroyi Fiesaly (from photograph in Prasse, 1957b); fig. 8. Gymnopleurus geoffroyi Fiesaly (from photograph in Prasse, 1957b); fig. 9. Sisyphus schaefferi (Linnaeus) (from photograph in Prasse, 1957b); fig. 10. Scarabaeus semipunctatus Fabricius (from posed photograph in von Lengerken, 1951); fig. 11. Scarabaeus semipunctatus Fabricius (from posed photograph in von Lengerken, 1951).

In the special combination is very female balance on the male of the ball in the pushing, female is 1 point out by C and independent roll in the pushing. Fabre (Souv. 1: 2) are of the same
female balanced on top of the ball, as on a treadmill (fig. 12). But when the male of the same pair was rolling in open terrain, the female clung to the side of the ball and did not move, allowing herself to be rolled with it (fig. 13). This enabled the male to roll with astonishing rapidity over this terrain.

In the species of *Scarabaeus* observed, the pushing-and-pulling combination is very rare. It is normal for one beetle (the male) to roll the ball in the pushing position, and for the other to follow, walking a short distance (not over 3 cm) behind the roller (fig. 11). This was first pointed out by Goggio (1926:11) in *Scarabaeus semipunctatus* Fabricius and independently confirmed for various species by Heymons and von Lengerken (1929). However, occasionally in *Scarabaeus* the two beetles roll in the pushing-and-pulling positions (fig. 10) seen in *Gymnopleurus* Fabre (Souv. 1:15) believed that this occurs usually when the beetles are of the same sex and when the puller is actually awaiting his oppor-
Fig. 13. Canthon h. humectus Say, pair rolling on open terrain. Male (left) is
pushing, female is clinging to side of ball. (From motion picture taken by the authors).

tunity to steal the ball. However, Heymons and von Longerken (1929: 579) note that in hot weather or hot climates (Algeria) Scarabaeus sacer
and S. semipunctatus show a sharply increased tendency to roll in the
pushing-and-pulling fashion, the beetles being of opposite sexes. Goggio
(1926:11, 21) notes that occasionally one of a pair of S. semipunctatus
will climb on the ball and be rolled with it. It may be that the normal
tendency of the female to follow the rolling male, instead of pulling or
climbing on the ball, may have something to do with the relatively small
size of the ball in Scarabaeus, as pointed out earlier in this section (fig. 5).

The Roles of the Sexes

Well-defined, separate roles for the sexes in joint ball rolling are
seen only in studied species of Scarabaeus and Canthon, where the male
is the active partner, and in some species of Gymnopterus, where the
female is the active partner who initiates the process and rolls it in the
pushing-and-pulling fashion, the beetles being of opposite sexes. Goggio
(1926:11, 21) notes that occasionally one of a pair of S. semipunctatus
will climb on the ball and be rolled with it. It may be that the normal
tendency of the female to follow the rolling male, instead of pulling or
climbing on the ball, may have something to do with the relatively small
size of the ball in Scarabaeus, as pointed out earlier in this section (fig. 5).

In some other species, during rolling by the female, 80% of the time
a female all the way (Linn. 1960), G. mopsus (Honda, 1927),
(1923:236). It was stated by the female partner, even in the pushing position
of this species: She plays the main part in pushing the ball and without
doubt that the female unaided by the male rolls the ball, and in Scarabaeus
in Sisyphus Fabricius

In Sisyphus

In this species, a (usually active) partner, even in the time comes for the
actual work of expression (Fabricius 1957b:604).
female is the active partner. The active partner is the one who at least initiates the process of making the ball (sometimes making it entirely), rolls it in the pushing position, and buries it. The passive partner in these species joins the active one during or after the ball-making process and plays a passive role in rolling and burial. As always, there are individual exceptions. Goggio (1926:17) observed that during rolling in Scarabaeus semipunctatus the pusher was the male 24 out of 27 times, being the female the other three times. We will see that in Scarabaeus the ball is question is the nuptial ball, not the brood ball. The brood ball is later made by the female alone, and rolled and buried by her alone. In Canthon pilulatus (Linnaeus), C. i. chevrolati Harold, and C. h. humecus Say the active partner is the male in all instances observed by the authors.

In some other studied species, the beetle in the pushing position, during rolling by a pair, will be of the following sex, by species: a female 80% of the time in Styphus schaefferi (Linnaeus) (Prasse, 1957b:600), a female all the time in Gymnopleurus geoffroyi Füessly (Prasse, 1957b:600), G. mopsus Fallas (Prasse, 1958:717), and G. sinaurus (Olivier) (Honda, 1927), but a male "as a rule" in G. miliaris Fabricius (Hingston, 1923:236). It will be recalled that in Styphus and Gymnopleurus the other beetle will usually be rolling in the pulling position, whereas in most canthonines (except Canthonella) it is balancing on the moving ball, and in Scarabaeus it is following a short distance behind.

In the species of Gymnopleurus the female is clearly the active partner, even in G. miliaris Fabricius, where the male is usually in the pushing position during rolling. Hingston (1923:262) writes of the female of this species: "She is the initiator, explorer, organizer of their lives. She plays the main part in changing the pellet; she goes off to seek out the trouble should the pellet cease to roll ... finally she is the excavator, and without doubt selects the place to dig." Prasse (1957b:604) reports that the female G. geoffroyi Füessly always buries the ball and male unaided by the latter, and Honda (1927) reports the same for G. sinaurus Fabricius.

In Styphus schaefferi (Linnaeus) the situation is not so clear-cut. In this species, as we have seen, either sex may be in the pushing (normally active) position, although it is usually the female. However, when the time comes for burial, the pulling beetle (usually the male) does the actual work of excavation, the female sitting passively on the ball (Prasse, 1957b:604).
Table 4

Roles of the sexes of some species of Scarabaeini when working in pairs

<table>
<thead>
<tr>
<th>Species</th>
<th>Ball making</th>
<th>Sex in pushing position</th>
<th>Position of other partner</th>
<th>Type of ball involved</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sisyphus schaefferi</td>
<td>In cooperation, initiated by Φ</td>
<td>Φ 80% of time</td>
<td>Pulling</td>
<td>Food or brood ball</td>
</tr>
<tr>
<td>Gymnopleurus geoffroyi</td>
<td>In cooperation, initiated by Φ</td>
<td>Always Φ</td>
<td>Pulling 1</td>
<td>Brood ball only</td>
</tr>
<tr>
<td>Scarabaeus semipunctatus</td>
<td>By Φ alone</td>
<td>Always Φ</td>
<td>Following 2-3 cm behind</td>
<td>Nuptial ball</td>
</tr>
<tr>
<td>Canthon pilularius</td>
<td>In cooperation, initiated by Φ</td>
<td>Always Φ</td>
<td>Balancing on top of ball</td>
<td>Brood ball only</td>
</tr>
</tbody>
</table>

1 Sometimes balancing on ball.
2 Rarely Φ.

Thus, taking the tribe Scarabaeini as a whole, and to the extent that it has been studied, there is no clear-cut distinction between the activities of the male and of the female regarding the preparation, rolling, or burial of the brood ball. The role of the sexes may be reversed in different species, and often in the same species. Of course, the preparation of the brood pear is the female's work exclusively, as in all Scarabaeinae (see Section 20).

In all genera studied except Scarabaeus, the ball that is being rolled by a pair of beetles is nearly always the brood ball, that is, the ball that will be the food supply of the larva. In Scarabaeus, on the other hand, it is apparently never the brood ball, but rather the "nuptial" ball. This ball is usually made entirely by the male, from beginning to end, and is rolled entirely by him, the female following behind a few paces (fig. 11). If the ball is removed from the male by the observer, the female loses interest and ceases to follow him (Heymons and von Lengerken, 1929: 580). When the ball is buried (by the male), and the two beetles are underground with it, they copulate and consume the ball together. It is difficult to avoid a sort of "anti"-philosophy, but the known in some species of Scarabaeini seems to be the usual one.

Three observers (Heymons, Wagner, and Matthews) have observed the direction in which a Scarabaeus ball is rolled. They adhered to this line of investigation in the course of their observations and concluded (given the results obtained) that the beetle will always roll in a straight line, by deviating its hind leg, both middle and both middle and both middle and middle leg, both middle and both middle and both middle and both middle and both middle and middle leg, both middle and both middle and both middle and both middle and both middle and... causes great interest.

Matthews (1923: 269-272) observed that a Scarabaeus ball is rolled in a more or less straight line, by deviating its hind leg, both middle and both middle and both middle leg, both middle and both middle and both middle and both middle and both middle and... causes great interest.

Wagner (1923: 269-272) observed that a Scarabaeus ball is rolled in a more or less straight line, by deviating its hind leg, both middle and both middle and both middle and both middle and both middle and... causes great interest.
When a ball is being rolled that is, the ball that on the other hand, "nuptial" ball. This thing to end, and is few paces (fig. 11).ter, the female loses in Lengkerken, 1929; the two beetles are ball together. It is difficult to avoid the interpretation that this ball is made by the male as a sort of "enticement" or "present" for the female—a type of behavior known in some Diptera and other insects—and the term "nuptial ball" therefore seems appropriate.

The somewhat confusing differences in the roles of the sexes regarding the common ball are summarized in Table 4 for the four best-studied species of Scarabaenini.

**Directions in Which Balls are Rolled**

Three observers have paid particular attention to the matter of the direction in which a ball is rolled in relation to spacial factors. Hingston (1923:269-272) noted that Gymnopleurus miliaris Fabricius rolls in a straight line directly away from the dung source, and that the beetles adhere to this straight course with great tenacity. Attempts to deviate the course of rolling beetles by placing them on a rotating platform (rotated up to 20 times), or by other manipulations, did not cause any loss in the sense of direction. It has been noted by all observers that a beetle will always try to surmount an obstacle, rather than go around it by deviating its course even a few centimeters. Hingston removed one hind leg, both hind legs, both hind legs and one middle leg, and finally both middle and both hind legs of some beetles, without impeding them from rolling in a straight line. It is not clear how a beetle can roll with both middle and hind legs missing. Removal of even one foreleg, however, causes great inconvenience.

Matthews (1963a) noted that Canthon pilularius (Linnaeus) rolls in a more or less straight line only about half the time, not counting enforced direction changes due to obstacles, and that the initial direction chosen will be influenced by the slope of the ground, the wind direction, and the position of the sun, in that order of priority. Specifically, the beetle will tend to roll uphill, with the wind, and directly toward or away from the sun (rather than at an angle), all other factors being equal.

Wagner (1957) noted a loss of orientation when rolling beetles, probably a species of Canthon, entered shaded patches in their course and concluded that the position of the sun is used for guidance in maintaining a straight course. He further noted that the beetles tend to roll directly toward the sun.
Finally Hingston (1923:238, 273) made a curious observation concerning *Scarabaeus sacer* Linnaeus in India. He reports that "in the desert" all the individuals may be seen to approach a dung source from the same direction, and then to roll the completed balls back to the "cardinal point" they originally came from, all the beetles thus rolling in the same direction. Suspecting the influence of the position of the sun on rolling directions, Hingston attempted to alter the course of rolling *Gymnopuleurus* by using a mirror to alter the sun's apparent position, without effect.

**Distances Rolled**

The species of *Gymnopuleurus* and *Sisyphus* studied by Prasse (1957b:601) roll 2-9 m in the field, and those of *Scarabaeus* studied by Heymons and von Lengerken (1929:554) roll 30 cm to 15 m, the shorter distance being exceptional. Halfster (1961:251) noted that *Canthon h. humecus* Say and *C. i. chevrolati* Harold roll 2-5 m. Matthews (1963a) measured the actual distances rolled by *Canthon pilularius* (Linnaeus) in the field by tracing the course behind the beetle and measuring all the twists and turns. He found that food balls are rolled 15 — 830 cm, and brood balls 90-1060 cm. His unpublished data on other Canthonina are as follows: *Canthon imitator* Brown — 198-1650 cm. *C. chalcites* Haldeman — 120-640 cm. *Boreocanthon probus* (Germar) (a much smaller species) — 38-160 cm. Most of these were probably food balls. Luederwaldt (1911:431) notes that in Brazil the necrophagous *Canthon curvipes* Harold rolls for considerable distances, up to five or six meters, especially if the soil is hard. The equally necrophagous *Canthon tristis* Harold, in contrast, rolls the ball for much shorter distances. There can be no doubt, of course, that the difficulty of the terrain greatly influences the distances rolled.

We are in need of studies of comparative ball-rolling distances among species of a single fauna, to determine whether there is an adaptation for apportioning the available terrain around a food source, by having different species consistently rolling different distances when working together.

**Burial of the Ball**

In most ball-rolling beetles the ball is buried after having been rolled a certain distance. This applies to both the food ball and the brood ball, Exception: *Sisyphus* Schaef.

Even though as may be that of a search subsoil before burial of burial spots initiating the burial of ball. It is not clear at its final choice behavior, leaving then usually not buried.

Both the terrain under natural conditions. For it the burial of ball, because this is the Tippmann (1959) in one location in spot. A serious however, unknown modern the "choice"

As previous burying the ball on the ball and *Sisyphus* Schaef which does the burial of those used by all nearby first, then excavation is dug all sides, in such a way they are simultaneously ball at the surface of the beetle, presumably it, will emerge and observed, the pass will then help the This has not yet be
The observation confirms that "in the dung source from back to the 'carthus rolling in the direction of the sun on the use of rolling Gym-

studied by Prasse arabaeus studied by 0 15 m, the shorter that Canthon h. Matthews (1963a) lararius (Linnaeus) and measuring all 15 - 830 cm. Other Canthonina 30 cm. C. chalcites (Germar) (a much probably food balls, rophagous Canthon 5 live or six meters, this C. tristis dis- tances. There can a greatly influences all-rolling distances er there is an adap- a food source, by en distances when ball, Exceptions may be found under Group IV and Aberrant Nidification Behavior in Section 20.

Even though the purpose of rolling does not seem to be primarily that of a search for a burial spot, there is some evidence of testing of the subsoil before burial takes place. There may be up to four or five tests of burial spots before one is finally selected. This testing is done by initiating the burial process, sometimes to the extent of half-burying the ball. It is not clear to the observer what factors prompt a beetle to arrive at its final choice. Often beetles seem to execute a type of reconnoitering behavior, leaving the ball for short excursions of a few centimeters and then returning to it. It is not clear what this accomplishes, as the ball is usually not buried in the area of the excursion.

Both the time and the distance rolled vary greatly under the same conditions. For instance, Canthon pilularius (Linnaeus) rolls 2-23 minutes under natural conditions (Matthews 1963a). In some instances, it may be that terrain features force a concentration of burials in one small area, because this is the only one where burial is possible. This was found by Tippmann (1959) for many individuals of Sisyphus schaefferi (Linnaeus) in one location in Yugoslavia, where about 20 balls were buried in one spot. A serious obstacle may often force burial at its foot. In general, however, unknown factors not associated with the immediate terrain govern the "choice" of a burial spot.

As previously mentioned, only one beetle does the actual work of burying the ball when a pair is involved, the other one sitting passively on the ball and being buried with it. In all observed species except Sisyphus schaefferi (Linnaeus) it is the roller in the pushing position which does the burying. The burial movements are quite different from those used by all other tribes of Scarabaeinae. A burrow is not dug nearby first, then the ball brought in, whole or in pieces, but rather the excavation is dug directly beneath the ball, the soil being pushed out on all sides, in such a manner that both ball and beetle (and partner, if any) are simultaneously interred. It may be that during the burial process the ball at the surface slips a little to one side; in that case the burying beetle, presumably no longer feeling the pressure of the ball on top of it, will emerge and pull it back into position. In the European genera observed, the passive partner, once it has been fully interred by the other, will then help the other in the process of excavating the nest chamber. This has not yet been verified in Canthon or other New World genera.
19. FEEDING BURROWS

In the genera Ateuchus, Ontherus, Dichotomius, Copris, Onthophagus, and some species of Phanaeus, it is common to find individuals alone in simple burrows with dung packed into the blind end. Two of these burrows are represented in figs. 14 and 17. It seems likely that this type of burrow is one dug by single beetles to store food for themselves, but only in some species of the genus Copris has this been actually verified. For instance, Matthews found many small burrows of Copris fricator (Fabricius) in North Carolina in the spring before nidification had actually begun in the area. These burrows were very shallow and contained only a small quantity of dung packed into the enlarged end, and contained only single beetles, of either sex. Frequently the dung supply was largely consumed, leaving mostly straws and beetle excrement in the burrow. Rommel (1961) and other observers of Copris hispanus (Linnaeus) report similar feeding burrows for that species.

In Phanaeus the burrows usually contain two individuals, a male and female, but these burrows do not contain a brood pear. They have the dung simply packed, either into a side branch (Ph. vindex McLeay, fig. 15) or into the end of an unbranched burrow (Ph. palliatus Sturm, fig. 16; Ph. mexicanus Harold).

Even burrows which are just in their initial stage, without yet containing dung, may be being dug by a pair of beetles in cooperation (author’s observations). Unfortunately we do not yet have any complete sequences of observations to be able to interpret these data. As a pure guess, we would say that in Phanaeus temporary pair bonds are formed very early in the active season, in May in Mexico, and that the pair dig and provision a single burrow which will serve as a joint feeding burrow. When the buried food is jointly consumed, the same pair, or a new partnership, will dig another food burrow, and so on until the arrival of the breeding season in September. At that time a brood burrow will be dug (see Sections 20 and 22), again by a pair but probably not the same one that started in the beginning of the active season (although this is possible).

In Dichotomius carolinus (Linnaeus) it is also common to find two individuals of different sexes in a single burrow with dung packed into the ends of one or more branches. The burrows may have only one
Copris. On the other hand, it is likely that this mode of life has been actually verified for Copris fricator, but that the modification had advanced only in shallow and consequently the dung piles of the enlarged end, and beetle excreta of the enlarged end, and excreta of Copris fricator, which species.

Individuals, a male and male, and females in cooperation have any complete data. As a pure bond is formed and that the pair feeds as a joint feeding, to the same pair, or and so on until the time a brood burrow is completed. A pair but probably the active season common to find two

Fig. 14. Phanaeus mexicanus Harold, feeding burrow of single female. Ixtapan, State of Mexico. In this and subsequent figures, dung is indicated by stippling; pile of loose soil is at surface. (Original).

Fig. 15. Phanaeus vindex MacLeay, feeding burrow of pair. North Carolina. (Original).

Fig. 16. Phanaeus palliatus Sturm, feeding burrow of pair. Ocoyoacac, State of Mexico. (Original).
Fig. 17. *Dichotomius carolinus* (Linnaeus), unbranched feeding burrow of single beetle, Guatemala. (Original).

Fig. 18. *Dichotomius carolinus* (Linnaeus), two-branched feeding burrow of pair, Honduras. (Original).

branch, two branches frequently such wholly consumed, spite of the last cases, at least, into a brood ball.

In the South, the ball dig with ball (except more feeding burrows less elaborate...
branch, two branches, or three branches (figs. 17, 18, and 19). Frequently such burrows are found abandoned with the dung partly or wholly consumed, indicating that they were purely feeding burrows, in spite of the fact that they contained a pair of beetles. However, in some cases, at least, a feeding burrow, or one of similar design, is converted into a brood burrow (see Group 1 of Section 20).

In the Scarabaeini observed, all those species which normally bury the ball dig what we might call a feeding burrow to consume the food ball (except most Gymnopleurus, which do not make food balls). This feeding burrow is shallower (often barely beneath the surface) and less elaborate than the burrow which contains the brood ball.

Fig. 19, *Dichotomius carolinus* (Linnaeus), three-branched feeding burrow of pair. Ixtapan, State of Mexico. (Original).
NIDIFICATION BEHAVIOR

A few thorough and detailed studies are available on nidification behavior, nearly all of them (after Fabre) being in the German literature. We have to rely on these careful studies to be able to place the remaining amount of scattered, superficial, and fragmentary data in some sort of perspective. Our purpose here is not so much to compile and repeat these data, following an artificial arrangement as was done by von Lengerken (1954), but rather to construct a phylogenetic scheme, however provisional, which can be used as a framework for future investigations.

The four major behavioral groups proposed below represent different grades of behavior, probably independently achieved in different phyletic groups and not necessarily representing consecutive evolutionary stages. The proposed phylogenetic relationship between the groups is represented in fig. 39. Within each of the four major groups, a number of "variations" usually represent separate evolutionary lines which have achieved a given grade of behavior in parallel. The discussion of these groups is followed by descriptions of "aberrant" behavior, that is, behavior shown by a small minority of species of various different taxa.

The following is a summary of the nidification categories to be discussed at greater length in the next section:

**Group I.** Egg(s) is (are) laid directly in a food mass packed into the blind end or branch of a burrow dug near or under food source.

*Variation 1.* One egg is laid in a relatively small dung mass packed into the end of a burrow. *Ateuchus, Uroxys, Dichotomius* (part), *Bubas, Chironitis, Onthophagus, Oniticellus*.

*Variation 2.* Several eggs are laid in a very large dung mass accumulated in a spacious chamber. *Onitis*.

**Group II.** Egg is laid in a sphere or pear which is specially modelled over its entire surface by the female parent and is provided with an outer shell of soil. Sphere is constructed underground near or under food source. Usually one sphere per burrow, sometimes several. No brooding.

*Variation 1.* Egg only is enclosed in a hollow ball made of clay and situated on top of food mass, which is simply packed in end of burrow. *Gromphas*.

*Variation 2.*

**Group III.** Sphere or pear under food source (or over food source in cases of *onthophagus*, which is a fungus-like cake) which is a sphere or pear, each containing one egg. Female, and sometimes male, waits at the entrance of the burrow for the larva of larval food, *Synapsis, Catharina*.

**Group IV.** Sphere or pear under food source and rolling it on sand from food source.

*Variation 1.*

**Malagocyphon*.

*Variation 2.*

*Deltochilum*.

*Variation 3.*

*Aberrant Ni*.

*Variation 1.*

*Materialis, Drepanocerus*.

*Variation 2.*

*Neocassida*.

*Variation 3.*

*Conradya* (part), *Oxymorpha* (part).
to place the tertiary data in some method to compile and present it in a manner as was done by a phylogenetic scheme, work for future representation of different phyletic evolutionary stages.

Variation 2. Both egg and food mass are enclosed in a clay shell, in separate compartments. Boilites, Phanaeus, Oxysternon, Dichotomius (part), Helcocoris.

Group III. Construction of a spacious underground chamber near or under food source, containing first a large mass of dung (the dung cake) which is compacted and then divided into several brood ovoids each containing one egg. Ovoid usually not enveloped in a clay shell. Female, and sometimes also male, remains in nest chamber some or all of time of larval development (this is here termed brooding). Copris, Synapsis, Catharsius?

Group IV. Fashioning a ball of food on surface at food source and rolling it on surface, to be provided later with an egg some distance from food source.

Variation 1. Brood ball buried, coated with clay shell in burrow. Malagoniella, Canthochilum (part).

Variation 2. Brood ball not buried, coated with clay shell on surface. Deltochilum, Eurysternus (part), Sisyphus (part), Nesosisyphus.

Variation 3. Brood ball buried, not coated with clay shell, but often with a thin outer layer of soil or dung and soil mixed. Canthon (part), Scarabaeus, Gymnopleurus, Sisyphus (part).

Aberrant Nidification Behavior.

Variation 1. No nidification, the larva living loose inside the food material. Onitis (part), Onthophagus (part), Liatongus (part), Drepanocerus, Trichilium.

Variation 2. Canthonina which make several brood pears simultaneously directly from the food source. Canthon (part).

Variation 3. Scarabaeini unable to make or roll balls. Nidification procedure unknown. Eucraniina, Canthochilum (part), Canthon (part), Canthonidia, Eurysternus (part).
20. Description and Discussion of Nest Types

Group I. Egg(s) is (are) laid directly in a food mass packed into the blind end or branch of a burrow dug near or under food source.

Variation 1. One egg is laid in a relatively small dung mass packed into the end of a burrow. *Ateuchus, Uroxys, Dichotomius* (part), *Bubas, Chironitis, Onthophagus, Oniticellus*.

The type of nesting behavior included here is considered the most primitive because the brood burrow does not differ in principle from the adult feeding burrow and it is the least elaborate. Most forms in groups II and III continue to use the same type of burrows for feeding, but their nesting behavior is more elaborate. The types of nests seen in this category are basically similar to those of most Geotrupinae.

*Ateuchus histeroides* Weber digs vertical, unbranched burrows 10 or 12 inches deep beneath cow manure in woodlands in the Eastern United States. "A single egg is laid in a cell near the upper end of the vertical pellet of dung packed into the lower end of each tunnel" (Ritcher, 1945). *A. granigerum* (Harold) digs and provisions similar burrows beneath the debris chambers of *Atta* nests in Brazil (Eidmann, 1937, cited in von Lengerken, 1954:183).

The only behavioral data we have on the genus *Uroxys* are provided by Ohaus (1909:88), who found the brood "balls" of two species (then undescribed) in eastern Ecuador under cow and horse dung. The nest is as in *Onthophagus*, that is, the egg is laid in a mass of dung packed into the end of a burrow. The brood ball is "larger than that of *Onthophagus* and the egg chamber is relatively smaller". The larva is "longer and slenderer" than in *Onthophagus*.

A nest of the same type is made by the common *Dichotomius carolinus* (Linnaeus). Lindquist (1935) states of the subspecies *colonicus* Say in Texas that "the egg is deposited in a mass of manure, which has the appearance of being pushed into a shapeless cavity branching away from the tunnel. The egg is enormous, about one-half by one-fourth inch in diameter". Likewise Ritcher (1945) says the egg of this species in Kentucky is laid "in a mass of manure packed in the burrow". After a many-year search, the authors finally located two *Dichotomius carolinus* nests near Cuernavaca, Morelos. Although the adults were not found in these particular burrows, other possibilities were considered. The essential features, described by Ohaus and Ritcher, ex. (actually in 1945), each contained one egg is packed, not massed, in one end of the deeper burrow and what the procedure, shallow, near-homogeneous provisioned with a mass of a sausage. The tunnel is present to a depth, enlarged and continues from the upper burrow in the mass, where the dung is packed into a small quantity of a diameter and 3. burrow, in contrast to the burrow, where the parents eat a huge, evidence strongling strong, in provisioning the brood. One nest uncovered contained both a larva and evidence that the male was present, and larvae.

The brood briefly described belong to Group II.

We will now briefly described (actually *Bubas* observed by Fabian) many-branched burrows, an egg cavity near the burrow when an egg is laid before and respect *Bubas* actually...
mass packed into the food source.

Dung mass packed into burrows, Dichotomius nicellus.

Considered the most principle from the forms in groups feeding, but their

shaped burrows in the Eastern upper end of the tunnel, each containing one larval cell. It is clear from the design of the nests what the procedure was in constructing them (refer to fig. 20). First a shallow, near-horizontal tunnel is dug beneath the cow dung and is provisioned with a large quantity of dung packed into the tunnel in the form of a sausage. Then a new shaft is sunk at an angle from the shallow tunnel to a depth of 20-40 cm. The bottom end of this shaft is slightly enlarged and carefully rounded, then (selected?) dung is brought down from the upper branch and carefully packed into this end. An egg is laid in the mass, which is then covered over with a layer of soil and more dung is packed above this layer, creating a second cell. A surprisingly small quantity of dung is provisioned for the larva — a mass 3.3 cm in diameter and 3.0 to 4.5 cm long. The dung amassed in the feeding burrows, in contrast, is 9 to 30 cm long for each branch (depending on the burrow), while being of the same diameter, which indicates that the parents eat a huge amount of food in comparison with the larva. All evidence strongly suggests that both parents cooperate in digging and provisioning the nest, as they do the feeding burrows (see Section 19).

One nest uncovered during the construction process, in the same locality, contained both a male and a female. In this particular case it appeared that the male was eating the dung in the lower branch, intended for the larva.

The brood balls of several other species of Dichotomius have been briefly described, but all are modelled, not simply packed, and therefore belong to Group II (q.v.).

We will now consider some of the Onitini. Babas bison (Linnaeus) (actually Bubas bubalus [Olivier], according to Chobaut [1929]) was observed by Fabre (Souv. VI:25-31) in France. It builds rather short, many-branched burrows, each branch packed with dung and each with an egg cavity near the bottom of the food mass. This means that the egg is laid before most of the food mass is accumulated, and in this respect Babas acts exactly like some of the known Geotrupinae.
Fig. 20. *Dichotomius carolinus* (Linnaeus), nest showing two larvae in their respective dung supplies and empty horizontal tunnel near surface. Pile of loose soil is blocking entrance. Cuernavaca, Morelos. (Original).

The nest of *Chironitis pamphilus* (Ménétries) was described by Medvedev and Medvedev (1958) in Central Asia. Whereas the larval food mass appears to be packed in the usual way (in an unbranched burrow, however), the pupal cell is separated from the exterior by a series of layers made of dried dung, each layer well separated from the next (fig. 21). It is not clear whether these layers are made by the parent beetle or the larva. Medvedev and Medvedev seem to imply the former, but the layers give the appearance of having been made by the larva successively as the food supply dwindled.

The remaining species belonging to this group.

Fig. 21. *Chironitis pamphilus* (Ménétries) and successive layers (Medvedev and Medvedev 1958).

We will now be indebted for our knowledge to Burmeister (*Chironomus chicorius* Linnaeus). Alt of Group I, the oval mass by plastered with a then brought down and spread out carefully successive conc. the cell is almost then filtering plug of leading to this...
The remaining known Onitini are discussed under Variation 2 of this group.

We will now consider the large genus Onthophagus. We are indebted for our detailed knowledge of nidification in this genus largely to Burmeister (1930), who observed the four European species O. nu-chicornis (Linnaeus), fracticornis Preyssler, coenobita Herbst, and ovatus (Linnaeus). Although the larval food is packed as in other representatives of Group I, there appears to be an effort in some species to create an oval mass by first digging out a special cell which is alongside the main shaft. The walls of the cell are prepared by the female by being plastered with a cementing substance of unknown nature. The dung is then brought down from the surface in "armfuls", each load being spread out carefully inside the cell such that the food mass consists of successive concentric layers, each layer representing a load. When the cell is almost filled, a small cavity is molded in the end of the dung mass and an egg is laid in it, the cavity then being covered over with a filtering plug of dung fibers and soil. The branch or section of the tunnel leading to this cell is then filled with soil and a new cell begun higher.
up, at least in the European species studied. Burmeister (1930) described important differences in the design of the nest in different species. For instance, in O. ovatus the higher cells are horizontal in position, the lower ones vertical. In O. coenobita the burrow is unbranched, with the cells lying one above the other. In the other two species, the burrow is branched, but all the cells are more or less vertically oriented. There are also specific differences in the location of the row of cells first completed. For more details and figures see also von Lengerken (1954:205-235).

Onthophagus taurus (Linnaeus), observed by Pabre (Souv. V: 151) and Main (1922), and O. furcatus (Fabricius), observed by the former author, make simple vertical galleries, about 2 inches long, having the ends packed with a quantity of dung which, when extracted, has the form of a thimble. The food mass occupies the lower 2/3 of the thimble, the upper third being occupied by an egg chamber covered over with a thin layer of dung. According to Main (1922), the egg is cemented to a wall of the burrow before most of the dung is brought in.

Outside Europe, many United States species of Onthophagus have been observed — or rather, their nests have been described, as the direct observations of Burmeister have not been duplicated. Some notes may be found in the literature on O. allius Howden and Cartwright (as anthracinus Harold, Lindquist, 1935), hecate Panzer (Lindquist, 1933; Ritcher, 1945), pennsylvanicus Harold (Lindquist 1933; Ritcher, 1945). subaeneus (Falisl), as cribricollis Horn, Sim, 1930), and landolli texanus Schaeffer (Howden, 1957). Howden and Cartwright (1963) recently summarized the known behavior of the North American species, including some original data on most of the above species and adding new data on O. striatulus (Falisl), oklahomensis Brown, tuberculiforms Harold, browni Howden and Cartwright, and medorensis Brown. The brood cells of O. hirculus Mannerheim and O. incensus Say, both in South America, have been briefly described (Ohaus, 1909).

The American species all seem to dig unbranched, vertical or winding burrows 1-9 inches long and packed at the enlarged end with a "wad" of dung forming only a single cell in each burrow. This cell is 1½ times as long as wide and is almost horizontal; in the upper (outer) end of it one egg is laid in a small cavity. The egg is attached by one end to the side of the cavity. The cells measure 6-11 X 10-16 mm (Howden and Cartwright, 1963). That of O. hirculus measures 1 X 2-3 cm (Ohaus, 1909). We do not know whether the other aspects of development can be predicted from this ovary cell.

A single female, or in some species, a lekking activity, and a few or several females may be present. The number is not mentioned, and the nest of O. incensus contains only one ovary cell.

Leaving O. hirculus, which we know has been observed in Europe and in the United States, we return to Oniticellus (Ehrenberg). Howden (1958) states that four eggs in cases of O. ancon are packed in a packed, thimble-like nest. The lower part, and the cavity occupied by the eggs, is packed with wads of dung, not mud. The cells do not extend 1 inch in length. Behavior below ground is mentioned in Ohaus (1909).

**Variation**

The type of behavior described by Howden (1958) for O. incensus is not mentioned in the literature on the American species. It seems that the American species ovary cells do not exist.
Gardner (1929) reports that Oniticellus (0.) cinctus (Fabricius) in India buries brood "balls" under dung and that these measure 13 mm in diameter. Medvedev (1952:224) reports that Oniticellus (Paronicicellus) festius Steven (as Liatongus) buries brood "pears" under dung. All authors are probably referring to packed dung wads, not modelled balls or pears in the true sense. Some other Oniticellini do not nidificate at all and are discussed under Aberrant Nidification Behavior below.

Variation 2. Several eggs are laid in a very large dung mass accumulated in a spacious chamber. Onitis.

The type of behavior included here was described by Oberholzer (1958) for Onitis calicus Boheman and by Skalé (1953, quoted by Oberholzer, 1958) for Onitis aygulus (Fabricius), both in South Africa. It seems that the female beetle accumulates a large mass of dung in the previously dug brood chamber and makes a number (about 5) of spherical cm (Ohaus, 1909:27). Data are not exact enough for us to be able to tell whether there are any specific differences in nest construction or other aspects of behavior. None of the native American species is reported to make branched burrows. One species (O. tuberculifrons) digs shallower burrows in moist habitats than in xeric ones (2-3 inches vs. 6-7 inches) (Howden and Cartwright, 1963:88).

A single female O. l. texanus may make three to 30 cells in captivity, and a female alluvius 20-40 cells, according to Howden and Cartwright (1963). 43-67 cells according to Lindquist (1935). In any case, the number is far larger than that seen in scarabs with more elaborate nidification behavior, even though Onthophagus still has the highly reduced ovary characteristic of Scarabaeinae (see Appendix II).

Leaving Onthophagus, we will now pass to the tribe Oniticellini, of which we know very little. Fabre (Souv. V:151) observed a female Oniticellus (Euonicicellus) fulvus Goeze (as O. flavipes Fabricius) lay four eggs in captivity in the course of three days. The eggs are contained in a packed, thimble-shaped mass of dung 1 mm wide and 15 mm high. The lower part of this mass is filled with dung, the upper part is hollow and cup-shaped, with the egg fixed in the bottom in a vertical position, and the cavity covered over by a thin layer of dung. This species thus nidificates much like an Onthophagus. Paulian (1945:129) describes a branched nest for this species, much like that of the European Onthophagus described above. Gardner (1929) reports that Oniticellus (O.) cinctus (Fabricius) in India buries brood "balls" under dung and that these measure 13 mm in diameter. Medvedev (1952:224) reports that Oniticellus (Paronicicellus) festius Steven (as Liatongus) buries brood "pears" under dung. All authors are probably referring to packed dung wads, not modelled balls or pears in the true sense. Some other Oniticellini do not nidificate at all and are discussed under Aberrant Nidification Behavior below.
egg cavities in this mass, without separating it into discrete ovoids. The larvae then feed on the mass communally, each constructing a pupal cell of dried fibers at the end of the two-year development period. It is not clear whether the female remains with the larvae during the latter's development, but Oberholzer reports that she continues to bring in more dung after the first eggs have been laid.

Several authors have claimed that the species of Onitis behave like Copris, breaking the dung mass up into separate ovoids and brooding these (Paulian, 1941:61; Janssens, 1951:6). The former author says: "Au Sénégal, j'ai pu constater qu'O. senegalensis Lansb. fabriquait, à partir de l'amasse stercoral, quelques ovoïdes comparables à ceux des Copris", and the latter author claims: "D'après Chobaut et Paulian et ce que nous avons pu constater nous-même, la plupart des Onitis ont une industrie qui se rapproche davantage à celle des Copris..." In spite of the rather emphatic assertions of these authors, doubt continues to remain, primarily because of the absence of supporting details. It is possible that these authors were influenced by Chobaut's (1922) claim that Onitis belial Fabricius nidificates like Copris and his refutation of Fabre's statement that it nests like Babas or the Geotrupinae. Fabre's remarks were based on observations communicated to him by Mayet. The latter author amplified his account in a separate paper (Mayet, 1901) in which he described and figured a short, sausage-type dung mass attributed to Onitis belial. Chobaut claims that the nest described was not of Onitis, but probably of Babas bison (Linnaeus), and then proceeds to describe a nest containing a female Onitis belial attending a large "gâteau stercoraire". He did not see this dung cake cut up into separate ovoids, but made the following inference: "Car, je n'en doute pas, ce volumineux pâté était destiné à être transformé en outres ou en poires, comme cela se passe chez les Copris" — an inference which is probably incorrect, in view of Oberholzer's observations mentioned above. We are in need of independent and detailed studies of the behavior of Onitis to clear up this matter; in the meantime, both Chobaut's and Oberholzer's actually observed facts support the contention that the dung mass is not cut up into ovoids in this genus.

Group II. Egg is laid in a sphere or pear which is specially modelled over its entire surface by the female parent and is provided with an outer shell of soil. Sphere is constructed underground near or under food source. Usually one sphere per burrow, sometimes several. No brooding.
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We are in need of
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ised with an
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oral. No brooding.

Variation 1. Egg only is enclosed in a hollow ball made of clay and
sitated on top of food mass, which is simply packed in end
of burrow. Gromphas.

Gromphas lacordairei Brullé (as inermis Harold) and G. aeruginosa
Perty 1 were studied by Judulien (1899), who communicated some data
which were published by Fabre (Souv. VI:76). The behavior of both
studied species of this genus is very interesting in that it is intermediate
between that of Group I and that of the other known Phanaeina (Vari-
ation 2 below). The food mass for the larva is packed and not modelled,
but the egg is enclosed in a clay shell (fig. 22).

Variation 2. Both egg and food mass are enclosed in a clay shell,
in separate compartments. Bolbites, Phanaeus, Oxysternon, Di-
chotomius (part), Heliocopris.

1 According to von Lengerken (1954.238) the species discussed by Fabre as
Gromphas de Lacordaire is G. aeruginosa Perty (= G. lacordairei Blanchard, sot
Brullé), but this is not an Argentine species, not being included in Martinez's catalogue
(1959). It seems probable that only G. lacordairei Brullé (= inermis Harold) was
studied by Judulien and Fabre.

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It will be immediately appreciated that the type of behavior described here is a striking advance over previous ones in that the larval food mass is modelled, not simply packed. That is, the beetle moves in a space all around the mass and sculpts it to the required shape. In feeding behavior, on the other hand, the members of this category (and also those of Group 111) retain the primitive packing method.

The brood pears of Bolbites onitoides Harold and Phanaeus (Phanaeus) menelas Laporte (as splendidus, not Fabricius) were studied by Judulien (1899), who communicated with Fabre (Souv. VI:71, 73). Those of Phanaeus (Metallophanaeus) saphirinus Sturm, Ph. (Phanaeus) floriger Kirby, Ph. (Phanaeus) lunaris Taschenberg, and Ph. (Phanaeus) dejeani Harold were studied by Ohaus (1909; 1913), those of Ph. (Phanaeus) triangularis Say by Lindquist (1933), Ph. (Coprophanacus) milon Blanchard by Judulien and Fabre (Souv. VI:80), Frenguelli (1939), and Barattini and Saenz (1953). Ph. (Phanaeus) vindex McLainy by Ritcher (1945), Phanaeus sp. (cited as Ph. conspicillus Laporte, a synonym of floriger Kirby) by Sauer (1956), and Ph. (Megalophanaeus) ensifer Germar by Teichert (1959). We here add new data on the brood ball of Ph. (Phanaeus) quadridens Say and Ph. (Phanaeus) palliatus Sturm. All observers are agreed that the brood ball is coated with a clay shell, sometimes very thick, and in the cases where the ball was examined internally before the eggs could hatch, a clay layer was found to exist between the cavity containing the egg and that enclosing the food mass (fig. 25). However, Ohaus (1913) claims that the outer cavity in Ph. floriger does not contain the egg but simply air, the egg being in another cavity hollowed into the main food mass inside the partition. He also states that the space around the brood ball is filled with earth except for an empty space at the tunnel end, which he calls the antechamber (Vorsaal). These observations have not been confirmed by subsequent observers.

The brood pears of Phanaeus are 25-45 mm in diameter, in keeping with the large size of the adults. They are usually nearly spherical, with one portion (that containing the egg chamber) slightly elevated from the rest. The food mass is more or less in the center of the pear and is spherical. The smoothness of the outer surface and general symmetry of form (of the recently made pear) have aroused the admiration of all observers.

The brood pears of Gromphas (V.) mass as well as the partition may be up to 1 cm thick except for the antechamber (Vorsaal), where it is thinner.

A detailed study of Phanaeus milon Blanchard by Judulien and Fabre (Souv. VI:80) has an outer layer which is slightly improved by the parent. The latter does not make the outer second layer which cover the brood pear is cemented by the parent. The outer layer of the various layers (unbranched) has an outer layer which is slightly improved by the parent.

Ph. (Phanaeus) palliatus Say, Mexico, by having finely set lines externally with one other with the food mass (unbranched) and therefore that arc burrow, but rather the transportation of the
The brood pear of *Phanaeus* is a logical step forward from that of *Gromphas* (Variation 1). The clay shell is extended to enclose the food mass as well as the egg. In both cases, the newly hatched larva must break through the earth floor of the egg cavity to get to the food supply, and this partition seems to be of minimal thickness. The outer clay shell may be up to two centimeters thick at the base and about one centimeter along the sides in *Ph. milon* (Fabre, Souv. VI:80). In *Ph. ensifer*, the largest species of the genus, the earth coat is only 10-12 mm thick (Teichert, 1959). In all the other studied species the earth coat is 0.6-1.5 cm thick except in the two northern species, *Ph. quadridens* and *Ph. vindex*, where the shell is only 1-3 mm thick.

A detailed description of a late larval ball of *Ph. (Coprophanaeus) milon* Blanchard is given by Barattini and Saenz (1953). They note that the late larva is enclosed in a thin clay layer; this is then overlaid at the top of the ball with a series of small cavities in a similar clay layer, the whole being covered by a cap of fragments of the same material which makes up the outer clay shell, but newly cemented together. They surmise that the inner two layers are made of fine cemented soil particles which have passed through the larval gut, and that the cavities in the second layer were made by the larva thrusting its head through to the cut side to cement the broken fragments of shell together in the outer cap. The latter does not show the many tibia marks of the mother beetle which cover the outside of the clay shell elsewhere, hence it was not made by the parent. No air hole is seen, and air presumably filters through the various layers. In this same species, which is a carrion feeder, Fabre (Souv. VI:80) notes that the original carrion mass inside the clay shell has an outer layer of carrion-soil mixture, and that the thick outside shell is slightly impregnated with "carrion juice".

*Ph. (Phanaeus) quadridens* (Say) was studied in the state of Hidalgo, Mexico, by Halfter. It makes a brood pear 36-42 mm in diameter containing finely selected cow dung arranged in concentric layers and covered externally with a thin 1-mm clay shell. This is buried singly, or sometimes with one other pear, about 20 cm down, usually a small distance away from the food source. The feeding burrows of this species are simple (unbranched) and located immediately below the dung supply. It seems therefore that a feeding burrow is not later converted into a brood burrow, but rather the latter is dug separately after some overland transportation of the dung (for an account of food transport in *Phanaeus*...
see Section 17). Also, the times of feeding (Reifungsfrass) and nidification are quite separate, the former coinciding with the earlier part of the rainy season, the latter with the end (September).

In *Ph. (Phanaeus) vindex* McLeay (studied by Matthews), the feeding burrow is often two-branched (see Section 19) and occupied by a pair of beetles. The latter seems to be a general rule for the feeding burrows of *Phanaeus*, but according to Lindquist (1933), only about a third of the burrows of this species and *Ph. difformis* Leconte, taken together, have a pair of beetles in them (in Kansas). A brood pear, found in Georgia and almost certainly belonging to this species, measured 32 mm in diameter and was covered with a stone-hard clay shell 2-4 mm thick. Although the larva was well advanced in development, one could still see the air canal passing through the shell at the place where the egg chamber was. This was marked on the outside by a sort of nipple.

Nidification in the rather rare *Phanaeus (Ph.) palliatus* Sturm was studied by the authors in Ocoyoacac, State of Mexico, in September. The brood pears are found singly 13-15 cm below ground surface at the end of simple curved burrows (fig. 23). The brood pear is in a chamber which forms a space 7-11 mm all around the sides and top of the pear. The inside wall of the chamber is smoothly polished. The pear itself measures 37-43 mm in diameter and 42-47 mm in height, and has a surprisingly thick (8-10 mm) outer layer of clay. The egg chamber measures 6 x 6 mm and is not lined by any special secretion, and apparently does not have an air canal leading to the exterior. The food mass is separated from the egg chamber by a thin layer of clay and is perfectly spherical, measuring 23-28 mm in diameter (refer to figs. 24 and 25). We were able to surprise a female in the last stage of making the pear. She had completed all but the egg chamber, which had the form of a cuplike hollow in the clay shell at the top. The female was sitting over this opening, apparently about to oviposit (fig. 23).

Larvae of *Ph. palliatus*, *Dichotomius carolinus* (Linnaeus) and *Copris armatus* Harold, in their respective brood balls, were kept under identical conditions in captivity, but only those of the *Phanaeus* survived to adulthood. This seems to indicate that the clay shell (absent in the other two species) affords good protection for the larva under dry or other adverse conditions. The extremely dry winter season in central Mexico is undoubtedly passed inside the brood pear by *Phanaeus*, in its immature stages and as an adult awaiting favorable humidity conditions.

Fig. 23. *Phanaeus* about to oviposit in *Phanaeus palliatus* (Original.)

In the allied *D. Carolinus* (Linnaeus) has the larval food supply provided with a spherical "pot" or cup and provided with a nipple.

Passing now to *C. armatus* Harold, the larval food supply is provided with a nipple, and provided with a large chamber.

A detailed account of the habits and habits of the larvae of *D. Carolinus* (Linnaeus) has been given by Joseph (1920), and the larvae are abundantly abundant, their numbers reaching 1.50 meters before the mounds of earth are covered with the mold.
(frass) and nidification, in the earlier part of August.

Matthews), the nipple was dug and occupied by the female for the feeding of the young (Fig. 23), only about a week after the eggs were laid (Fig. 18). A brood pear, resembling the species, measured 2.4 x 2.4 x 2.4 mm in dimension, one could see the surface where the egg mass was deposited

allatus Sturm was collected in September. The clay shell over this opening, which forms the top of the pear. The pear itself measures 3.4 x 3.4 x 1.8 cm and has a surprisingly large mass of 6.0 x 6.0 x 6.0 cm, apparently does not collapse, but the mass is separated from the surrounding perfectly spherical, smooth clay mass by a door. We were unable to determine the size of a cuplike hollow which might be formed by this opening.

Linnaeus) and Cochlodes species were kept under Phanaeus palliatus Sturm, taken in Ocoyoacac, State of Mexico. (Original.)

In the allied genus Oxysternon, we have only the observation of Daniel (1940) that O. conspicillatum Weber in Colombia makes a spherical "pot" of mud, 5 cm in diameter, crowned by a slight margin and provided with "one or two eggs". This is buried 30 to 40 cm deep.

Passing now to the genus Dichotomius (= Pinotus), D. carolinus (Linnaeus) has been previously discussed under Group I, since it packs the larval food supply and does not make modelled brood pears. The few other studied species of Dichotomius seem to belong here in Group II.

A detailed account of the nidification of D. torulosus Eschscholtz is given by Joseph (1929) in Temuco, Chile, where this species is phenomenally abundant. The earth must be dug down to a depth of 0.60 to 1.50 meters before the brood balls are encountered, usually directly below the mounds of cow dung. The nesting season is July and August (the
winter) and brood balls containing full-grown larvae may be found from February to June. The dimensions of the brood pear are given by Kilian (1960) as 40 mm in diameter with a 6-9 mm earth coat. Their construction appears identical to that of Phanaeus just discussed.

Joseph (1929), by repeated excavations and observation, was able to reconstruct the entire series of activities employed by the beetles in making the nest, providing us with one of the very few complete accounts of this behavior in an American scarabaeine. First the descending winding tunnel is dug and the lower end enlarged into a spherical cavity 25-30 mm in diameter, which it brings down backwards into the terminal cavity. The procedure must be under Group 2 of the earth balls, not further, it makes a "perfect nut, which it brings out backwards. (Luederwaldt, 1876) Phanaeus regalis (Felsche) "mud ball" 2 cm...
may be found from the given by Kilian et al. Their construc-
d. D. torulosus creates the separate earth coat or shell around the mass of dung by loosening the soil all around the mass and compressing it into the surface of the dung with powerful pressure exerted by the forelegs. The pressure reduces the volume of the soil, creating an air space on the outside of the earth coat. The beetle thus works its way all around the mass, pushing against it with the forelegs and using the earth at its back to exert pressure. In this way, the central mass of dung, coated with soil, is compressed into a separate ball. The beetle works on the lower surface of the ball by digging upside down under it and lifting it up while it compresses the surface with the forelegs. The beetle is careful, while compressing, to eliminate all pebbles from the protective coat. It makes a thicker, cone-shaped layer at the top of the ball and digs a funnel-shaped hollow in this portion, leaving only a thin layer between this hollow and the spherical food mass inside. It then plasters the inside surface of the hollow with a “special secretion” and lays an egg in it. The hollow is now closed over by prolonging the edges of the funnel into a loose soil layer covering the egg. The egg is oval, the lower end a little larger, and measures 6-8 mm in length.

The above procedure takes about 15 days. Once finished, the female begins another nest (after “contemplating” her finished work for a few hours) by digging a new branch from the same tunnel. Joseph estimates that one female makes three or four brood pears in one season.

Concerning other species of Dichotomius, we have only some fragmentary data. D. bosqui (Pereira) in Argentina makes distinct brood balls, not further described (Martínez, in litt.). D. ascanius (Harold) makes a “perfectly round” ball of excrement, about the size of a hazel nut, which it buries 15 cm to 1 m deep in soil in the São Paulo region (Luederwaldt, 1914). The same author also mentions balls of D. singularis (Felsche), found 20-30 cm deep. D. belus Harold makes a “small mud ball” 2 cm in diameter in Colombia (Daniel, 1940).
We thus see that within the single genus *Dichotomius* one species at least — the abundant *D. carolinus* (Linnaeus) — nidificates in the primitive Group I manner, while other species have evolved a behavior quite similar to that of *Phanaeus*. We also see, thanks to the excellent account of Joseph, how the latter behavior was derived from the former, since it incorporates the former as a preliminary phase. Nevertheless, this is the only instance we have of a single genus belonging to two behavioral groups.

The species have seldom been studied. Paulian (1945:60) gives behavior similar to that of *Phanaeus* for spherical and conical spheres. Some of 3-12 (H. bucephalus) to four inches (A. ater) long. The nest chambers are eight feet deep, reports an access.

The literature states that the balls, which are said to be close but are not, simply close but do not stay with the brood balls, in this genus and in *Dichotomius*. However, this is not the case in many species.

Group III. Other species, or under food spheres which are said to be simply close but are not. The food spheres are eight feet deep, reports an access.

Female, and some of the behavioral group. Only *Copris* in *Heliocopris* (Group III).

In *Copris*, the behavior is more the same as the uniformity of the dung-sphere, which are constant in all of the individuals.
The species of *Heliocopris*, among the bulkiest of all Scarabaeinae, have seldom been directly observed. Remarks by Arrow (1931:10), Paulian (1945:67), and Balthasar (1963[1]:299) seem to indicate a behavior similar to *Copris*. However, in *Heliocopris* the brood balls are spherical and coated with a thick layer of clay. They may be in groups of 3-12 (*H. biceps* Fabricius) and measure two (*H. gigas* Linnaeus) to four inches (*H. dominus* Bates and *tyrannus* Thomson) in diameter. The nest chamber may measure 15 × 18 cm (Paulian, 1945:67) and be eight feet deep in the ground (Arrow, 1931:10). However, Paulian reports an access tunnel only 20 cm long in *H. hamadryas* Fabricius.

The literature is not convincing as to whether *Heliocopris* really behaves like *Copris*. Is there an initial dung cake cut into separate ovoids, or are the balls separately made from the food source? Are the balls, which are said to be found in groups, together in a single chamber or simply close but separate under the same food source? Does the female stay with the brood during their development? The thick clay shell around the brood balls of *Heliocopris* suggests that there is, in fact, no brooding in this genus and that the behavior is probably quite similar to that of *Dichotomius*. *Heliocopris* is placed in the subtribe Coprina by all investigators, but this must be for geographical reasons, since an examination of its morphology places it in the Dichotomina.

**Group III.** Construction of a spacious underground chamber near or under food source, containing first a large mass of dung (the dung cake) which is compacted and then divided into several brood ovoids each containing one egg. Ovoid usually not enveloped in a clay shell. Female, and sometimes also male, remains in nest chamber some or all of time of larval development (this is here termed brooding). *Copris, Synapsis, Catharisius*?

Only *Copris* and *Synapsis* are definitely known to belong to this behavioral group. *Catharisius* probably belongs and there is a possibility that some species of *Onitis* (discussed under Group I, Variation 2) and *Heliocopris* (Group II) may belong.

In *Copris*, the well-known basic pattern of nidification — accumulation of the dung cake, to be cut up into several separate ovoids or spheres which are brooded by the female until their metamorphosis — is constant in all observed species, but minor variations are known to
exist. In the first place, the oviposition procedure described for *C. hispanus* (Linnaeus) by Fabre (Souv. V:103-150) differs from that described for *C. incertus* Say by Thomas (1961) and seen by us in *C. lugubris* Boheman. Fabre states that the brood ovoid is first completely separated from the rest of the dung cake and molded into shape; then the top portion is hollowed out and an egg laid in the hollow, which is then closed over. In *Copris incertus* and *C. lugubris* the egg is laid directly in the dung cake and then the ovoid is carved out around it. We were able to verify this in the latter species in Morelos. A female was discovered in the process of making a brood ovoid from the dung cake (three other completed ovoids, containing eggs, had already been made). The fourth ovoid had not been completely detached from the cake, but was demarcated by a deep groove (fig. 26). Yet an egg was already located in the upper portion of this ovoid, in a round cavity just below the surface (indicated by the dotted outline in the figure), showing that it must have been laid first directly in the cake, the ovoid then being cut out around it.

![Fig. 26. *Copris lugubris* Boheman. One completed brood ovoid and one partially completed, still attached to dung cake. Dotted outlines indicate position of egg in egg chamber. Cuernavaca, Morelos. (Original.)](image)

The behavior of *Copris incertus* and *lugubris* could be a step in complexity (but not in phylogeny) following that of *Onitis*, which also lays eggs directly in a large dung cake, but which does not then carve out any ovoids (Group I, Variation 2). That of *Copris hispanus* may represent a more advanced step within the genus itself.

Intraspecific variation may be seen in the nest construction of *Copris hispanus* itself. One type of nest is that described for the European individuals by various authors (Fabre, Souv. V:103-150; von Lengerken, 1954).
described for C. lugubris the egg ovoid is first condensed into shape; in the hollow, the egg is carved out. Yet this ovoid, in a dotted outline directly in the eggshell and one partially detached image (fig. 26). Yet this ovoid, in a dotted outline directly in the eggshell and one partially detached image (fig. 26). Yet this ovoid, in a dotted outline directly in the eggshell and one partially detached image (fig. 26). Yet this ovoid, in a dotted outline directly in the eggshell and one partially detached image (fig. 26). Yet this ovoid, in a dotted outline directly in the eggshell and one partially detached image (fig. 26). Yet this ovoid, in a dotted outline directly in the eggshell and one partially detached image (fig. 26). Yet this ovoid, in a dotted outline directly in the eggshell and one partially detached image (fig. 26). Yet this ovoid, in a dotted outline directly in the eggshell and one partially detached image (fig. 26). 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brought clown to the deep one, in an exchange which Siyazov was not able to observe directly. This behavior (also seen in Synapsis tmolus Fischer in the same area) is explained by Siyazov as being due to the extremely harsh climate of Central Asia. Only a very brief activity period in spring separates the frigid winter from the very hot, dry summer. The brood chamber must be dug very deep to avoid the summer heat and desiccation, but if a deep chamber were dug directly, it would take a very long time to both dig and provision it, with the risk of losing much of the dung at the surface in the meantime. Bringing it down quickly into a shallow chamber keeps it humid and safe while the deep chamber is dug.

![Fig. 26-c. Copris armatus Harold, completed brood ball in external view, Salazar, State of Mexico. (Original.)](image)

Further differences, of an interspecific nature, may be seen in the poorly studied American species. Central American forms, such as C. aspericollis Gillet and C. lugubris Boheman dig somewhat deeper nests than the North American ones studied (see Matthews, 1962, for a brief summary). Interspecific differences also seem to exist as to whether the entrance tunnel is blocked with earth or not, and as to the length of time the male participates in nidification. Data are too few for an analysis at this time, however.

From three i...
From three nests of *Copris armatus* Harold found in different stages of completion by the authors in Salazar, State of Mexico, it is apparent what the actual construction procedure is. First the nest tunnel and chamber are dug, then dung is packed into the chamber, filling it completely (fig. 27). Then a space is dug out all around the dung mass, probably by removing a layer of soil about 1 cm thick all around (fig. 28). The identical procedure was surmised to occur in the nest con-

![Diagram of nest construction](image)
struction of *Copris hispanus* by Spaney (quoted in von Lengerken, 1954:332). This procedure is also similar to that employed by *Dichotomius torulosus* (already discussed) in making its brood ball, with the important difference that in *Dichotomius* (and *Phanaeus*) the soil loosened from around the dung mass is pressed into the mass itself, while in *Copris* it is removed altogether, leaving the dung mass, or cake, free of soil and surrounded only by an air layer. This sets the stage for the subsequent compacting of the dung cake, oviposition, and the cutting up of the dung cake into separate ovoids (fig. 29). The two blind tunnels issuing horizontally from the chamber of the nest illustrated are probably a little unusual.

The number of brood ovoids per nest in *Copris* does not seem to exceed eight, and averages about five. Several other aspects of the behavior of *Copris* are discussed in some other sections of this work (see Section 19, 22, 23, and 28).

*Synapsis tmolus* (Fischer), a very large coprine, was observed together with *Copris hispanus* (Linnaeus) by Siyazov (1913) in Central Asia. It also digs two chambers, makes a dung cake and ovoids, broods the larvae until metamorphosis, and in other known respects does not differ in behavior from *Copris hispanus* in that region.

For *Catharsius*, about the only concrete data we have are that the brood pears are distinctly pyriform, not ovoid as in *Copris* (Paulian, 1945:69, citing de Cooman). The genus is said to nest like *Copris* (Paulian, loc. cit.; Balthasar, 1963[1]:305).

**Group IV. Fashioning a hall of food on surface at food source and rolling it on surface, to be provided later with an egg some distance away from source.**

The Scarabaeinae placed in this group are most of the tribe Scarabaeini, the ball rollers. The Scarabaeini which are known not to roll balls are discussed in the last grouping of this section (Aberrant Nidification Behavior). The ability to roll a ball of food over the surface of the ground sharply distinguishes most Scarabaeini from previous groups. Many *Phanaeus* can roll food overland, but this is usually a piece of excrement which is already more or less round, and the method used (butting) is quite different from that seen in the

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*Variation IV. Malagoclyta Malagoclytina.*

This variation which have retained this ability to roll in the Scarabaeini, digging ability, this behavior is retained in *Malagoclyta*. The two subfamilies mentioned above two are the *Malagoclytina*. The genus *Malagoclyta vivida*, Malagoclytina vivida is 3 cm high, with a relatively thick cuticle. The body shape of *M. bicolor* is similar to that of *M. vivida*, and are buried in the ground (Lengerken, 1954:242). The diurnal habits of the *Phanaeus*, which enclose the food mass in a thin external clay layer in both summer and winter. In this respect they resemble *Malagoclyta gibbosum* (Fabricius).
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Scarabaeini (see Section 17). The morphological adaptations to ball

rolling in the Scarabaeini often mean a partial or complete loss of
digging ability, hence we do not see elaborate nests or impressive

cavations in this tribe. The variations which follow are based on whether

brood hall is buried or not, and whether it receives a separate

earth shell. These categories are not sharply defined and several genera

belong to more than one, as the Scarabaeini seem to be a homogeneous

group behaviorally.

Variation 1. Brood hall buried, coated with clay shell in burrow.

Malagoniella, Canthochilum (part).

This variation includes the behaviorally most primitive Scarabaeini,

which have retained a fair digging ability. It will probably be found

that a large number of canthonine genera are included here, but the

above two are the only ones presently known to belong. They place

a relatively thick clay shell around the brood hall, which is buried.

Malagoniella violacea (Blanchard) makes pears 2.5 cm in diameter and

3 cm high, with a 3 mm clay shell (Richter, 1918). The brood balls

of M. bicolor (Guérin) are of about the same size and construction

and are buried about 10 cm down (Judulien, 1899; von Lengerken,

1954:242). The brood balls of Malagoniella, while earth-coated like

those of Phanaeus, differ in the important detail that the clay does not

enclose the food and egg chamber in separate compartments, with a

clay layer in between. Instead, the shell is entirely external (fig 30). In

this respect it also apparently differs from that of Deltochilum gibbosum (Fabricius) (see below).

Fig. 30. Malagoniella violacea (Blanchard), section of brood ball, showing entirely external clay shell, Argentina. (From Richter, 1918.)
Canthochilum n. sp. (cited as C. histeroides Harold) makes clay-coated brood balls about 1 cm in diameter, in keeping with the beetle's small size, but buries these proportionately very deep at 7-10 cm depth (Matthews, 1963b). This species was induced to nidificate in a trap directly below the dung source, something not previously recorded for the Scarabaeini. All the species of Canthochilum observed by the authors in Puerto Rico may bury themselves directly below the dung, in the dichotomine manner, although all except one were observed to make and roll balls as well.

Some species of Deltochilum probably belong to this variation, as Martínez (in litt.) reports that D. orbignyi Blanchard buries its ball very deep (up to 60 cm).

**Variation 2. Brood ball not buried, coated with clay shell on surface.**

*Deltochilum, Eurysternus* (part), *Sisyphus* (part), *Nesosisyphus*.

*Deltochilum gibbosum* (Fabricius) in Florida leaves its brood pear, which is about 4 cm in diameter, in a depression about 5 cm deep in the ground, protected by leaves or some overhanging object. The pear is coated with a 1.5 cm thick coat of mixed clay and small leaves (Cartwright, 1949; Howden and Ritcher, 1952). The egg is apparently placed in a separate cavity in the outer shell (von Lengerken, 1954:297, fig. 196), separated from the food mass in the manner of *Phanaeus* brood balls, but not those of *Malagoniella*. *Deltochilum brasiliense* Laporte and *D. dentipes* Eschscholtz in Brazil also make clay-coated brood balls; it is not known whether these are buried or not (von Lengerken, 1954:301).

*Eurysternus plebejus* Harold in Ecuador leaves its "cherry-sized" brood balls lying on the surface of the ground. Each has an egg in a central chamber, attached to the wall with a darker cementing substance, according to Ohaus (1909:94). *Sisyphus quadricollis* Gory in South Africa attaches its brood ball to a grass stem (Arrow, 1931:68). It is not mentioned whether an earth shell is present. The four species of *Nesosisyphus* on the island of Mauritius deposit their brood balls above ground under some kind of shelter or dead leaves and coat them with a thick "clayey material" (Vinson, 1947).

This variation has been more or less operable over long distances (Scarabaeinae), more or less operable over long distances (Scara, climates (representations of careful studies). The omission of its burial at most makes it more suitable to the preparation of the brood pears. The brood pears of *Canthonina* are concerned here, of a pure-clay shell, mixed soil-dung or not at least in *Scarabaeinae*. The entire process was observed in detail by Füssy and G. geoffroyi Füssy here. The entire process was constructed jointly by the female. The entire process was not as described here. The entire process was observed in detail by Füssy and G. geoffroyi Füssy here.
This variation differs from the previous one only in that digging ability has been almost or entirely lost and the brood balls are not completely buried. Other members of the three subtribes included here (Canthonina, Eurysternina, Sisyphina) are known to bury the ball.

**Variation 3. Brood ball buried, not coated with clay shell, but often with a thin outer layer of soil or dung and soil mixed.** *Canthon (part), Scarabaeus, Gymnopleurus, Sisyphus (part)*.

The omission of a clay shell around the completed brood ball, and its burial at moderate depths, are characteristics of the adept hall rollers of temperate or dry climates. The species involved occur in more or less open situations and have evolved the ability to roll balls over long distances. Nidification is preceded by rolling and the brood ball is well buried at depths of 6 (Canthon pilularius [Linnaeus]) to over 30 cm (*Scarabaeus* spp.). Some of the species occurring in temperate climates (representing four different subtribes) have been the subjects of careful studies. Their above-ground behavior is dealt with in detail in Section 18 of this work, devoted to ball making and rolling. We are concerned here only with the underground behavior involving the preparation of the brood pear by the female.

The brood pears of the species belonging to this variation are devoid of a pure-clay shell, but some have a thin (less than 1 mm) soil or mixed soil-dung outer layer. This is placed on deliberately by the female, at least in *Scarabaeus, Gymnopleurus, and Sisyphus* (see below). The brood pears of *Canthon* observed by the authors have a thin outer layer of sand particles which may or may not have been placed on deliberately by the female.

The process of brood pear formation and oviposition has been observed in detail in *Sisyphus schaefferi* (Linnaeus) and *Gymnopleurus geoffroyi* Fuessly by Prasse (1957b), and his account is worth repeating here. The entire process occurs underground in the nest chamber constructed jointly by the male and female. The nest is a small, simple chamber with a short entrance shaft, as in all known Scarabaeini which bury the brood ball. As soon as the male departs, the female *S. schaefferi* and *G. geoffroyi* begins to reconstruct the brood ball completely, tearing it apart and putting it back together again, working from the middle outward, transforming it into a more dense, compact (gummiartig).
ball than the original. This takes 40-50 minutes. Then the female clings
to the side of the ball and grasps a quantity of dung from the upper
part and pulls it down. She does this two or three times, then moves
2-3 mm to the right or left and repeats the process, continuing in the
same direction all around the ball, converting it into an urn-shaped
form. She then climbs into the upper concavity and smooths the walls
of what will become the egg chamber. Probably a secretion is put on
the walls by mouth. Preparation of the egg chamber takes 1½-2 hours
for each species.

The Gymnopleurus female oviposits by stretching the end of the
abdomen over the chamber opening, with the middle legs around the ball
and the hind legs flanking the opening. The Sisyphus female sits directly
in the egg chamber with the forelegs on the rim. In side view only
the head and prothorax are visible over the rim. Oviposition takes from
five to 30 minutes.

In both species the beetle then resumes its position at the side of
the ball, reaches over the opening to the opposite rim and pulls it
toward her to the middle of the opening. She moves to one side and
repeats the process, going all around. Only a barely visible opening is
left in the middle (the air canal). To give it its final pear shape, the female pushes
dung up from the sides toward the apex. Finally, soil is taken from
the floor of the nest chamber (never from the walls) and spread evenly
over the surface of the pear. The processes of preparing the brood pear
take 2-3 hours in S. schaefferi and 3-4 hours in G. geoffroyi, without
any pause. Her work completed, the female abandons the pear.

Regardless of the size of the brood pear, the egg chamber is always
the same distance from the upper end. In smaller pears, this places the
egg practically in the center.

From the data given by Fabre (Souv. V:1-92) on Scarabaeus sacer
Linnaeus, it seems that a similar or identical process is employed by
this species in making the brood pear, but Fabre was not able to observe
every step involved.

In the brood balls of Scarabaeus the egg is attached by its narrower
end to the top of the egg chamber and hangs down into it (Heymons

and von Lengerken, 1954). In the baeinae, including our Scarabaeus, the egg simply lies on

Aberrant

We have previously shown that dung beetles are known to differ
to a greater or occasionally lesser extent, in their tribe.

Variation 1

Oviposition

(continued)

Various species of dung beetles have been found to change their manner. Gardner
(1956) and others have found that the larvae live in dry dung, extruding a
buried dung mass. Other cases in this category were found living in dry dung
or occasionally in dry dung. In S. schaefferi adults, in Ajijic, were found living
to be found in tunnels (see Section 8); O. bernhardus adults were found loose
be found in tunnels (see Section 8); O. bernhardus adults were found loose
were found loose inside caves (see Section 7). The adults in A. schaefferi
live normally in small tunnels. A. schaefferi adults inside fresh dung
wardly dried dung, and adults inside fresh dung and adults inside fresh dung
t there pupate, as there pupate, as

It is undoubtedly a characteristic to live in this manner, but also
Onthophagini, which...
the female clings from the upper times, then moves continuing in the to an urn-shaped name smooths the walls secretion is put on and takes 1 1/2 hours 

the female sits directly 2 

the female pushes soil is taken from and spread evenly 

the pear. 

chamber is always 

this places the 

larvae simply living loose inside the fecal material, Onitis (part), Onthophagus (part), Liatongus (part), Drepanocerus, Trichillum.

Various species have been observed to live in this "aphodiine" manner. Gardner (1929) reports that some Onitis larvae in India live loose inside cow dung. This is not so incredible when we remember that the larvae of Onitis caffer Boheman live communally in a large buried dung mass. One of us (Halffher) has discovered three additional cases in this category, as follows: Liatongus monstruosus (Bates) larvae were found living free in the debris of an Atta nest, together with the adults, in Ajjic, Jalisco (although the adults and larvae may occasionally be found in tunnels dug in the decomposed lower part of the debris; see Section 8 for more details); Onthophagus rufescens Bates larvae, pupae, and adults were found either loose in Atta debris or at the ends of vertical tunnels dug through the decomposed lower part of the debris (refer to Section 8); Onthophagus vespertilio Howden, Cartwright, and Halffher were found loose inside bat dung in a cave near Acuitlapan, Guerrero (see Section 7). The species of Drepanocerus in the Congo are said to live normally in the aphodiine manner (Jaessens, 1953:5). Finally, Trichillum sp. was reported by Ohaus (1909:88) in Ecuador to live as adults inside fresh cow or horse dung, but to lay its eggs in older, outwardly dried dung, where the larvae eat out tunnels in the periphery and there pupate, as in Aphodius.

It is undoubtedly no coincidence that nearly all the species reported to live in this manner belong to the tribes Onitini, Oniticellini, and Onthophagini, which represent the behaviorally most unspecialized cate-
gory (Group I), together with some Dichotomina (tribe Coprini). Groups with more elaborate nidification behavior would not have been able to modify it sufficiently to live loose in the food material. The aphodiine way of life is undoubtedly not primitive in these groups, but is secondarily acquired in response to the unusual ecological conditions of having the food material concentrated in deposits of considerable depth (making burial of the food impossible), under the stable humidity and temperature conditions obtaining in Atta nests and bat caves (rendering burial unnecessary). The case of Trichillum sp. (a dichotomine) is not so clear, as it does not live in a cave or nest (one Argentine species previously mentioned, however [Section 7], does live in vizcacha nests).

The larva of Liatongus monstrusus (Bates), collected by Halffter and Reyes, is not humped like all other known scarabaeine larvae, but has a straight, sub-cylindrical body reminiscent of that of a cetonine. The humped shape is an adaptation to living inside a spherical cavity (see Section 26), hence it is no longer needed by a free-living larva. This striking modification of the larva demonstrates the extent to which L. monstrusus has become adapted to this type of myrmecophily.

**Variation 2.** Canthonina which make several brood pears simultaneously directly from the food source. Canthon (part).

Whereas the general rule among Scarabaeini is that the brood ball will be converted into a single brood pear (hence a nest will contain only one pear), there are indications that more than one pear may be placed in a single nest in some South American Canthon. Unless these multiple pears are made from a single ball which has been previously rolled overland (which seems very unlikely), the habit of making more than one pear is closely associated with a great reduction or even loss of ball rolling, with consequent nest construction directly below or beside the food source. Hence this variation overlaps (perhaps completely) with the next, which includes Scarabaeini known to be unable to roll balls.

For a long time we had only Judulien's (1899) observations to indicate that some Canthon in Argentina make more than one brood pear per nest. According to that author, C. bispinus Germar makes two pears 15 cm deep in the soil, C. muticus Harold makes six 10 cm deep, and C. edentulus Harold makes nine 20 cm deep (the numbers must vary).

The nests of Scarabaeini contain beetle eggs. The brood balls are not spheres, as in a normal pear, but resemble a food mass. The larva is more strongly humped and develops more strongly and rapidly. The body is more strongly humped and develops more strongly and rapidly.

Recently, some confirmation of Judulien's observations was provided by Marti (1940). The larvae of Trichillum sp. are more strongly humped than any other larva known to me, and are not in the details of their development the same as the larva of Canthon virgatus Germar, which is more strongly humped and develops more strongly and rapidly than any other larva known to me.

**Variation 3.** Scarabaeini which make only one brood pear per nest. Canthochilus (part).

Food transport is discussed in Section 26. The habit of transporting the food mass in a single piece, making at least, "makes the brood develop". We have seen this.

Among the Scarabaeini some species have lost the ability to roll balls.

**Canthochilus** is a genus in which individuals were found one night by the writer. The habit of being able either to transport the food mass or to develop it more strongly is the key feature of the group.
The nests appear to be very deep in relation to the size of the beetles. The brood pear of *C. bispinus* consists of two superimposed equal spheres, as in a figure 8, the upper one containing the egg, the lower one the food mass. The brood pears of the other two species are of the normal pear shape.

Recently, some hitherto unpublished data have tended partly to confirm Judulien's observations. As previously mentioned (Section 4), *Canthon virens* (Mannerheim) makes 2-3 brood pears from the contents of the abdomen of a single *Atta* queen, burying them at shallow depth. Secondly, Martinez (in litt.) has found that *Canthon edentulus* (one of the species studied by Judulien) makes 2-3 pears at a time, but does not bury them, placing them directly on the ground beneath the excrement (supporting Judulien in the basic fact of multiple pear formation, but not in the details).

The very unexpected brooding behavior ascribed by Judulien (op. cit.) to two of the same species of *Canthon* in Argentina (*bispinus* and *edentulus*) and to *Malagoniella bicolor* (Guerin) and *M. puncticollis tubericeps* (Gillet), requires confirmation. If confirmed, this behavior represents the independent acquisition by some Scarabaeeini of the brooding behavior known elsewhere only in the Coprina (Coprini).

**Variation 3.** Scarabaeeini unable to make or roll balls. Nidification procedure unknown; Eucraniina, Canthochilum (part), Canthonidia, Eurysternus (part).

Food transportation in the Eucraniina, which is not by ball rolling, is discussed in Section 17. Martinez (in litt.) reports that *Anomiopsoides*, at least, "makes very regular spheres where it lays its egg and the larvae develop". We have no other information on nidification in this subtribe.

Among the Canthonina, the following species are known to have lost the ability to roll, and burrow directly beneath the food supply.

*Canthochilum oakleyi* Chapin, which was observed in Puerto Rico one night by the authors. At no time did this species show any indication of being able either to make or roll a ball. The following morning individuals were found buried directly below the dung supply. *C. oakleyi* is more strongly modified morphologically for digging than the other species of the genus (all ball rollers), possessing a developed prothorax...
and strong forelegs, especially in the male. A similar morphological
development of an African genus of Scarabaeini (Pachylomera; Scarabaeina)
raises the question whether this genus also may have lost the ability to
roll.

*Canthonidia rubromaculata* (Blanchard) buries pieces of dry
excrement, without making a ball, directly below the dung source about
10 cm down. Many individuals may also be found embedded in the dung
mass at the surface (Martínez, in litt.).

*Canthon e. edentulus* Harold, previously mentioned in connection
with its ability to make more than one brood pear at a time in a single
nest, is said by Martínez (in litt.) never to roll balls, always being found
in dung or directly beneath it. It is possible that the other multiple-pear
species of *Canthon* (*muticus*, *bispinus*) also do not make or roll balls at
the surface.

*Canthon conformis* Harold, a necrophagous species in Brazil, digs a
burrow directly beneath the edge of the cadaver and provisions it with
pieces of carrion, without making a ball (Luederwaldt, 1911:429, 431).
*C. septemmaculatus* (Latreille) may behave the same way (op. cit.:431).

Among the species of *Canthon* described from Patagonia by
H. F. Howden, 1909:94, a pair of the species just mentioned made three ba-
A pair of the species just mentioned made three balls without making a hall
suggested coprolite-derived material. *Eurysternus* rubromaculatus was
ever to roll balls, always being found in dung or directly beneath it. It is possible that the other multiple-pear
species of *Canthon* (*muticus*, *bispinus*) also do not make or roll balls at
the surface.

*Canthon conformis* Harold, a necrophagous species in Brazil, digs a
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pieces of carrion, without making a ball (Luederwaldt, 1911:429, 431).
*C. septemmaculatus* (Latreille) may behave the same way (op. cit.:431).

Fossilized coprolites, described from various localities in Patagonia,
occurred in very small numbers, and can be no doubt that the burrowing habit
is accurately observed, and clearly in the feeding habits of the young beetle.
Frenguelli's coprolite contained the round exit of a burrow leading to a chamber. This
similar to those of *Phanaeus* and *Bombus*, those of fossil balls with a fossilized organic matter which was
without the open cavity and filled with decayed organic matter. The chamber itself, decayed organic matter and hollow balls. Material which may have been from Patagonia.

![Cow Dung](image)

Fig. 31. *Eurysternus magnus* Laporte, nest. Chipinque Mesa, Nuevo Leon. (From
field sketch supplied by H. F. Howden.)
Among the Eurysternina, *Eurysternus magnus* Laporte was found by H. F. Howden (*in litt.*) in a large cavity under the edge of a dung mass in an oak-pine woodland on Mesa del Chipinque, Nuevo León, Mexico. A pair of the beetles had buried a quantity of dung of which they had made three balls (fig. 31). We do not know whether the balls had been made on the surface or below ground, but the nature of the nest strongly suggests coprine, not scarabaeine, behavior. No one has actually observed *Eurysternus* rolling balls, although the shape of the hind legs suggests a ball roller and the genus is therefore placed in the Scarabaeini. Ohaus (1909:94), reporting on another species, claims that the brood balls are left exposed on the surface, in a form of behavior totally different from that observed by Howden. Obviously, the genus *Eurysternus* is much in need of observation.

21. **Fossil Scarab Balls**

Fossilized balls which can be attributed to scarabs have been described from various Tertiary deposits in South America, where they may occur in very large numbers (see especially Frenguelli, 1938). There can be no doubt that these are, in fact, the brood balls of scarabaeine, or more accurately, the fossilized clay shells around brood balls. Some show clearly in the interior impressions which look like tibia strokes of the young beetle, or perhaps scratches from the larva (a few balls from Frenguelli's collection were examined by the authors). Most also show the round exit opening, corresponding to the location of the original egg chamber. This opening can be seen in the old brood balls of extant *Phanaeus* and *Dichotomius* after the adult has emerged. In general, the fossil balls with exit openings are filled with the same sedimentary material which makes up the stratum in which the balls are found. Those without the opening are completely hollow. This is evidently because the organic matter which made up the food supply for the larva, and the larva itself, decayed completely, but the intact walls of the ball did not allow entry of the sediments. Evidently the beetles never emerged from these hollow balls. No balls were found with the egg chamber intact, but some from Patagonia show a thin floor across the bottom of the large opening. This floor perhaps represents the original partition between the egg cavity and food cavity of the ball, such as we see today in *Phanaeus* and *Dichotomius* In these balls the egg apparently did not hatch. In
one hall, the partition is perforated by a small hole. This perhaps represents the point where the recently hatched larva penetrated the floor of the egg chamber to reach the food mass, dying soon after. Other perforations seen in the balls Frenguelli attributes to parasites.

The various balls found differ principally in size, all being spherical. Those of the earliest deposits (Lower to Middle Oligocene of Patagonia) are 29-39 mm in diameter, with walls 6-7 mm thick, leaving an internal space about 20 mm in diameter and an exit opening 10 mm in diameter. One large Oligocene ball measured 41 mm in outer diameter, and a single Miocene ball, 31 mm in diameter, was also found. All these Frenguelli attributes to *Megathopha* on the basis of their size.

A large quantity of smaller balls (11-27 mm in diameter, with 4 mm walls) was found inside a glyptodont skeleton of Middle Pleistocene age near Paraná (Entre Ríos). These Frenguelli attributes to *Canthon*. Finally, two enormous balls, 82 and 87 mm in diameter, with 20 mm walls and a 16 mm opening, were found in an Upper Pleistocene deposit in Santa Fe Province, together with remains of large mammals. Frenguelli ascribes them to *Phanaeus* (although larger than any contemporary ones), and notes that this period coincides with gianism among the mammals.

In a second work, Frenguelli (1939) discusses similar fossil balls previously described by Roselli (cited in Frenguelli) as being of Cretaceous age (red sandstone of Colonia, Uruguay). Frenguelli points out that the actual age of the deposits is Miocene. In this same work he describes additional balls from Neuquén and Río Negro provinces which date from Upper Oligocene to Pliocene. The balls are found in incredible numbers, often in their original groupings of three or four. A chemical analysis of the dark layer which lines the inside cavity of the balls shows the presence of organic matter in the process of mineralization. The balls vary from 35.5 to 59 mm in diameter and seem to belong to *Phanaeus*. Some cylindrical masses, 17-37 mm in diameter and hollow for about 2/3 of their length, were also found intermixed with the above-mentioned balls. Frenguelli attributes them to *Onthophagus*. Actually, no known dung beetle makes a clay-covered cylinder. The cylinders may represent simply tunnels partly filled with sediments, in which case they could easily belong to *Phanaeus* or several other genera.

Sauer (1956) describes numerous hollow fossilized scarab balls, which he calls *Coptinsphaera ecuadorensis*, from deposits of consolidated volcanic ash from the Pichincha Volcano near Quito, Ecuador. The balls are round opening...
This perhaps penetrated the floor soon after. Other parasites.

all being spherical. (|ne of Patagonia) leaving an internal 0 mm in diameter. diameter, and a. All these Fren-

meter, with 4 mm Pleistocene age attributes to Canthon.

Pleistocene deposit mammals. Frenquelli points out four. A chemical of the balls shows the condition of the brood balls, it is not possible to identify them with certainty even to genus. On the basis of what we see today, it seems most probable that species of Phanaeus or Dichotomius, or both, are involved in all cases. Frenquelli’s determination of some of the fossils as Megathopa (=Malagoniella in part) is another possibility, but his suggestion that some balls were made by Canthon appears highly improbable, as no Canthon today are known to place a thick clay shell around their brood balls.

The main interest of the fossil balls is that they demonstrate nidification behavior at a fairly advanced (Group II) level in Scarabaeinae as early as the Lower Oligocene, which coincides with the earliest fossil remains of the subfamily in Europe (Balthasar, 1963:79).

22. SEXUAL RELATIONSHIPS

Encounter and Recognition of the Sexes

following the period of Reifungstrass, the gonads are mature or almost so and reproductive behavior begins. Without any known exceptions, sexual encounters occur at the food source or in relation with the

volcanic ash ("cangahua") dating from the last interglacial period in Ecuador. The balls measure 5-8 cm in diameter and most have a 1-2 cm round opening.

Kilian (1960) describes almost identical hollow spheres (smaller in size, however) from weathered clay in Chile, found abundantly from Temuco to Puerto Montt. These are actually recent and are made by Dichotomius torulosus (Eschscholtz). Joseph (1929) mentions that the balls of this species are found in enormous numbers during excavations below the foundations of Temuco. Judging from the age of the buildings involved, these balls must have been there for at least 50 years. When the adult beetle emerges it leaves the hollowed clay shell, about 6-9 mm thick, and the inner lining of larval excrement, which are very durable and become stone hard with age. These observations on the recent Dichotomius torulosus clearly explain the origin of the fossil balls of Ecuador, Argentina, and Uruguay, although the same species or even genus are not necessarily always involved.

Since the fossils are known only from the clay shells surrounding the brood balls, it is not possible to identify them with certainty even to genus. On the basis of what we see today, it seems most probable that species of Phanaeus or Dichotomius, or both, are involved in all cases. Frenquelli’s determination of some of the fossils as Megathopa (=Malagoniella in part) is another possibility, but his suggestion that some balls were made by Canthon appears highly improbable, as no Canthon today are known to place a thick clay shell around their brood balls.

The main interest of the fossil balls is that they demonstrate nidification behavior at a fairly advanced (Group II) level in Scarabaeinae as early as the Lower Oligocene, which coincides with the earliest fossil remains of the subfamily in Europe (Balthasar, 1963:79).
ball (if any), by what appears to be accidental contact. The “search” for the opposite sex is therefore an indistinguishable part of the search for food. The only behavior which appears to be aimed specifically at facilitating sexual encounters is the strong tendency for beetles to congregate at only a few food sources, when many of these are present in an area. This has previously been discussed (Section 10, Aggregation). Only *Sisyphus schaefferi* (Linnaeus) presents an exception to this tendency to congregate at food sources, according to Prasse (1957a:441).

Aronw (1931:20-21) observes that the males of Scarabaeinae, unlike some other scarabs, do not show any unusual development of the antennae, which are often used to locate the females in insects. This is because both sexes use the antennae only for locating food, and obviously both sexes have to be equally adept at this. The only known exceptions are two species of *Onthophagus*, one from India (*O. igneus* Vigors) and one from Borneo (*O. egregius* Arrow). The males of which have exceptionally developed antennae. A figure of the antenna of the latter species is given by Balthasar (1963[2]:340). Arrow notes that it is significant that the females of these species are not known, and he surmises that they must be unusually secretive (subterranean and wingless?) and that this may explain the males’ antennal modifications.

In the ball-rolling beetles (Scarabaeini), whose activity is largely above ground, we have the following data on sexual encounters and recognition. As far as we know, the beetles cannot recognize one another’s sex without direct contact or very close approach. This is effected by a head-to-head contact, of about \( \frac{1}{2} \) second in the species of *Gymnopleurus* and *Sisyphus* studied by Prasse (1957b:593), and of unknown but very short duration in *Scarabaeus* and *Canthon*. Recognition seems to be effected through contact of the antennae and maxillary palpi, and is hence chemotactic in nature (Prasse, loc. cit.). This is, of course, in keeping with the whole nature of behavior in the subfamily, where visual stimuli appear to play little part.

If a ball has already been formed, and if the beetles are of the same sex, hostile behavior immediately follows the contact. This usually takes the form of active combat (see sub-section on combat below). If the beetles are of opposite sexes, and not already attached to a partner, there will be immediate acceptance and formation of a partnership in *Scarabaeus*, *Gymnopleurus*, and *Sisyphus*, while in the two species of *Canthon* best studied (*C. orientalis* and *C. fulvus*) a brief combative period is led by the male, and the sexes immedi­ately accept each other.

In *Copris hispidus*, the female rolls a ball, and the male burrows until he has located and attached to the female in her burrow. In this, as in *Copris setosus*, a visioning period is involved.

In *Pha­naeus*, the period is preceded by the male rehearsing the sequence by visioning the female in Istapan. In the sub­sequent period (*Section 17*) the female begins rolling or burying a piece of dun­ger, in *Pha­naeus*, she follows her if she rolls a piece, or he if he buries. Recognition of “interested” behavior is therefore similar mechanism: the male in *Pha­naeus* and the female behav­ior of *Pha­naeus* is united before the but­terfly is suggested, before the butterfly is suggested.

On the other hand, *Pha­naeus* and *Pha­naeus* are united before areas are suggested.

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The "search" phase, of the search sequence is described specifically at this point. There are several species of beetle to consider, but it is known that these are present in C. pilularius Linnaeus and C. h. humectus Say) there will be a brief combat, lasting a few seconds, before the female will be accepted by the male. This may possibly be due to failure to recognize the other's sex immediately (authors' observations).

In tribes other than Scarabacini, the observations are much fewer. In Copris hispanus (Linnaeus), the males will seek out the female feeding burrows during the Reifungsfrass period. The male intrudes upon the female in her feeding burrow and the two then partake of the meal in the burrow. In this manner, a pair bond (Zusammengehörigkeitsgefühl) has been formed which lasts throughout the long nest construction and provisioning period in this species (Remmel 1961).

In Phanaeus nimrod Harold, actual nest construction seems to be preceded by a lengthy period of trial and error during which the sexes rehearse the future nidification activities and form temporary associations in connection with the food. According to the authors' observations made in Ixtapan, State of Mexico, in September, the female begins the activity sequence by rolling a piece of horse dung (pushing with the head, see Section 17) a certain distance and then burying it. At any time during the rolling or burying phases she may be joined by a male, who will simply follow her if she is rolling or, if she is burying, will eat directly from the piece of dung. The male may then help the female in burying the rest of the piece. It is certain that only the female rolls the food on the surface, and this form of behavior, aside from serving a transportation function, may also represent a way of soliciting a partner. During the pre-nesting trial period observed by the authors, the male was evidently much more "interested" in the piece of horse dung than in the female who was rolling or burying it. We have seen (Section 18) that in Scarabaeus a similar mechanism operates, but in this case it is the male which attracts the female by making and rolling a nuptial ball.

On the whole, the incomplete data we have on some species of Phanaeus and Dichotomius carolinus (Linnaeus) indicate that the pair is united before the digging of a feeding burrow, which is then dug in cooperation by both members. A number of joint feeding burrows may be thus dug in succession throughout the long Reifungsfrass period before the brood burrow or burrows are dug. It is not clear whether the same pair stays together throughout this period. In any case, it seems
that in these two genera the act of digging a burrow together is that which cements the pair bond, rather than the act of feeding together as in Copris.

We have no data on encounter and recognition in other genera and species.

Copulation

It is extremely unusual to observe a pair of Scarabaeinae in coitum. In many genera, even such common ones as Copris, Phanaeus, and Dichatomius, copulation has never been seen. Burmeister (1930), who observed four species of Onthophagus at great length, was unable to see copulation, and in fact the only data we have on this for this genus is a remark by Fabre (quoted in von Lengerken, 1954:207) that Onthophagus copulate on the surface in the spring.

In the Scarabaeini we have the following data. Pairs of Gymnopleurus mopsus Pallas copulate on the surface, on top of the ball or the dung, probably also underground (Prasse, 1958). Gymnopleurus geoffroyi Fieslly copulates underground, in the presence of the brood ball (Prasse, 1957b:595). Copulation takes 20-40 minutes. Sisyphus schaefferi (Linnaeus) copulates "continuously" underground, in the presence of the food ball, occasionally above ground during formation of the brood ball (Prasse, loc. cit.). A single copulatory act takes 15-20 minutes in S. schaefferi. Scarabaeus semipunctatus Fabricius copulates underground in the presence of the nuptial ball, which had been made and rolled by the male (Heymons and von Lengerken, 1929:584). In captivity the beetles would copulate only above ground, and this took 20-30 minutes. (It should be noted that all the observations of Prasse were also made in captivity.) Canthon pilularius (Linnaeus) copulates underground soon after the brood ball has been buried by the pair (Matthews, 1963a). The duration of copulation is unknown in the latter.

The actual copulatory positions have been described only by Prasse (1957b:595) for G. geoffroyi and S. schaefferi. The male climbs on to the back of the female, moves backward so that his fore claws are grasping the female's elytral bases, his middle legs are encircling the female's elytra, and his hind legs are on the ground. The aedeagus is inserted into the female's cloaca from this position. Both beetles remain still during copulation, or the female may eat or work on the brood ball.
together is that of Gymnopleurus and Onthophagus, or the dung beetle genus of Onthophagus and Gymnopleurus. The aedeagus is shed during copulation. Heymons (1930) made a study of the reproductive organs of Scarabaeus sacer Linnaeus and Scarabaeus semipunctatus Fabricius and included some data on the relative positions of the genitalia during copulation and the subsequent fate of the sperm. It will be necessary to refer to fig. 32 to follow the present discussion. The anal region of the female ends in a cloaca which receives both the dorsal alimentary and ventral genital openings. These are separated only by a feebly transverse fold. Fouling of the genital opening is avoided because the feces are wrapped in the peritrophic membrane. Immediately inside the female genital opening is the bursa copulatrix which leads to the U-shaped, strongly chitinized seminal receptacle (rs), in which sperm is stored. The vagina leads through a separate opening into the bursa copulatrix. During copulation, the sclerotized portion of the
male aedeagus (basal piece and parameres) is not inserted, but only the membranous internal sac, which enters the bursa. The end of the internal sac has a narrow “praepe­nis” which is inserted into the copulatory canal. The sperm, which is in the form of a stringy spermatophore, thus bypasses the vaginal opening and enters the copulatory canal. The introductor muscles of the female (mid and mis) probably help in bringing in the spermophore. After the aedeagus is removed, the sperm must still get up into the seminal receptacle, and Heymons does not believe this is done either by peristalsis or by active swimming. The ductus receptacularis (dr) has no muscles, and the sperm, when it reaches the seminal receptacle, is not uniformly oriented in a way that would indicate a chemical attractant. Instead, the introductor muscles of the copulatory canal and the muscles of the receptacle, working alternately, pump the sperm up into the receptacle. These same muscles, working in reverse order, presumably pump it out again at the time of fertilization, Heymons points out that only the honey bee is known to have a similar (but not homologous) sperm-pumping mechanism. Much of the sperm perishes, as just after copulation the entire bursa, canal, and duct, as well as the receptacle, are filled with sperm, whereas later only that which is in the receptacle survives. Further aspects of the reproductive system are discussed in Appendix II.

Pair Bonds and Male-Female Cooperation

Scarabaeines show a strong tendency to form a close temporary association between one male and one female (pair bond), which lasts from the time of first encounter to the completion of nidification during the reproductive season. Nidification in the subfamily is nearly always a cooperative endeavor of the pair. Experimental data are lacking on the extent to which the bond is oriented to a particular individual of the opposite sex, but field and captivity observations show that once a bond is formed, it is usually not broken voluntarily by either individual until after the nest has been dug and provisioned in cooperation.

Only in the genus Onthophagus is a pair bond known not to occur. However, even here there is a certain degree of cooperation in nest building (Burmeister. 1930). Generally, a female does all the work involved in nest building and provisioning, but sometimes a male will help at the surface, pushing soil away from the burrow entrance and bringing the female food. However, this male is not necessarily the one who inseminated the female he is helping. In other words, a male will help any female, not a particular one.

Among the digging scarabaeines, cooperation in nidification has been observed in Copris (many authors), Phanaeus (authors' observations), Bubas (Fabre Souv. VI:25-31), and is said to occur in the other Onitini (Janssens, 1953:6).

The joint provisioning of burrows of Diabrotica species also there.

The joint provisioning is observed by one author's observations on Bufo bufo. The dung (rabbit pelle) is laid apparently, though simultaneously. The male carries dung over the entrance, and then the female carries out the underground nest building. In the previous dig, the male also fed the female, and was rarely fed by her.

Something similar was observed by Harold, on the Japanese species also there.

In Copris and Phanaeus, a pair bond between male and female is not necessary since the dung supply is sufficient for the single female (at least in Copris). In Phanaeus rudius and C. lugubris Boheman, the female is not the one in digging out a space into which the pupa is put, but she begins to make a hole. This is continued by the male, who then shapes the bursa. The male Copris may be very active in quieting the brood entrance, while the female is busy pushing away soil from the entrance. The male Copris, when the female is absent, seems to have a place in the brood entrance, and in the feeding of the dung supply, which Rommel's report (Souv. VI:15-24; T. E. Harold, with C. T. T. Matthews, 1962). C. rufus, C. fricator Fabricius, 1807, (T. E. Harold, 1960), and C. alater.

To determine any stage of the cooperation, if any, of any stage of any spider.
only the membranous
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is in the form of
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the copulatory canal
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umably pump it out
by peristalsis
s, and duct, as well
which is in the recep-
(1953:6). The frequent occurrence of a pair of beetles in feed-
ing burrows of *Dichotomius carolinus* (Linnaeus) indicates that in this
species also there is probably cooperation in digging and provisioning.
The joint provisioning of a *Phanaeus* (probably *vindeix McLeay*) burrow
observed by one of us (Matthews) in Florida differs from described
observations on *Bubas* and *Copris* in that the beetles were transporting
dung (rabbit pellets, in this case) from source to storage place indepen-
dently, though simultaneously. In *Copris hispanus* (Linnaeus), the male
carries dung over the surface to the female, who waits at the burrow
entrance, and transfers the dung to her (Rommel, 1960). Thus she
carries out the underground phase of provisioning, and he the surface phase.
In the previous digging of the nest, the same relationship is seen—the female
digs the main tunnel and brood chamber, passing the soil back
to the male, who then pushes it up to the surface.

Something similar may occur in *Phanaeus palliatus* Sturm and *Ph.
nimrod* Harold, observed by the authors in Mexico. Frequently the male
is the only one of the pair seen at the surface, but the exact nature of
cooperation, if any, was not discerned.

In *Copris* and *Synapsis* alone, as far as we know, cooperation be-
 tween male and female goes beyond nest digging and provisioning. Once
the dung supply is fully accumulated, the male seals the tunnel entrance
(at least in *Copris hispanus* [Linnaeus] [Rommel, 1961] and perhaps
*C. lugubris* Boheman [Matthews, 1962]) and proceeds to help the female
in digging out a space all around the dung mass and compacting the mass
into what is called the dung cake. This is accomplished by both beetles
incessantly wandering over the surface of the mass, patting it with the
tibiae. This is the limit of the male's role; the subsequent cutting and
shaping of the brood ovoids from the cake is done by the female alone.

The male *Copris hispanus* spends the rest of the summer aestivating
quietly in the brood chamber or elsewhere (at least in North Africa, to
which Rommel's remarks apply). More or less the same cooperative role
of the male appears to be indicated for *Copris lunaris* (Linnaeus) (Fabre,
Sey. VI:15-24; Teichert, 1960) and a few American species studied: *C.
Iricator* Fabricius, *C. aspericollis* Gillet, *C. lugubris* Beheman (Mat-
thews, 1962), *C. minutus* Drury (Ritcher, 1945), *C. incertus* Say (Tho-
mas, 1960), and *C. armatus* Harold (authors' observations).

To determine whether the male's presence is necessary for comple-
tion of any stage of nest construction or provisioning in *Copris hispanus,
Rommel (1961) removed him at several points and found that the female can continue alone. Fabre found the same thing for *C. lunaris* and in *C. fricator* Lindquist (1933) and Matthews (1962) found many uncompleted nests with only a female present. Lindquist (1935) does not even mention the male in his account of nidification in *C. remota* Leconte. In general we may conclude that the male's presence during nidification is normal but not obligatory in most species of *Copris*.

In the ball-rolling scarabs, as we have seen, pair bonds are formed some time during the ball making or rolling processes and continue throughout rolling, burial, and nest construction. The exact role of each sex differs according to the species (see Section 18). In the European species of *Scarabaeus*, pair bonds, if we may call them that, are formed only in connection with the nuptial ball—the ball used by a male to attract a female—and not the brood ball, which the female must subsequently make, roll, and bury all by herself (Heymons and von Lengerken, 1929:586).

The ball-rolling scarabs are the only ones in which a pair bond may be broken occasionally through combat between members of the same sex. If the intruder wins the fight, it replaces the loser in the partnership and is apparently immediately accepted by the other member (see subsection on combat which follows).

There is no courtship of the ritualistic sort in the *Scarabaeinae*. As the purpose of such courtship, when it occurs, is species recognition, it may be that the prolonged cooperation in nidification seen in *Scarabaeinae* partly serves the same purpose by bringing the two members of the pair into repeated contact before copulation takes place.

**Combat**

One generalization that may be made is that individual combat has been seen in all *Scarabaeini* carefully observed, but not in any single member of any other tribe of the subfamily.1 We can, therefore, im-

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1 Arrow (1951:111) claims that "In Africa it has been noticed that contending males of the Elephant dung beetle (*Heliocopris gigas*) are sometimes found dead with horns interlocked ..." We know of no reliable direct observations of combat in these beetles, or any other horned *Scarabaeinae*. Only in the *Dynastinae* are horns known to be used for combat.
found that the female of C. lunaris and in C. remotus (1935) does not bond during nidification

bonds are formed and continue exact role of each In the European that, are formed and heterosexual female must sub-

with a pair bond may fight only between members of the same species recognition, it seen in Scarabaeinae and von Lenger-

individual combat has not in any single species. It is therefore, im-

noticed that contending times found dead with the horns of combat in these Sciarabaeinae are horns known

immediately dismiss the notion that the horns and other ornamentation of the head and thorax, seen in all tribes except Scarabaeinae, serve any combat function. On the contrary, it seems that the absence of horns and greater agility of the Scarabaeinae are among the factors which enable them to engage in frequent combat.

Another factor which may lead to overt combat is the beetles' reliance on chemical and tactile stimuli, rather than visual ones. This precludes the evolution of the threat displays which are developed as combat-substitutes in many visually-oriented animals. Auditory threats may play a role in some Coprini (see Section 28), but have not been developed in the Scarabaeinae. Territory, which permits and in fact requires the evolution of grades of hostile behavior ranging from threat displays to actual combat, is a negative factor in the Scarabaeinae — the beetles must clump, not disperse. With many individuals working together in close proximity, it seems that actual physical combat is the most efficient way to communicate hostility. Whatever the reason, the Scarabaeinae are extremely combative, but fights seldom if ever result in injury to the participants. Fights are invariably between members of the same species and nearly always the same sex.

Combat is intensified at the time of reproductive activity and is therefore a form of sexual behavior, even though the immediate object of contention is always the ball, not the member of the opposite sex. We see again the close connection between food and sexual activity, also exemplified by the fact that sexual encounters occur at the food source or during transportation of the food.

Prasse (1958b) made a special study of combat in Sisyphus schaefferi (Linnaeus) and Gymnopleurus geoffroyi Fässly. He found that, of the two, Sisyphus was much the more combative, the individuals fighting continuously from three days after emergence. Gymnopleurus tends to fight only during the reproductive season. Fights are always between two beetles only. Both sexes are equally combative. Fights occur only in connection with the preparation, transport, or burial of a ball. In other words, only when an intruder is very close to the ball of the proprietor. In Sisyphus fights may be between individuals of the same sex or of opposite sexes during the Reifungsfrass period, only between individuals of the same sex during the reproductive period. In Gymnopleurus fights are only between individuals of the same sex at all times. This was noted also by Honda (1927) in Gymnopleurus sinuatus Fabricius. Goggi-
Avoidance of intersexual combat may be illustrated by the following observations. When a rolling female Scarabaeus meets another female, they fight and the winner gets the ball. When a female roller encounters a male, as soon as the sexes are recognized the female will cede her position on the ball, allow the male to roll it, and follow behind at a short distance (Heymons and von Lengerken, 1929:576). A similar observation was made once on Canthon indigaceus chevrolati Harold by the authors, when a rolling female ceded her position to allow a newly arrived male to roll the ball she had made. In an observation made by Prasse (1958b:90), a female Gymnopleurus geoffroyi Füessly approached a pair of which the female was in the process of burying the ball and male, as is the custom. The intruder female proceeded to start eating the ball and male, completely unmolested by the male sitting on top of it. The proprietor female, unaware of the intruder, proceeded to bury the ball, the male, and the intruder female together. Only underground do the two females meet. The encounter is marked by upheavals of the ground surface, followed by the precipitous emergence and departure of the intruder female. Several other examples of this sort may be found in the works mentioned above.

The actual combat motions seem to differ in different genera. In Sisyphus schaefferi the aggressor jumps into the back of the opponent, holds on with the middle and hind legs, and pummels the head of the other with the forelegs. This position may be reversed several times, the winner being the one last in the top position. In Gymnopleurus geoffroyi both individuals attack at the same time, with the result that they remain front-to-front and engage in a "boxing" match, tumbling over and over. The loser is the first to disengage. In Canthon pilularius and other species of the genus, more use seems to be made of the head (Matthews, 1963a, and authors' observations). The beetles "butt" each other, often succeeding in throwing an opponent some distance away. Close grappling, in the manner of Sisyphus and Gymnopleurus, may also be observed, however. In Scarabaeus semipunctatus, the beetles fight front-to-front with the legs, as in Gymnopleurus (Goggio, 1926; Heymons and von Lengerken, 1929). In all cases the difference between "winner" and "loser" is that the latter disengages from combat and departs. No combat injuries have ever been directly observed.

As previously noted, dung is the essence of the tribe other than the objective, without such a situation, such as in Copris hispanicus (Fabre on), animals, such as the pestiferous dung beetles, are yet without combat.

In all insects, dung during the rearing of larvae is the most prominent. In Copris hispanicus (Fabre on), ants and other insects are often seen close to the dung of the dung beetle in the early stages of development. The dung beetle is the important factor in the propagation of dungs, it is claimed to occur throughout the tropics, although its importance as a crop pest is yet without mention.

The purpose of dung in the rearing of larvae is the consequence. When these mature, the dung beetle may be seen, for the entire body, mixed with the dung, the larvae to mature and leave the insect. The dung beetle is the parent of the insect.
As previously mentioned, combat is not observed in species of any tribe other than Scarabaeini. Even in a potentially conflict-producing situation, such as that observed by the authors when three female *Phanaeus nimrod* Harold were attempting to take possession of the same small piece of dung, the individuals simply strive simultaneously to achieve their objective, without showing combative behavior toward one another directly.

**23. Parental Care**

A beneficial contact between one or both parents and their offspring is the essence of social behavior in insects. When this relationship takes the form of the continued presence of the parent during the early stages of development of the brood ("brooding", *Brutpflege*), but nothing more, we may perhaps term it sub-social. Such sub-social behavior is known to occur in the genera *Copris* and *Synapsis* only. It has also been claimed to occur in the genera *Catharsius*, *Heliocopris*, and *Onitis*, but as yet without convincing documentation.

In all investigated species of *Copris* the continued presence of the female during larval development has been observed. These species are *Copris hispanus* (Linnaeus), *lunaris* (Linnaeus) (many observers from Fabre on), *arizonensis* Schaeffer (Howden, in litt.), *armatus* Harold (authors' observations), *fricator* (Fabricius), *incertus* Say (Matthews, 1962), *lecontei* Matthews (Howden, in litt.), *lugubris* Boheman (Matthews, 1962), *minatus* Drury (Ritcher, 1945), and *remotus* Leconte (Lindquist, 1933). All but the first two are New World species.

The purpose of the female's presence in the nest has not been satisfactorily determined. One obvious, visible effect of removing the female is the consequent growth of molds on the surface of the brood ovoids. When these moldy ovoids are returned to the female, she cleans them off (von Lengerken, 1954:343; Matthews, personal observation). The female may be seen wandering incessantly over the surface of the ovoids for the entire brooding period, patting them with the forelegs and apparently tasting the surface. In captivity it is possible to rear *Copris* larvae to maturity in the absence of the female, but the incidence of brood survival seems to be lower in that case. Matthews (unpublished thesis) noted that in *Copris fricator* (Fabricius) the survival rate for
unattended larva e was seven out of 12 ovoids observed (58%) and for attended larva e it was 13 out of 14 ovoids observed (93%). These observations were made in captivity.

In Synapsis tmolus (Fischer), nidification behavior is as in Copris and the female remains in the brood chamber tending the ovoids. In this species, however, the female dies in the chamber before her brood's emergence (Siyazov, 1913:130). In all Copris, the female emerges from the brood chamber with her offspring and may begin a new nest (at least in C. remotus, according to Lindquist, 1933). In Synapsis the mother beetle apparently places a coating of clay around the late brood cvcid, probably just before she dies (Siyazov, 1913:127). It would indeed be remarkable if the female placed this coating on the ovoids as a compensation for her impending death. In coprine beetles which do not brood the larvae (Phanaeus, Dichotomius), the brood balls are coated with a clay shell, as a rule (Section 200 Group II). Probably in all species of Copris and Synapsis the male plays an unusually important part in nidification. He not only aids in digging and provisioning the nest (as in most Scarabaenae), but also collaborates with the female in preparing the dung cake by compacting it (see Section 22). Whereas earlier authors claim that the male plays no defensive role in the nest, Rommel (1961) describes an instance where a male C. hispanus rushed toward her when the nest was opened, then turned around and proceeded rapidly to push up a wall of soil to close the breach in the chamber, all the while stridulating. However, this seems to occur only when the male is actively participating in nidification. Later, during the brooding period, the male, if present, shows no interest in defending the nest or helping in brooding. On the other hand, he does not eat the dung supply meant for the larvae, either. Rommel found both beetles' gut empty during the brooding period, which lasts four months. Von Lengerken (1954:347) and previous observers have also noted that the adult fasts completely during the brooding period.

Brooding is also said to occur in three species of Canthon in Argentina (Judulien, 1899) (see Section 20). As this behavior departs so radically from what we have observed in other Scarabaenae, it seems best to await confirmation of the data before discussing them further.

Species of Scarabaenae which attack the food supply of their hosts seem to be limited in Scarabaenae to the Scarabinae (by Aphodius), Phanaeus igneus and Onthophagus (Howden, 1957), as well as the above-cited A. hispanus. The second case involves 'deliberate' accidental attacks and may involve "deliberate" accidental attacks by the parent Aphodius larvae which occur in cow dung and attacking Ont. 

In Argentina, dung beetles are attacked by ants. The dung balls move rapidly, thus starving the host larva and killing it by the parent dung beetle staying at the surface.

A group of ants relationship was noted and perhaps some of these flies have "phoresy" for...
These ovoids are as in *Copris* [5]. In this case, the female emerges from a new nest (at emergence, *Synapsis* the male plays an active part in digging and then, together, they collaborate in sealing it (see Section 22). There are no defensive mechanisms associated with the nest where a male may already have been turned, then turned over again close to the breach of the nest. This seems to occur accidentally. Later, during the late brood period, the adult may not be seen again but the larva may be found in the surrounding area. In five instances recorded by Howden, each host larva was killed, and its supply eaten, by a single *Aphodius* larva. However, *Aphodius lividus* larvae may also be found in cow dung at the surface, hence this species does not specialize in attacking *Onthophagus* nests.

In Argentina, the brood pear of *Malagienella violacea* (Blanchard) is attacked by an oitid fly, *Tetanops sanguinipes* Wied., which develops more rapidly than the scarab larva, consuming its food supply and thus starving it (Richter, 1918). Several flies may emerge from a single host pear, and Richter believes the fly eggs were brought in accidentally by the parent beetle with the dung, as the fly commonly breeds in dung at the surface.

A group of flies which appear to have an obligatory cleptoparasitic relationship with the ball-rolling scarabs is the borborid genus *Ceropera*, and perhaps some other borborids. The following summary of the habits of these flies is taken from Grandi (1951:459-460).

"Belonging to this ecological group [of coprophagous borborids] are the sphaerocerids [= borborids] symbiotic with scarabaeid beetles. All of them, as far as we know, included in the genus *Ceropera* Macq. and found in Southern Europe (Spain), Africa, and Ceylon. The first account of the subject was that of Meigen (1838), who then redescribed his *Borborus rajitarsis* (1830) as *Limosina sacra* (now *Ceropera rajitarsis* [Meigen]) on the basis of specimens found in Spain on *Scarabaeus sacer* L. Lesne (1896), as we mentioned elsewhere, coined the term 'phoresy' for this behavior, which was incorrectly interpreted, Roubaud..."
in effect discovered, regarding C. nasuta Willem., that the fly, after being transported by the beetle, deposits its egg in the dung collected by the scarab at the moment in which this is being stored under the soil. We are therefore dealing with a more obligatory form of symbiosis [than phoresy].

Knab (1915) found that in the United States of North America these habits are proper to two species of "Borborus". However, these insects fly over the beetle (at least in some cases), instead of settling on it.

Apparently the European species cling to the back of the beetle while the latter is rolling the ball, while the American species run or fly behind the rolling beetle. H. E. Howden (personal communication) photographed what appeared to be one of these borborids running and flying rapidly behind a rolling Canthon indigaceus Leconte in Durango, Mexico.

Of particular interest to us here are cases of cleptoparasitism of scarabaeine nests by other Scarabaeinae. Lea (1923:353) reports that in Australia Pedaria geminata (MacLeay) (originally described as an Aphodius) "habitually uses, for its own young, dung-balls formed by other species of Coprides". Martínez (1959) writes that Trichillum externepunctatum Preudhomme in Argentina feeds on the brood balls of Dichotomius bosqui (Pereira) (presumably as an adult), but this Trichillum may also be found in excrement at the surface.

Arrow (1931) records a number of species collected by G. M. Heury in Colombo, Ceylon, in balls of Scarabaeus gangeticus Laporte. These apparent cleptoparasites were: Caccobius aterrimus Fabricius (op. cit.: 143), C. rufipennis (Motschulski) (op. cit.: 158), Onthophagus ochreatus d'Orbigny (op. cit.: 167), O. cryptogenus Boucomont (op. cit.: 220), and O. paullus Fabricius (op. cit. 322).

Kolbe (1905:485) cites Kolpänti (1846) to the effect that Onthophagus clavatus Brullé (referred to as O. trochiscobius Kolpänti) deposits its eggs in the balls of Gymnopileurus. Kolpe (op. cit.) also mentions that Onthophagus saturnal Périnquey (cited as O. buplagnus Périnquey) and O. pullus Roth (cited as O. brevicornis Fehr.) in South Africa oviposit in the brood of Scarabeus. Likewise, adults of Onthophagus chevroleti Harold may be found inside the dung cake of Copris armatus Harold in Salazar, State of Mexico (Halffter, 1959:168), but is also frequently found elsewhere. Finally, Fabre (Souv. V:83) notes that the hips of Scarabaeus may sometimes contain, in addition to the Aphodus Schreber" (unwith the dung materials.

Thus, with some borborics specializing in brood balls of Scarabaeine, we have no idea if these brood balls can be found in the small chamber and the published account made it desirable, the study involved, the published account.

Very little and their mitosis studies have been published. Evans and Krantz (1959) species of Macrocheles phoretic associated to Filipponi genera Copris, Geotrupes. This is a purely ph.
...that the fly, having found the dung egg in the dung ball, is being stored in the obligate form. In North America these insects fly in the evening, these insects fly after sunset on it."

The beetle while running or flying behind the dung (photographed and flying rapidly at outdoor, Mexico).

Reports that leptoparasitism of Onthophagus (Caccobius [Linnaeus]) brought down with the dung. Thus, with the exception of Pedaria geminata (MacLeay), and some borborid flies, no species or group of insects has succeeded in specializing in any sort of parasitism of scarabaeine nests or larvae. This attests to the effectiveness of the defenses built into the nests and brood balls of Scarabaeinae. On the other hand, mites may frequently be found in the nests of Scarabaeinae, occasionally even in the egg chamber and larval feeding space of the brood mass. We know of no studies which define the role of these mites in the scarab nests, and have no idea whether their presence is even detrimental.

25. Associations with Mites

In Section 24, dealing with cleptoparasitism, we mentioned several species of flies which can be found in the nests of Scarabaeinae. The table presented by Balthasar (1963:75-78) lists the mites known to be found on Scarabaeidae, but it omits a number of references, even when published some years previously. Furthermore, a number of recently published acarological works dealing with mites found on scarabs have made it desirable to prepare a new table indicating the scarabaeine species involved, the mite species, and the source publications.

Very little is known concerning the relationship between the scarabs and their mites. The mites are believed to be phoretic, but no detailed studies have been made to discover the type of association which exists. Evans and Hyatt (1963:327) claim: " Females of the coprophilous species of Macrobeles are facultatively parthenogenetic and display a phoretic association with insects, particularly coprid beetles." According to Filipponi and Dojmi di Delupis (1963:277), various species of Macrobeles are active predators attacking primarily eggs of Musca domestica and rhabditoid nematodes and, to a lesser extent, Collembola. Krantz (1965) recently revised the Old World macrochelid genus Neopodocinum, which is entirely phoretic on coprophilous scarabs of the genera Copris, Catharsius, Heliocopris, Synapsis, Onitis, Scarabaeus, and Geotrupes. "The association between the mite and the beetle apparently is a purely phoretic one, and the mites may leave the beetle in the dung..."
substrate to feed on small arthropods. Only adults and nymphs are found on the beetles, the larvae apparently remaining in the substrate until the first molt.

It may be assumed that specimens found between the mandibles of the host beetle are in close contact with the food material being utilized by the beetle, and are perhaps feeding on the same substances. It is also conceivable that the very presence of numbers of *Neopodocinum* in the feeding apparatus of the beetle may significantly reduce the availability of food for the beetle, primarily because of the physical barrier produced. Specimens of *Neopodocinum* may attain a length of 1000-2000 μ, and have been found in such numbers as to virtually block the passage of food into the oral cavity of the beetle carrier.” (Krantz, 1965:140-141).

The same author also notes that certain similarities between phoretic macrocheilids, such as *Neopodocinum*, and the family Pachylaelaptidae, which is entirely phoretic, are probably due to convergence because of similar phoretic behavior in both groups.

According to Rommel (1962), adults of *Copris hispanus* (Linnaeus) and *C. lunaris* (Linnaeus) are continuously afflicted with mites of the genera *Uropoda*, *Cilliba*, *Macrocheles*, *Peletiphis*, and *Pachylaelaps*, and unidentified members of the family Laelaptidae (all belonging to the suborder Parasitiformes). There may be individual differences with regard to the species of mite involved. For instance, individual beetles from the same locality in Tunis bore either *Uropoda orbicularis* Müller exclusively or *Cilliba copridis* Oudemans exclusively. On adult beetles only the yellow or brown deutonymphs or adult mites were found, and Rommel naturally asks where the white larvae and protonymphs may occur. On opening brood ovoids of *Copris lunaris* (Linnaeus) both in captivity and in the field, she found the eggs and larvae of the beetles frequently infested with the white early instars of the mites. Rommel concludes from this that the association between the mite and beetle is not exclusively one of phoresy, but also one of commensalism.

Siyazov (1913:131) also found mites within the egg chambers of *Copris hispanus* brood ovoids, and Matthews (unpublished thesis) found mites of the family Parasitidae inside the egg chamber of *Copris fricator* (Fabricius) ovoids in captivity on two occasions, in both cases with a dead egg.
### LIST OF SCARABAEINAE WITH ASSOCIATED MITES

<table>
<thead>
<tr>
<th>Beetle</th>
<th>Mite</th>
<th>Author</th>
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<tbody>
<tr>
<td><strong>SCARABAEINI</strong></td>
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<td><strong>CANTHONINA</strong></td>
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<tr>
<td>Canthon principalis Burmeister</td>
<td>Macrocheles boxi Evans and Hyatt</td>
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<td>Deltochilum lobipes Bates</td>
<td>Macrocheles baccatus Evans and Hyatt</td>
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<td>Macrocheles floridanus Evans and Hyatt</td>
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<td>Eudinopus dytiscoides (Schreber)</td>
<td>Macrocheles argentinus Evans and Hyatt</td>
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<td>Malagoniella argentina (Gillet)</td>
<td>Macrocheles nevinsoni Evans and Hyatt</td>
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<td><strong>GYMNOPLEURINA</strong></td>
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<td>Gymnopleurus azureus (Fabricius)</td>
<td>Macrocheles rhodesi Evans and Hyatt</td>
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<td></td>
<td>Macrocheles vernalis Berlese</td>
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<td>Copris elphanor Kling</td>
<td>Pelethiphis gegeri Ryke and Meyer</td>
<td>Ryke and Meyer, 1957</td>
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<td>Copris hispanus (Linnaeus)</td>
<td>Ciliiba copridis Oudemans</td>
<td>Rommel, 1962</td>
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<td>Coprolaelaps caputmedusae Berlese</td>
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<td>Uropoda orbicularis Müller</td>
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<td>Copris incertus Say</td>
<td>Macrocheles kraepelini (Berlese)</td>
<td>Krantz and Filipponi, 1964</td>
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<td>Eviphis pterophillus Berlese</td>
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<td>Macrocheles glaber Mull.</td>
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<td>Copris spp.</td>
<td>Parastus heliocopridis Oudemans</td>
<td>Balthasar, 1963</td>
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<td>Heliocopris bicepsFabri</td>
<td>Olaefia trifolium (Oudemans)</td>
<td>Oudemans, 1901</td>
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<td>Eviphis hastatellus transvalensis Ryke and Meyer</td>
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<td>Heliocopris spp.</td>
<td>Parastus heliocopridis Oudemans</td>
<td>Balthasar, 1963</td>
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IMMATURE STAGES

In the Scarabaeinae there are always three larval instars, the last of which usually undergoes an inactive phase called the prepupa, and a pupal instar. The embryonic and other immature stages are passed underground within the dung mass or ball prepared by the parent, with the few exceptions enumerated in Section 20. This provides the immature stages with relatively constant humidity and temperature conditions, an assured food supply, and good protection against predators and diseases.

It also makes observation of the larva very difficult. In spite of this, a few European observers have made excellent studies of larval behavior. Undoubtedly the most thorough such studies are those of Prasse (1957c) on the immature stages of Gymnopleurus geoffroyi Füessly and Sisyphus schaefferi (Linnaeus), and of Burmeister (1930) on Onthophagus spp.

This is not the place to go into detail on larval morphology. The essential features of the scarabaeine larva which concern us here are the fully developed mouthparts with strong mandibles (far less specialized than the adult mouthparts), the eyelessness, the relative immobility, and the "coprine hump" — an enlargement of the dorsal portions of all or some of the first six abdominal segments, enclosing coils of the middle and hind guts (see Appendix I). This hump is also very important in aiding the movement of the larva inside the cavity of the dung ball, as we shall see. The hump is much more marked in some genera (Onthophagus, most Scarabaeini) than in others (Copris, Phanaeus, Dichotomius), but an enlargement of the dorsal area is always evident, except in the free-living larva of Liatongus monstrosus (Bates) (Sections 8, 20).

A consequence of the relative immobility of the scarabaeine larva is a reduction in the extent and development of the body bristles, including the raster — the stiff, curved bristles on the venter of the last abdominal segment. Although the raster is still present in many scarabaeine larvae, it does not achieve the level of development seen in most pleurostictics. Ghilarov (1949:61-64) points out that the traditional C-shape of the scarabaeid larva is more correctly an S-shape, as far as the living larva is concerned. The free-living scarabaeid larva propels itself through the underground tunnels maintaining contact against the ceiling of the tunnel with the dorsum of the anterior abdominal segments and against
the floor with the venter of the last segment, the body being in an open-S position. The dense bristles normally seen on these parts of the body are therefore used to give purchase. The legs of scarabaeid larvae play no part in locomotion and are reduced and feeble, although always present. The scarabaeine larva continues to use the dorsum of the anterior part of the abdomen as a surface of support and locomotion, but the other contact surface is no longer the venter of the last abdominal segment but the specially flattened anal area (the "trowel" of Fabre and others). The legs continue to play no part in locomotion. The body is maintained in a constant C-position, having lost the S-shape of the free-living scarabaeid larva.

We know of no studies that have been made on nutrition and digestion of scarabaeine larvae, hence we do not know whether the enlarged mid-gut houses symbiotic micro-organisms to digest the cellulose often found in the dung food. The intestine of coprophagous scarab larvae is distinguished from that of other scarabs by the absence of gastric caeca and greater length relative to the body (see Appendix I). The copious excrement, which is used as mortar, is stored in the enlarged hind gut only (Prasse, 1957e:1035). The very different nature of the larval mouthparts, as compared with those of the adult, suggests that the consistency of the larval food is very different from that of the adult. The larvae have strong, cutting or crushing mouthparts, and the food particles reaching the intestine must therefore be in the form of rather coarse chunks. The adult mouthparts, on the other hand, are highly membranous and sensory and capable only of an extremely fine trituration. The food reaching the adult intestine must therefore be in the form of liquids and very fine particles in suspension (see Appendix I for a more complete discussion).

26. Duration of Development

There are few studies that give the duration of development in Scarabaeinae in a precise manner. The normal time lapse from egg to adult appears to be 30-50 days. Some known examples are: Onthophagus spp. in North America - 35-42 days (Howden and Cartwright, 1963); Nesosisyphus spp. on Mauritius - 30-34 days (Vinson, 1947); Canthochiletum n. sp. on Puerto Rico - 40-50 days (Matthews, 1963b); Gymnopileurus Geoffroyi Füesly - 36-46 days; Sisyphus schaefferi (Linnaeus) - 38-39 days (Linnaeus) see Lengerken, 1957.

It should be noted that interruptions during unfavorable conditions usually contains two up to four pupal which are summer. Development follows, according to the larva, overwinters as an adult, overwinters as an adult, emerging in May. The life cycle is then less than two years.

Even in the tropics, less than a month, the life cycle (egg to adult) may follow. This is because of the feeding which occurs in the gonads. These feedings often up to four times per year to the winter. The female annually gives birth. This would bring these data are that the dry climate, continuous, super-pupal, which have no pupal stages observed each year among the scarabaeid larvae of Puerto Rico respectively.

On the whole, the duration of development and shorter than...
The body being in an S-shape in these parts of the scarabaeid larvae although always motion, but the last abdominal "prowl" of Fabre notion. The body of the larva is the S-shape of the

on nutrition and suggest the cellulose ophagous scarab by the absence of nutrition. (see Appendix 1). Enlarged in the enlarged present nature of the adult, suggests that that of the adult. Adults, and the food the form of rather abundant, are highly by fine triturations.

in the form of Appendix I for a more

velopment in Scarabaeinae. From egg to adult Onthophagus spp. (Chen, 1963); Can-

thophilus schaefferi (Linnaeus) — 41-49 days (Prasse, 1957c); Copris remotus Leconte — 38-39 days (Lindquist, 1933). We then get a number of species, mostly large in size, with much longer development periods. Copris hispatus (Linnaeus) seems to need four months for full development (von Lengerken, 1954; Rommel, 1961). The immature period of Dichotomius torulosus (Eschscholtz) in Chile is 18 months (Joseph, 1929), and that of Onitis caffer Boheman in South Africa is two years (Oberholzer, 1958).

It should be noted that when development takes over a year, this includes interruptions due to unfavorable weather. The delaying influence of an unfavorable climate is best noted in Central Asia, where each year contains two unfavorable seasons — the cold winter and the dry summer. Development of Synapsis tenuis (Fischer) in Uzbekistan is as follows, according to Siyazov (1913:129): Year I: egg to mature larva, overwintering as larva; year II: mature larva, pupa, and teneral adult, overwintering as adult in original brood ball; year III: adult emerging in March, feeding, and beginning nidification in early summer. The life cycle from egg to emergence of the adult is therefore a little less than two years.

Even in those cases where actual development takes little longer than a month, as in most species of Onthophagus, the complete life cycle (egg to egg) may still take a full year in temperate climates. This is because of the need for a Reifungsfrass period — a period of feeding which the newly emerged adult must undergo for ripening of the gonads. This period probably takes well over a month on the average, often up to four months (see Section 13), which brings the beetles up to the winter. Lindquist (1933) claims that three or four broods per female annually are normal for Copris remotus Leconte in southern Texas. This would bring about a superposition of individual life cycles, but these data are based on individuals kept in captivity and it is not clear that the dry climate would normally allow such continuous activity. Continuous, superposed life cycles seem to be the rule on tropical islands, which have no marked seasonal changes. Both Vinson (1947) and Matthews observed the continuous presence of teneral adults throughout the year among the forest-inhabiting Scarabaeini of Mauritius and Puerto Rico respectively.

On the whole, it appears to be a general rule in the Scarabaeinae that the duration of the immature stages is far shorter than that of the adult, and shorter than the corresponding immature stages of pleurosticts. We
do not actually have many data on adult longevity, but even if the complete life cycle lasts only one year in temperate climates, the fact that all immature stages together normally take only 30-50 days (see above) means that the rest of the year (10-11 months) must be spent in the adult instar. Such evidence as we have indicates that the adult lives longer than a year. Lindquist (1933) kept a female Copris remotus Leconte alive in captivity for over 21 months, and Balthasar (1963[1]:42) believes that an adult longevity of 2-3 years is normal for the subfamily. We have already noted that the newly emerged beetle has no food reserves to begin reproduction immediately, hence the larva was provided with only just enough food to carry it through metamorphosis.

27. LARVAL BEHAVIOR

If we combine the accounts of Fabre (Souv. V:71-92) for Scarabaeus sacer Linnaeus, Burmeister (1930) for Onthophagus spp., von Lengerken (1954:271-288) for Scarabaeus semipunctatus Fabricius, and Prasse (1957c) for Gymnopleurus geoffroyi Füssly and Sisyphus schaefferi (Linnaeus), we obtain a good picture of larval behavior, probably applicable in principle to the whole subfamily. The accounts are not all complete enough to permit a comparative analysis at this time.

The newly hatched larva continues to derive nourishment from the yolk which fills the mid-gut, and so does not feed externally for one to four days after hatching. It begins feeding on the side walls of the egg chamber, and also perhaps on the egg shell. After some additional days (on the 8th to 10th day in Onthophagus) the larva begins to eat the floor of its chamber, and thereafter continues to eat its way downward, depositing its own excrement on the ceiling of the chamber. Most observers agree that the larva responds to gravity in directing its feeding, but in the American species of Onthophagus at least (and some European ones), where the cell is horizontally oriented, the larva must eat its way in horizontally. In any case, the larva does not move continuously in one direction, but wanders about inside the food mass (von Lengerken, 1964: 275-277).

As soon as the larva begins to eat its way into the main food mass, it creates a perfectly spherical space around itself, by rotating as it eats. The diameter of this space is exactly correlated with the size of the larva and, indeed, the larva is completely dependent on the exactness of this diameter to be in the space, with the dorsum of the forebody free to change position but contact now being "swings".
the fact that all adult lives longer than 10 days (see above) may be spent in the pupal stage. Leconte (1871:42) believes the adult family. We have provided food reserves to be spent in the adult lives longer than 10 days (see above) and thus Leconte alive at 15 years (fig. 1).

Eventually for one to understand how the larva moves about, we see that the characteristic, seemingly distorted shape of the scarabaeine larva is nothing more than an adaptation for efficient movement inside a spherical space, a fact apparently first pointed out by Prasse (1957c). When we understand how the larva moves about inside its food supply, we see that the characteristic, seemingly distorted shape of the scarabaeine larva is nothing more than an adaptation for efficient movement inside a spherical space. With an enlarged space, the larva is unable to wedge its hind body and therefore lies rather helplessly on the floor. However, it soon begins to rasp away at the food within reach, at the same time depositing excrement along the upper surface of the space. This excrement hardens and gradually reduces the space to its requisite diameter.
Ronchetti (1949:161) in relation to the larva of Scarabaeus affinis Brullé. The hump is thus seen as an important means of locomotion and support. The legs, while present, are nearly immovable and quite useless for locomotion, as we have mentioned, but the anterior pair is directed forward and may aid in feeding.

As the larva eats its way into the bulk of the food, it leaves a trail of its own excrement mixed with a certain amount of inedible frass. Even though the larval excrement is deposited mostly on the posterior (upper) face of the space, in the course of the larva’s rotation inside the space it smears some of its excrement evenly over the entire surface, and consequently eats it again with the food. In the Scarabaeini at least, it seems that most of the food material passes through the larval intestine at least twice. Excrement is not normally ejected to the outside except in Deltochilum gibbosum (Fabricius) (Howden and Ritcher, 1952) and Synapsis tmolus (Fischer) (Siyazov, 1913:127), and probably others. The exuviae are not eaten, but usually only the head capsule of the first two molts can be found afterwards, and only with difficulty.

A faint scraping noise can be heard from the outside while the Scarabaeus larva is feeding (von Lengerken, 1954:283).

The behavior of the larva when repairing a breach in its brood hall was first described by Fabre, then confirmed by all subsequent investigators. This behavior seems to be common to all scarabaeine larvae. Soon after the hole is made, the larva’s head appears and it proceeds to deposit an oral secretion, variously described as yellow to brown, along the edge of the hole. The anus (which is near the head because of the larva’s bent shape) now appears and a drop of excrement, dark brown in color, is pressed against an edge of the hole for a minute or so. The anus is then moved a little and another drop applied, this process being continued around the entire hole. The excrement quickly hardens on exposure to air. If the breach is very large, as in an experiment by von Lengerken (1954:287) in which half of a brood pear was removed, the excrement is used as mortar to cement dung fibers together to rebuild the entire missing surface. In this work the mandibles and anus are used together (not the legs). A similar experiment, with similar results, was made by Joseph (1929) with larvae of Dichotomius tortulosus (Eschschoitz).

Fabre’s experiments prove that it is not the light entering the hole which makes the larva aware of it. Larvae behave normally in light coming through glass, as the larva detects the air entering through the break.

Thus we see larvae maintain the inner lining of the shell around the larva lines the inner lining lining with cemented soil particles in the larval food supply. According to Kilian (1946), (1953), and Siyazov, species there is also of larval excremen in the larval food supply. According to Fabre (Halffeter) observations, consisting only of a small intestine. A puparia of fly puparia.
Rabaeus affinis Brullé.

This is a very active scarab, and its motion and support system is rather remarkable.

As the larva grows, it leaves behind a trail of inedible frass. Even the posterior (upper) portion inside the space it created is used for exuviae. In at least one species, it seems that the larval intestine at least partially fills the space except in Deltochesion (von Lengerken, 1952) and Synapsis others. The exuviae of the first two molts are buried outside while the exuviae of the third molt are deposited in its brood hall (von Lengerken, 1954:287). Thus we see that the larva detects the hole by the different physico-chemical properties of the air entering through it (von Lengerken, 1954:288).

Thus we see that the scarabaeine larva has a remarkable ability to maintain the integrity of its brood ball and to seal itself off completely from the outside world. It is not clear what natural agents normally cause breaks in the brood ball. It is likely that the major agent is the larva itself, whose movements inside the ball may cause cracks to appear, particularly as the larva gets larger and the walls get thinner.

As the larva reaches the end of the food supply it faces the problem of providing a pupal cell for itself. In those genera which form a clay shell around the brood ball, this shell serves as pupal chamber, but the larva lines the inside of the original shell with a thinner layer of very fine cemented soil particles, which represent sand that was originally included in the larval food and which has passed through the larval intestine. This inner lining has been described for Dichotomius torulosus (Eschscholtz) by Kilian (1960), Phanaeus milon Blanchard by Baratti and Saenz (1953), and Synapsis molus Fischer by Siyazov (1913). In the latter species there is no outer shell initially, since this is one of the brooding scarabs, but at the time of pupation there is an outer layer of clay bearing the tibia marks of the mother beetle. Siyazov believes that the outer layer is also of larval excrement, extruded by the larva and plastered evenly over the ball by the mother beetle. In Copris armatus Harold, one of us (Hafner) observed an ovoid completely consumed by the larva and consisting only of a shell of cemented soil, presumably also from the larval intestine. A pupal cell of larval excrement is made by Copris gopheri Hubbard (Hubbard, 1894) and undoubtedly by other species of the genus, though not all.

In Onthophagus, the pupa is found in an oval shell ("double-walled") according to Sim, 1930) made by the larva within what is left of the food supply. We were able to verify that the larva of O. rufescens Bates, which lives in the debris of Atta nests, makes a hard cocoon for pupation. On microscopic examination this cocoon is seen to consist of very small sand grains cemented together with fine fibrous vegetable matter, probably larval excrement. Ohaus (1909:27) states that the cocoons of O. circulus Mannerheim, made of larval excrement, are hard and black, reminiscent of fly puparia. The larva of this species (and also that of O. incensus through glass, and appear to be quite insensitive to it. It seems that the

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Say) eats about one third of the available dung, the rest being eaten by the newly-emerged adult (no one else has observed this).

None of the observed species of Scarabaeini make cocoons; rather the larva leaves a portion of the dung uneaten and this shell of dried dung serves as a pupal chamber, except in those species where the brood ball has an outer clay shell.

28. Pupal Adaptations

The described pupae of Scarabaeinae all share a feature seldom seen in other scarabaeid pupae — projections issuing (depending on the species) from the middle of the pronotum, meso-, and metathorax, and from the middle, sides, and end of the abdomen. Few species have projections on all these places, but those on the sides of the abdomen at least are always present. The projections along the middorsum of the thorax and abdomen serve to support the full weight of the pupa; those along the sides and end of the abdomen apparently serve to keep it away from direct contact with the walls of the brood ball.

The position of the pupa of Gymnopleurus gеоfгоуі Fiessly in its cell is indicated in fig. 36, taken from Prasse (1957c:1040). It will be seen that it lies upside down, resting on the series of short projections which emerge from the middle dorsum of the pterothorax and abdomen (not seen in the figure) and with the sides supported by projections issuing laterally from the abdomen and directed downward. This upside-down position of the pupa is also reported for Sisyphus schaefferi (Lинновеус) (Prasse, 1957с:1040), Scarabaeus semipunctatus Fabriceus (von Lengerken, 1954:276), and Onthophagus (four European species) (Burmester, 1930). In the latter case, the pupa lies head-downward, resting most of its weight on two short projections issuing from the middle of the front edge of the pronotum (see also von Lengerken, 1954:234-235). Assuming that this upside-down position is normal for all Scarabaeinae, fig. 37 shows the appearance of a pupa of Canthochilum n. sp. from Puerto Rico in its presumed natural position (the actual position was not observed). It will be seen that the unusual filamentous projections of the pronotum and abdomen are in contact with the cell walls, while the pupa rests principally on the short support projections of the middle of the thorax and abdomen. A ventral view of this same pupa may be seen in Matthews (1963b). Similar filamentous projections, in the same loca-
being eaten by oocoon; rather the oocoon is shell of dried egg where the brood are seldom seen depending on the netathorax, and species have projections the abdomen at idorsum of the pupa; those projections to keep it away from Füessly in its it will be of support projections of the metathorax and abdomen are assisted by projections of the underside. This 185

Fig. 36. Gymnopleurus geofroyi Füessly, pupa in natural position in cell, posterior view, showing support function of projections. Fig. 37. Canthochilum n. sp., pupa in presumed natural position in cell, lateral view, showing support function of projections.
Through the courtesy of H. F. Howden of the Canada Department of Agriculture and D. M. Anderson of the U. S. Department of Agriculture, we were able to examine pupae of the following species of Scarabaeinae: Canthon pilularius (Linnaeus), Copris fricator (Fabricius), Copris n. sp., and Deltochilum n. sp. near scabriusculum Bates, plus some pupae of Bolboceras, Geotrupes, and Osmoderma for comparison. All the Scarabaeinae except Deltochilum possess small support projections on the middle of the tergum of the mesothorax and, of these, all but Copris minutus on the metathorax as well. All but the Deltochilum also possess conical lateral projections on abdominal segments 3, 4, 5, and 6. The Deltochilum has two very small bumps in the middle of the pronotum, a pair of short, rounded projections on the sides of abdominal segments 4 and 5, and two short projections in the anal region behind the pygidium ("anal palpi"). It will be noted that in all of these positions Canthochilum (fig. 37) and Nesosisyphus have long, filamenteous projections, also on abdominal segment 3.

The non-scarabaeine pupae examined were all devoid of mid-dorsal support projections, but the two species of Geotrupes examined (splendidus Fabricius and blackburnii Fabricius) had low, setose, rounded projections on the sides of abdominal segments 2-4 and 2-5 respectively, plus distinct anal palpi. The lateral projections were not conical or filamentous as in Scarabaeinae. The other genera did not have any projections at all.

This highly preliminary survey indicates that the presence of projections is a characteristic of the scarabaeine pupa, but not an altogether exclusive one. Within the subfamily, there is considerable variation in the location and shape of the projections. As far as we know, the purpose of these projections is to keep the pupa away from direct contact with the walls of the brood ball. Why this should be necessary we cannot guess at present.

Arrcw (1934a, 1934b) and Darlington (1934a, 1934b) independently, licens. What other mechanisms are involved, is a problem and an unfortunately not fully understood.

In the Scarabaeidae, the pupae examined for both sexes of Canthochilum (1934a, 1934b), Bdelys (Martinez, 1925, 1934), and for the present author, Heliocopris (Martinez, 1925, 1945:67; equal.

"The margin of each of the abdomen are a finely striated" or heard to stridulate. The coxal mechanism of the "strialement ridges are largely less musical sound."
OTHER ASPECTS OF BEHAVIOR

29. STRIDULATION

Arrow (1904) made a survey of stridulation in the whole family Scarabaeidae and showed that stridulatory mechanisms have appeared independently, and in widely different forms, in several groups of lamellicorns. What is still lacking is field observation to show whether these mechanisms are actually used for sound production and if so under what circumstances. Alexander, Moore, and Woodruff (1963) discuss this problem and make valuable observations on a number of Scarabaeidae, unfortunately not including the subfamily Scarabaeinae.

In the Scarabaeinae, stridulatory mechanisms have been described for both sexes of Copris, Helicocoris, and Synapsis (Arrow, 1904; Marcu, 1934a, 1934b; Dieter, 1953), Dichotomius mormon Ljungh (Marcu, 1934b), Bdelyrus sp. (Ohaus, 1909) and several species of Malagoniella (Martinez, 1950).

The species of Copris are well known to be strong stridulators and just about every species observed, and every species collected by the present authors, can be induced to stridulate when picked up. The mechanism is of the elyto-dorsal type seen also in Trox, that is, the downturned sutural edges of the elytra bear microscopic teeth which rub against a patch of transverse microscopic ridges on the middle of the fifth (true seventh) abdominal tergite. The edges of the elytra are held in line by a deep groove in the propygidium (sixth, or true eighth, tergite). Stridulation is brought about by moving the abdomen back and forth along the elytral ridges.

Helicocoris is said to stridulate strongly, sounding like a bat (Paulian, 1945:67; Arrow, 1931:85). As in Copris, both sexes stridulate equally. "The stridulating plate is minute and occurs near the inner margin of each hind coxa, while the inner half of the inturned part of the abdomen against which the coxa revolves is similarly but rather less finely striated". (Arrow, 1904:722). Synapsis timolus (Fisher) has been heard to stridulate in the field by Syuzov (1913). It has a ventro-metacoxal mechanism similar to that of Helicocoris, but the coxal portion of the "instrument" consists of very short, stout bristles, and the abdominal ridges are coarser. The effect is to produce a "much harsher and less musical sound than in Helicocoris" (Arrow, 1904:723).
No species of *Dichotomius* has yet been heard to stridulate, Marcu's (1934b) study being on dead specimens. According to Marcu, *Dichotomius mormon* Ljungh has a pronoto-mesoscutal stridulatory mechanism in both sexes. That is, there is a triangular field of very fine ridges on the inside (inflexed) surface of the back of the pronotum (pars stridens) rubbing against some other very fine ridges on the mesoscutum (plectrum).

*Bdelyrus* sp. is a species inhabiting bromeliads in Brazil (mentioned also in Section 3 of this work). According to Ohaus (1909:26), when the *Bdelyrus* are seized with forceps they emit a squeaking noise, which is produced by rubbing the middle and hind femora against the broadened elytral epipleurae. The femora have a number of fine longitudinal grooves near the "knee" and the epipleurae have a carina with fine tubercles and bristles. In some individuals the grooves of the middle femora are poorly developed.

Martinez (1950) cites the following species of *Malagoniella* (referred to as *Megathopa*): *M. p. puncticollis* (Blanchard), *M. p. aeneticollis* (Waterhouse), *M. p. tubericeps* (Gillet), *M. bicolor* (Guérin), *M. chalybea* (Blanchard), and *M. magnifica* (Balthasar), which, at the moment of capture, usually produce a noise resembling that made by certain acridids in flight, but less intense. This noise is produced by contractions of the abdomen, the stridulating apparatus being located on the apices of the elytra and the seventh abdominal tergite, which rub against each other.

It will be noted from the above that all the stridulating genera have evolved different mechanisms to produce sound, only *Heliocopris* and *Synopsis* having a somewhat similar mechanism. All the above-mentioned genera except *Dichotomius* and *Malagoniella* are known or suspected to be sub-social or at least gregarious. Ohaus (op. cit.) always found *Bdelyrus* in groups of four or five in bromeliads.

The important question is whether stridulation serves purely an alarm function, or whether it is also a means of communicating other types of information to members of the same species, such as calls to congregation (as suggested for *Trox* by Alexander, Moore, and Woodruff, 1963), species identification, warning to rivals, etc. The various observers of *Copris hispanus* (Linnaeus), from Fabre on, have spent a great many hours carefully watching all phases of the behavior of these beetles. At no time did they hear stridulation being used for any other purpose than alarm directed toward an outside intruder (the observer).
Nor have any other Scarabaeinae been heard to stridulate except when handled or when their nest was opened.

Paulian (1943:147) notes that an auditory sense has never been experimentally demonstrated in beetles. However, even if this is so, the numerous vibrating hairs present on the antennae, mouthparts, legs, etc. of most insects have been demonstrated to serve at least partly as sound receptors, and we need not doubt that beetles can hear noises.

Larval Scarabaeinae, like most scarabaeid larvae, have the mandibular-maxillary "stridulating apparatus", consisting of a row of teeth on the maxilla, rubbing against a ridged area on the mandible. However, this apparatus is usually very rudimentary, the mandibular area having disappeared, and scarabaeine larvae have never been heard to stridulate, even when handled.

Until a special study is made of stridulation in Scarabaeinae, we must remain in the dark as to the purpose of the sound-producing apparatus.

30. PROTECTIVE BEHAVIOR

Under this category we include any behavior or other adaptation which serves to protect the adult individual against members of other species. Unfortunately we know very little of this subject, as no specific studies have been made. We are forced back on descriptive observations and deductions from dead specimens, which may sometimes be misleading.

Perhaps the most convincing evidence that protective mechanisms do, in fact, occur in Scarabaeinae is the fact that color mimicry is to be observed among some unrelated species living together. Arrow (1931:33-34) describes some instances of mimicry in African Scarabaeinae in the following words:

"It is interesting to find in Africa a series of species belonging to the genera Onthophagus and Phalops associating with different species of ball-rollers of the genus Gymnopleurus found in different parts of the continent, and in each region mimicking, in extraordinary detail, the appearance of the particular Gymnopleurus occurring there: a small black and white species in West Africa, a large blue one in Rhodesia, a particular one in Abyssinia, vivid crimson upon the anterior half and blue upon the posterior half, etc —each is accompanied by a mimicking
Onthophagus or Phalops. That the species of Gymnopleurus are the models and the others the mimics is indicated by the fact that in several of the former a patch of white hairs at the side of the body, which is exposed owing to the cutting away of the elytra behind the shoulders characteristic of this genus, is simulated in the other by a patch of hairs situated, not upon the abdomen, which is not exposed, but upon the elytra at the corresponding point, and found in these mimics alone. We may, therefore, conclude that the ball rolling Gymnopleuris have better natural protection than their mimics, which, of course, are found closely associated with them when all are engaged in collecting their food-material. I have given fuller particulars of the mimetic associations in Proc. Ent. Soc. Lond. i, 1926, p. 19. The three genera concerned are all represented in India, but no mimetic associations have been noted, up to the present, except in Africa".

One of us (Matthews) observed a case of scarabaeine mimicry in Hispaniola. In cow pastures on the Dominican side of that island, two species of Scarabaeinae may be seen flying and feeding together in the full daylight: Nesocanthus violaceus (Olivier) and Onthophagus albicornis Beauvois. The former species is a brilliant dark purple color with contrasting white antennal clubs and pygidium. The Onthophagus is shiny black with similarly pure-white antennae and with a pale area on the elytral edges above the pygidium. When the beetles are alive, both species wave the antennae, which are very conspicuous in contrast to the dark body color. As this is a very unusual color pattern, in either group, its occurrence simultaneously in two unrelated species active together cannot be a mere coincidence.

We have no data on what may be the protective mechanisms which make at least some species of Gymnopleurus and canthionines suitable models for mimics. It is probably a strong-smelling secretion which emerges from the anal region and which may be noted also in diurnal Canthion, but which has not been tested or analyzed. Because the mimicry involves color patterns, the predators are probably birds.

The most common behavioral adaptation for protection is thanatosis, or death-feigning. This may be expected to afford protection whenever the predator is dependent on the movement of the prey for locating it. In this connection, Goljan (1953) makes some interesting observations. He notes that in Poland in the early spring, when food is generally scarce, many birds are heavily dependent on coprophagous scarabs (mostly Aphodiinae and Pachybrachini) at the same time picking over other food is plentiful; and some scarabs that in spring have a very early emergence, while the predators (reptiles and birds) are still dormant, are not a success against in spring, the predators (reptiles and birds) is evidently to escape haphazardly at the first sign of danger. 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Aphodiinae and Onthophagus) for their food, and that they spend much time picking over horse and cow dung for the beetles. Later in the year other food is preferred. The dung beetles which are active in the early spring have a very short period of thanatosis, or none at all, when disturbed, while those occurring later display a longer-lasting thanatosis before burying themselves. In this case, we may deduce that thanatosis is not a successful protective behavior against birds and is selected against in spring species, but that it is successful against warm-weather predators (reptiles and amphibians), which are more dependent on the movement of their prey, rather than its form, for detecting it. To escape birds, it is evidently better to get out of sight as quickly as possible, while to escape herptiles it is better to remain immobile.

One of us (Matthews) has observed several instances of attacks on dung beetles (Canthon and Onthophagus) by reduviids and the carabid Pasimachus. In all cases the scarabs emerged unscathed through the protection of their thick exoskeleton. The attitude of the beetles under attack was always that of thanatosis, which in these cases apparently served to protect the extremities.

Halfpeter noted that the protective reaction of Deltochilum scabriusculum Bates is to remain completely immobile with the fore tibiae covering the sense organs of the head. The first movement on resumption of activity is the extraction of the antennae from the protection of the tibiae, and the opening of the club lamellae. This occurs before any movement of the legs.
EVOLUTIONARY TRENDS IN THE NATURAL HISTORY OF SCARABAEINAE

A phylogeny of the Scarabaeinae cannot be constructed at present because of the absence of a sound morphological basis for doing so. In spite of the fact that this is one of the best-studied groups of Coleoptera, and in spite of the voluminous literature dealing with it, the subfamily is still at an elementary level in this respect, barely having advanced beyond the alpha-taxonomic stage. Nevertheless, certain phylogenetic trends in nesting behavior may be detected and these correspond fairly well with established taxonomic categories. Certain other trends in regional ecological adaptation, displayed by various taxonomic groups in parallel, may also be seen.

The family Scarabaeidae is closely associated with the soil. This association explains most of the adaptations seen in both the adults and the larvae of the family. We may therefore assume that the earliest scarabs encountered their food in the soil, at least when in the larval stage. There must have been an early separation into three main feeding groups: one feeding on live roots, one on dead wood, and one on fungi and dead vegetable matter other than wood (these are not sharply separable categories). From the latter group (the saprophages) arose the various coprophagous beetles (the Aphodiinae, Geotrupinae, and Scarabaeinae). We cannot say at what level in the evolution of dung beetles the switch was made from saprophagy to coprophagy, but in at least two of the subfamilies — the Aphodiinae and Geotrupinae — the acquisition of coprophagy was a late event, since many or most of their members are still saprophagous today. In the case of the Scarabaeinae, coprophagy became the dominant trophic adaptation very early, and today we know of no species which can conclusively be demonstrated to be primitively saprophagous, although there are several we suspect to be so (see Section 3).

The availability of abundant excrement, a result of the appearance of the larger terrestrial vertebrates of the Mesozoic, posed a challenge to the potential dung beetles — the saprophagous scarabs. The excrement was there, it was trophically assimilable because of its similarity to decaying vegetable matter, but it was on the surface, not in the soil, and probably frequently on exposed surfaces. Two ways of attacking this problem presented themselves: the dung could be eaten by the larvae in situ, on
the surface (the aphodiine way), or it could be buried by the adults for the larvae, (the geotrupine and scarabaeine ways). Because of the danger of desiccation, only massive deposits of dung, such as those of large herbivores, could be exploited in the aphodiine manner, and for full exploitation this dung had to be situated in sheltered locations. The geotrupine-scarabaeine way allowed for much more flexibility both as to the initial mass of the excrement and its location. The soil could provide the suitable physical conditions for the larvae. The geotrupine-scarabaeine behavior need not have evolved from the aphodiine, in fact it seems more probable that both represent adaptations independently evolved from soil-inhabiting saprophages, in response to the new challenge of vertebrate excrement. However, in the case of the Geotrupinae it seems that the habit of burying the food preceded the appearance of dung, as most geotrupines today seem to bury humus or other vegetable debris instead of, or as well as, dung (Howden, 1955). In discussing nidification, we refer to "aphodiine" and "geotrupine" levels of behavior. These are merely descriptive terms that do not imply that either of these two subfamilies necessarily gave rise to the Scarabaeinae.

Evolutionary trends in nidification behavior in the Scarabaeinae (other than Scarabaeini) appear to diverge radially from a primitive base in which the larval food is simply packed into the blind end of a burrow (fig. 38, Group I). Genera which seem to be still at this "geotrupine" level of evolution are Ateuchus, Uroxyx, some Dichotomius, Babas, Onthophagus, and Oniticellus, and probably many others not yet studied. These represent four tribes of Scarabaeinae (Coprini, Onitini, Onthophagini, and Oniticellini) which are therefore at least partially at the same level of behavioral evolution. The first tribe includes elements which have advanced greatly from this base, while the other three seem to have advanced little or not at all in this respect. The improvements on this simple nesting system in the Coprini all involve increased protection for the immature stages and the larval food.

Various ways of separating the egg from direct contact with the food material are seen in the subfamily. In Gromphas, the egg alone is enveloped in a clay shell, the food material still being packed into the burrow. In Phanaeus (and Deltochilum in the Scarabaeini) both egg

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1 Actually, some aphodiines seem to bury the food for the larvae, as Jerath and Unny (1965:91) report finding larvae of five species of African Aphodius "in small dung cells usually about 3-6 inches deep in the soil". 

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and food are in a clay shell, but the egg is in a clay compartment separate from the food. Other methods seen are cementing the egg upright in the egg chamber (Onthophagus), suspending it from the roof of the chamber (Scarabaeus), or lining the chamber with a dark secretion, which could conceivably be antibiotic (Copris, many Scarabaeini). The apparent purpose of all these methods is to isolate the egg from direct contact with the food material, possibly to discourage mold formation on the egg, which must be exposed to an air supply.

The methods of protecting the larval food in the tribes other than Scarabaeini show two major evolutionary advances departing from the
primitive base in which the food is packed or pressed into the end of a burrow (Group I). The first refinement on this may have been to line the burrow wall with a cementing substance before filling it with food. European Onthophagus have been observed to do this. This presumably forms a partially impermeable layer around the food and egg and protects them temporarily either from desiccation or flooding. A more elaborate advance from this, involving quite different behavior, is to surround the food and egg with a clay shell and to maintain an air layer between this shell and the burrow wall. This clay-air layer may be presumed to afford good protection against humidity changes and mold. It involved the evolution of a complex modelling behavior. The food is first packed into a carefully shaped oval mold (at the end of the burrow) (fig. 38, A, B), then a layer of soil is loosened from around the food and pushed with considerable pressure into the outer surface of the food mass. The compression of the soil reduces its volume and thus creates the air layer (fig. 38, C, Group II). The beetle thus works its way all around the food mass, not only compressing but also carefully smoothing the surface of the ball. This sequence involves the preliminary step of packing the food, as in the primitive groups, and hence is clearly derived from more primitive behavior. In fact, within the single genus Dichotomius we see two species which have been well studied, one of which (D. carolinus Linnaeus) simply packs the larval food, the other one (D. torulosus Eschscholtz) modelling a clay-coated brood ball in the manner described above. The genera which are known to have achieved this level of behavior (Group II) are, beside some Dichotomius, Phanaeus, Bolbites, Oxysternon, and probably Heliocopris.

An entirely different line of behavioral evolution was begun by Onitis and Copris independently, the former genus having achieved only the first step. Onitis packs a large quantity of food into a spacious underground chamber, then (presumably) removes a layer of soil from all around the mass and lays about five eggs in it. It is not known how long the female remains with the young. Copris goes through the same initial steps (fig. 38, C, Group III), but cuts away a portion of the large food mass after the first egg has been laid in it (fig. 38, D), then cuts away a second portion after the second egg has been laid, etc. (E), until the original mass is divided into a small number of separate ovoids, each containing one egg. The presumed advantage of this method over that of Onitis is that each larva is assured an adequate food supply and larval competition is eliminated. It should be noted that the early step of removing the soil layer and packing it away from the ball, as in Group II in the elaboration above, is similar to the "burrowing" behavior, but presses the soil away from the egg, which is, apparently, in contact with the ground. The degree of elaboration here, as pointed out the the above account the behavior of Group III, has reduced larvae competition. This in turn has led to an elaboration of this phenomenon appearing in the genera Phanaeus (Appendix II) and Heliocopris, in which the follicles of the female then tends to the young, by the degree of elaboration noted above, and sometimes the entire procedure of ball-making of Onitis is markedly similar. But
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the soil layer around the food (step C) differs from the equivalent step
in Group II in that the soil is not pressed into the food to create an earth
coat, but pressed away from the food (or possibly the food is pressed
away from the soil), so that now only air surrounds the food.

While we have retained Onitis in Group I, it can be seen from
the above account that its behavior could be a preliminary step toward Group-
III behavior, which is thus derived directly from Group I in a separate
line of evolution from that of Group II (fig. 39). The essential feature
of Group-III behavior is that the female beetle remains with the brood
ovaids and tends these until larval metamorphosis. The continued presence
of the female thus substitutes for the clay layer seen in Group II and
is, apparently, a more effective method of protecting the brood, judging
by the degree of ovarian reduction in Copris. However, it should be
pointed out that the ovary of no Group-II scarab has been carefully
examined.

The "brooding scarabs" (Group III) are known to include only
the genera Copris and Synapsis, and possibly Catharsius—all in the
subtribe Coprisina.

The elaboration of efficient nidification procedures in the subfamily
has reduced larval mortality and consequently the level of egg produc-
tion. This in turn is reflected in a reduction of the female reproductive
system to but a single ovary, and a single ovariole, on the left side. This
phenomenon appears to be general throughout the subfamily (see Ap-
pendix II) and is perhaps one of its most striking characteristics. As
nidification becomes progressively more efficient the number of egg
follicles of the ovariole becomes progressively less, until in Copris we
have but a single follicle.

The Tribe Scarabaeini (the ball rollers) does not fit into the above
scheme, as no members of this tribe are known to pack food into a pre-
viously prepared burrow. Even if a ball is not made, food is buried intact
by digging directly under it (undermining it). The brood pear, in the
cases observed, is made by tearing apart the original ball, rebuilding it,
then sometimes placing a layer of soil around the finished pear. This
entire procedure is totally different from that adopted by Group-II Cop-
prini in making the brood ball, although the finished products may be
quite similar. For these reasons, and especially because of the unique

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ball-rolling behavior not seen in any other tribe, the Scarabaeini represent a completely different evolutionary line which must have diverged very early in scarabaeine history.

The Scarabaeini have remained essentially homogeneous in their nidification behavior (see under Group IV in Section 20), however, there is some evidence of isolated but major divergences in behavior. Some Scarabaeini have habits (some Ca. possibly even a Co. Eurysternus). The scarabaeine family and much in need of revision which bury excrescences.

The profound procedure in the great ecological specialization and transport of their food, a minimum of care which bury excrescences.

Two groups, and Eurysterninae, the former has definitely, a change in the family of food transport.

The adaptation, physiological characteristic, not in the diet in affecting the environmental influence on food specialization and increased its own food supply, "sausages" of different case to behave in nidification. In most have been lost, we seek it or very stable habitats.

Coprophagy by the family but it has well, especially those to become adapted as in many other Scarabaeinae have whose mouthparts advanced Aphodius of the mouthparts under similar see...
Scarabaeini have abandoned ball rolling and acquired coprine nesting habits (some Canthochilum, Canthon, and Canthonidia) and possibly even a Copris-like brooding behavior (some Canthon and some Eury sternus). These “aberrant” tropical forms are all very poorly studied and much in need of careful field observation, which may completely change our ideas about them.

The profound differences seen in both adult feeding and nesting procedure in the Scarabaeini, in comparison with other tribes, are also of great ecological significance, as they reduce competition. The manufacture and transport of a ball of food permit the Scarabaeini to coexist, with a minimum of competition, in the same areas inhabited by other tribes which bury excrement directly beneath the source.

Two groups placed as subtribes of the Scarabaeini—the Eu craniina and Eurysternina—may really represent separate evolutionary lines. The former has definitely, and the latter may have, developed alternate means of food transport which cannot be derived from ball-rolling behavior.

The adaptational requirements of coprophagy, as well as the physiological characteristics of the excrement itself, have been dominant influences not only in the development of complicated nidification behavior, but also in affecting the behavior associated with adult feeding. The same environmental influences which require that the nest be protected from desic- cation and extreme temperature fluctuations, oblige the adult to protect its own food supply by digging tunnels which are then supplied with “sausages” of dung or by making balls to be buried later—in either case to behave in a manner similar to that of the simpler forms of nidification. In most of the cases in which this adult feeding behavior has been lost, we see either an abundance, and continuous supply, of food or very stable humidity and temperature conditions, or both.

Coprophagy has not only profoundly affected behavior in the subfamily but it has brought about radical morphological modifications as well, especially in the adult. Thus, the mouthparts of the adult have become adapted for processing a soft and pasty food. In this respect, as in many other morphological and behavioral ones, the evolution of Scarabaeinae has proceeded much further than that of the Geotrupinae, whose mouthparts are less modified from the general type. The more advanced Aphodinae, on the other hand, show similar modifications of the mouthparts for coprophagy, having undergone a parallel evolution under similar selective pressures.
The larvae of Scarabaeinae, which feed on a drier and therefore harder excrement, have not modified the mouthparts, which resemble the general type seen in the family. On comparing the extent of modification which coprophagy has imposed on the mouthparts of the adults and of the larvae, we can deduce not only that they consume it in a different physical state (that of the larvae being drier and harder), but also that they utilize it in a different manner: the adults ingest primarily the liquid and colloidal content (microorganisms and undigested food particles), while the larvae ingest primarily the solid content.

The digestive tract also shows modifications for coprophagy on a different scale in the adult and larva. In the adult the intestine is extraordinarily long and coiled, apparently in adaptation to the microphagous coprophagy of the adult (microorganisms, liquid and colloidal excrement). This type of intestine can be adapted easily to adult saprophagy and necrophagy, which are not very different from coprophagy. The intestine of the larva is more similar to the general type seen in the Pleurosticti; it even has an enlarged portion of the hind gut similar to the "fermentation chamber" of phytophagous larvae. This raises the possibility that it may contain microorganisms capable of digesting the cellulose which comprises a large part of the excrement of herbivorous mammals (especially when dry).

The modifications of the adult head and legs are not exclusive to Scarabaeinae, as they are found to a greater or lesser extent in many groups of Scarabaeidae and represent a very early adaptation to life in relation to the soil and organic detritus. The lengthening of the hind legs of Scarabaeini is, however, an important morphological characteristic of this group which reflects a vitally significant biological adaptation: the ability to manufacture and transport a ball of excrement. When this modification of the hind legs reaches an extreme (for instance in some species of Deltochilum), it begins to make burying more difficult, and these species tend to be poor diggers.

The larvae and pupae of the subfamily display characteristic morphological adaptations for living in a small, enclosed spherical space. These adaptations are discussed in sections 27 and 28.

So far in our discussion we have concentrated on the behavioral and morphological adaptations which accompany coprophagy, because coprophagy, and more particularly coprophagy in grassland biomes, is the dominant theme in the evolutionary trends in the group. We shall now try to manipulate and classify categories in the light of these specializations, hence the development of the phylogeny and regional evolution of invasion of biomes later on in this section.

Very little is known about Scarabaeinae and different groups of European fauna, but the distribution of biotopes occupied by the group is very important. As for the remaining geographical distributions, they should try to set in one or more environments of soil and vegetation, for example in grassland biomes. It is also necessary to consider all factors —insects, large mammals, the group of Scarabaeini, etc.—interdependent.

We have studied Scarabaeinae, or at least Scarabaeini, at least one biome (see Section 28), but abundance of concentration and humidity fluctuates, and there is a great abundance of forms. We have used powerful statistical techniques under certain constraints, as new adaptive specializations arise.

Forests, pastures, and savannas...
drier and therefore harder, which resemble the extent of modified parts of the adults they consume it in a drier and harder), but adults ingest primarily undigested food content.

For coprophagy on a certain level the intestine is especially adapted to the microphagous (colloidal excrement). It sapro- and necrophagy. The intestine of the Pleurosticti; it resembles to the fermentation possibilities that it may lose which composed elements (especially when the

are not exclusive to lesser extent in many adaptation to life in thinning of the hind biological characteristic biological adaptation: excrement. When this for instance in some more difficult, and

characteristic moul-
spherical space. 18

the behavioral and coprophagy, because co-
land biomes, is the dominant theme in the biology of the Scarabaeinae. Major evolutionary trends in the group emerged primarily as the beetles evolved new ways to manipulate and protect the dung food in grasslands. Major taxonomic categories in the subfamily tend to reflect the evolution of behavioral specializations, hence the latter are those which tend to correspond best to the phylogenetic subdivisions of the subfamily. However, important regional evolutionary trends in local faunas have resulted from the invasion of biomes other than the grasslands. These trends are discussed later on in this section.

Very little has been published on the relationship between Scarabaeinae and different biomes, except perhaps in connection with the European fauna, about which we have a fairly exact knowledge of the biotopes occupied by the various species. With respect to the rest of the world, the present work contains the first attempt to analyze this important point in some detail.

As for the relative importance of food vs. biotope in relation to the ecological distribution of Scarabaeinae, our idea is that we cannot, nor should, try to separate food from other environmental factors. Food is one more environmental factor, inseparable from those of the microclimate, soil, and vegetation. In our opinion, the distribution of Scarabaeinae (for example in grassland biomes) can be understood only when considering all factors — insolation, temperature, tree cover or lack of it, presence of large mammals, abundance of excrement, coprophagy, rolling behavior of Scarabaeini, feeding and nesting burrows of other tribes, etc. — as interdependent.

We have stated our reasons why we believe the subfamily Scarabaeinae, or at least its presently dominant elements, arose in a grassland biome (see Section 10). The Cenozoic grasslands, with both their abundance of concentrated dung and their special problems of temperature and humidity fluctuations, were without doubt the environment which gave rise to all the dominant evolutionary lines of Scarabaeinae. The abundance of food coupled with the harshness of the environment provided powerful selection pressures for developing burial and dispersal techniques under conditions of intense competition. It seems likely that as new adaptive radiations took place in the grasslands, elements of previous radiations were forced into marginal niches, particularly in forests.

Forests, particularly tropical forests, provided the environment for new adaptations. In these biomes the selective pressures are different:
desiccation ceases to be of prime concern, while the scarcity of large-mammal dung acquires special importance. Hence we see some evolution in regressive directions, such as in the partial loss of burial of the brood ball and food ball in *Deltochilum*, while on the other hand the new limiting factor—the scarcity of excrement—gives rise to many and diverse trophic specializations, which are largely limited to forests.

Forests have served as refuges for many forms, such as many small canthochilines and dichotomines, which have survived in many specialized niches on the sidelines of the intense competition of the grasslands, where the perfection of nesting techniques has become the determining factor in survival. In spite of the greater variety of Scarabaeinae in forests, ecologically there do not play as significant a role there as in the grasslands and probably the actual number of individuals is relatively less in forests. We cannot be certain about this since the required ecological studies have not been made in tropical forests. The leaf-litter inhabiting species are difficult to collect except by trapping, hence their real abundance is not reflected by their presence in collections.

In contrast to the Geotrupini, which are a predominantly Holarctic group abundant in temperate forests, the Scarabaeinae are basically inhabitants of warm climates. There are progressively fewer Scarabaeinae, both in terms of taxa and of individuals, as we approach the poles and, more importantly, they become progressively more restricted to non-forested areas. The extensive scarabaeine invasion of forests mentioned above is largely a tropical phenomenon.

The invasion of forests has tended to be accompanied by special adaptations such as secondary saprophagy, necrophagy, perhaps myrmecophily, and even more specialized types of associations, while the desertification of original grassland biomes has often led to radically and cavernicoly. Let us consider these adaptations in turn.

Secondary saprophagy nearly always involves attacks on fallen fruits, and must be distinguished from what we consider to be the primary, primitive saprophagy involving feeding on vegetable detritus. We have pointed out (Section 2) that whereas we believe some genera of Scarabaeinae to be primatively saprophagous (*Epilissus, Odontoloma, Onthobium, Saphobius, Panelus, Aphengium, and Bdelurus*), we have no conclusive evidence for this, since several genera found in forest leaf litter have proved on further study to be coprophagous (*Nesosisyphus, Canthochilum, Geocanthion, Pelecanthion, some others in *Neocanthidium, Neocanthina, etc.* are only those coprophagous.)

The most typical of the saprophages are the *Scarabaeinae* or other plant part-eating Scarabaeinae. As in the case of Saurophaga, most operate on the detritus of the forests inhabiting it. Nevertheless, they are a taxonomic group of many diverse genera. The saprophagous response to communities is widespread.

The prevalence of saprophagous species and the adaptations leading to them in this region are due in large part to the Geotrupini and Canthochilinae. Necrophagy, perhaps a more natural aspect of the same phenomenon, is undoubtedly widespread in the North American region.

In Section 2 we discussed historical factors which have operated in the Neotropical region, but it is undoubtedly true that there groups to adapt...
...due to the scarcity of large-...
...
...see some evolution in the burial of the brood hand the new limit-
...to many and diverse forests.
...
...such as many small 
...in many specialized 
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...fewer Scarabaeinae, 
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...restricted to non-
...forests mentioned 

...companied by special 
...perhaps myrme-
...while the deser-
...and caver-

...attacks on fallen 
...to be the pri-
...uble detritus. We 
...some genera of 
....(Canthochilum, Canthonella). Secondary saprophages may be seen in 
...somes others in fermenting fruits or other parts of higher plants, and 
...in fungi). The above genera 
...are only those containing species believed to be primarily or exclusively 
...saprophagous. Many other genera contain species which are only partly 

...The most unequivocal examples of saprophygy on decaying fruits 
...or other plant parts are to be seen in tropical-forest inhabiting species. 
...As in the case of necrophagy, the special conditions of this biome have 
...in the biology, especially the feeding habits, of the scarabaeines 
...inhabiting it. Neither saprophagy nor necrophagy are limited to any special 
...taxonomic group, but are manifested in a very similar manner in many 
...diverse genera, which have thus undergone a parallel evolution as a 
...response to common selective pressures.

...The prevalence of necrophagy in the Neotropical Region is striking, 
...and the adaptation is displayed by all three tribes of Scarabaeinae occur-
...cing in this region, but especially in the two dominant ones — the Scar-
...aeini and Coprini. This necrophagy, which elsewhere in the world is 
...an incidental manifestation, is the primary feature of the Neotropical 
...scarabaeine fauna. In this zoogeographic region it is not only the adults 
...which utilize dead animals as food (often exclusively), but also the larva. 
...that carrion is normally used for nest provisioning in these species 
...a phenomenon which is exclusive to certain Neotropical groups and 
...the North American elements derived from them.

...In Section 1 we enumerated the combination of ecological and 
...historical factors which in our opinion explain the prevalence of necrophagy 
...in the Neotropics. Among the ecological factors, the most important one 
...is undoubtedly the great extent of tropical forest in this zoogeographical 

...Necrophagy, like saprophygy, is not a decisive factor in the phy-
...logenetic evolution of the subfamily; it does not separate different tribes 
...or subtribes. Both types of trophic specialization may be found in widely 
...separated genera and species. The importance of these adaptations resides 
...in their influence on the evolution of regional faunas, and in enabling 
...groups to adapt to new biomes, especially tropical forests. Nevertheless,
the greater importance of necrophagy as an evolutionary influence is shown by the fact that entire groups at the subgeneric level (Coprophanaeus and Megaphanaeus) and the generic level (Deltochilum) have become entirely or largely necrophagous (equivalent saprophagous taxa are not known). Several other genera have exclusively necrophagous species (Canthon, Uroxys, Onthophagus) and many others have copro-necrophagous species.

Myrmecophily also appears repeatedly in many species of different genera (see Section 8), but only one supra-specific group — the subtribe Alloscelina of the tribe Scarabaeini — appears to be largely or exclusively myrmecophilous.

Whenever it has been studied, scarabaeine myrmecophily takes the form of feeding on the detritus accumulated by the ants (especially in the New World species associated with attine ants); it is therefore a form of saprophagy. But the myrmecophilous adaptation is more than a feeding specialization; it also involves responses to other environmental factors such as the constancy of the food supply and the stability of humidity and temperature conditions. These factors have profoundly influenced the nidification behavior of those species most strongly adapted to myrmecophily (e.g., Liatongus monstrosus [Bates] and Onthophagus rufescens Bates), by bringing about a near-loss of nidification procedures. This phenomenon provides indirect evidence for the extent to which the complex nesting behavior of Scarabaeinae is a response to harsh environmental factors causing rapid desiccation of the food and extreme oscillations in temperature and humidity. In the above-mentioned instances, and possibly in many others yet unstudied where these physical conditions cease to be limiting factors, nidification becomes simplified to a marked extent and larval development shows a convergence with that seen in Aphodiinae and the Pleurosticti.

Unlike saprophagy and necrophagy, myrmecophily is not clearly an adaptation to forest conditions. It may represent a way of surviving in an arid or otherwise unsuitable environment, and in the case of Liatongus monstrosus it has clearly provided a refuge for a relict species. Other adaptations which are not obviously correlated with any particular biome are endoparasitism (Section 6) and cleptoparasitism (Section 24). Predation (Section 4) and ectocommensalism (Section 5), on the other hand, seem to be associated with the tropical forest biome.

Other adaptations may adapt to environments different from the original one from which the former species of Scarabaeinae. A parallel phenomenon evidently for different areas the same — elements of the Palaeoamerican fauna suggest note that with the exception all the Scarabaeinae of the world (although they belong to the genus Macropodius) are ancient and are displays a very broad range.

In Argentina they have been seen there in some scarabaeine, Liatongus. and Onthophagus. Ecological conditions of nests.

Whereas the saprophagous and perhaps Scarabaeinae is becoming monstrosus, Ecological conditions of nests.

In the preceding trends in the subfamily of an initial adaptation of grassland biomes to the major adaptations of behavior. We have abandoned by some ecological conditions tropical forest, see.
coprophagy and from complex nidification behavior, and to substitute new trophisms and new associations with other animals. These new, non-grassland adaptations can be seen to be marginal in terms of the basic adaptive radiations of the subfamily, as they involve only "end branches" of the radiations (genera and species) as they entered the new biomes independently and in parallel. However, the invasion of the tropical forest, although marginal in a phylogenetic sense, involved so many lines that it may be said to be one of the major events in the history of the Scarabaeinae.

TENDENCIAS

Actualmente, debido a la mejora en el estudio de los Scarabaeinae, la importancia de los grupos se ha incrementado. A pesar de que la relación entre los adultos y larvario es distinta, se han encontrado coincidencias entre los grupos regionales, destacándose la familia Geotrupinae.

Esta relación entre los grupos se ha estudiado en profundidad. Muy probablemente, la presencia de grupos separados derivan de la evolución de las formas de vida y su adaptación a biomas diferentes. Los Scarabaeinae son los que hoy en día más se caracterizan por ser saprófagos, en el ecosistema trofico dominante. De los grupos conocidos, son saprófagos (sección 3).

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Actualmente, no puede establecerse una filogenia de los Scarabaeinae, debido a la falta de una base sólida de estudios morfológicos.

A pesar de que esta subfamilia es uno de los grupos de Coleoptera mejor estudiados, a pesar de la voluminosa literatura acumulada, el conocimiento de los Scarabaeinae permanece en un nivel elemental, que rebasa ligeramente el correspondiente a una taxonomía de tipo alpha.

Sin embargo, en este trabajo ha sido posible señalar las tendencias evolutivas que sigue la compleja nidificación de la subfamilia, tendencias que coinciden bien con las categorías taxonómicas establecidas. También se indican algunas otras tendencias relativas a adaptaciones ecológicas regionales, desarrolladas por varios grupos taxonómicos en forma paralela.

La familia Scarabaeidae está estrechamente asociada con el suelo. Esta relación explica muchas de las adaptaciones presentes tanto en adultos como en larvas. Suponemos que los primeros Scarabaeidae encontraron su alimento en el suelo, por lo menos durante su desarrollo larvario. Muy pronto se estableció la separación en tres grupos con alimentación distinta: aquellos que comían raíces vivas, los que consumían madera muerta, y por último, los que se alimentaban de hongos y materia vegetal muerta distinta de la madera (hay que advertir que no se trata de grupos separados en forma tajante). Del último grupo, los saprófagos, derivan los Scarabaeidae coprófagos: Aphodiinae, Geotrupinae y Scarabaeinae.

No es posible asegurar en qué nivel evolutivo la coprofagia hace su aparición; pero por lo menos en dos de las subfamilias: Aphodiinae y Geotrupinae, la adquisición de la coprofagia es un evento tardío, ya que hoy en día muchas o la mayoría de sus especies continúan siendo saprófagas. En el caso de los Scarabaeinae, la coprofagia es la adaptación trófica dominante muy pronto, hasta el punto de que actualmente no conocemos especies de las cuales se pueda afirmar con seguridad que son saprófagas primitivas, aunque en algunas se supone (véase Sección 3).
La presencia de excremento abundante, resultado de la aparición de los grandes vertebrados terrestres en el Mesozoico, dio la oportunidad a los escarabajos potencialmente coprófagos: los Scarabaeidae saprófagos. El excremento estaba ahí, tróficamente aceptable debido a su similitud con la materia vegetal en descomposición, pero estaba en la superficie —no enterrado en el suelo— y por lo tanto expuesto a la acción destructora de los elementos del medio ambiente.

Dos respuestas tuvo este problema: en la primera, el excremento era comido por la larva in situ: respuesta de los Aphodiinae1; en la segunda, enterrado por los adultos, para su posterior consumo y especialmente para la alimentación de la larva: respuesta de Geotrupinae y Scarabaeinae.

Debido al peligro de desecación, únicamente los depósitos masivos de excremento, por ejemplo los de los grandes mamíferos, pueden ser explotados en la primera forma o forma afodinoide; aún más, para que una explotación completa pueda verificarse el excremento debe estar situado en la sombra, protegido de la insolación directa.

Geotrupinae y Scarabaeinae tienen mucha mayor flexibilidad, tanto en relación con el tamaño inicial de la masa de excremento, como respecto a su localización. Gracias al enterramiento, el suelo da protección a la larva y al alimento acumulado para su consumo, o bien al alimento que el adulto almacena para su propio uso.

El comportamiento de Geotrupinae y Scarabaeinae no parece haberse desarrollado a partir del de los Aphodiinae. Más probable es que ambas líneas representen procesos de adaptación desarrollados en forma independiente a partir de Scarabaeidae saprófagos primitivos, como respuesta a las posibilidades derivadas de la presencia del excremento de los vertebrados. Sin embargo, en el caso de los Geotrupinae parece que el hábito de enterrar el alimento ha precedido a la aparición del excremento, ya que hoy en día muchos geotrupinos entierran humus o residuos vegetales en lugar, o lo mismo que el excremento (Howden, 1955).

Al discutir la nidificación de los Scarabaeinae nos referimos a los niveles "afodinoide" y "geotrupinoide" de comportamiento. Estos son meramente términos de dos familias haya.

Las tendencias incluyendo a los Scarabaeinae, finalmente otros much cuatro tribus de Dichotomacini. La primera a partir de poco o nada. El enterramiento por los Co el estado inmánico.

En la subfamilia del contacto directo el huevo sólo es rodeado de que el material en Phanaeus (Cómo el huevo está en la pared interna o suspendida capa de anexada del huevo son con-

La prueba del contacto directo o llo de hongos, al final de una

Los métodos de Scarabaeinae no partir de una base pa al final de una forma posiblem
La aparición de la familia Scarabaeeidae saprófita, dio la oportunidad de que una Scarabaeeidae saprófita estuviera en la superficie, debido a su exposición al excremento, que estaba en la superficie. El excremento de los géneros Geotrupinae y Scarabaeinae puede ser consumido y especializado en este sentido. Con la flexibilidad, tanto al alimento que se produce como la protección de los estados inmaduros, es que se desarrolla el sistema de nidificación de evolución. Los Scarabaeeidae no parecen haberse desarrollado en forma primitiva, como respectivamente en la subfamilia Geotrupinae, que está en el excremento de los géneros Geotrupinae. Los scarabaeae se describen del excremento, y están representados en cuatro tribus de Scarabaeeidae: Coprini, Onitini, Onthophagini y Oniticellini. La primera tribu incluye además elementos que avanzan notablemente a partir de esta base, mientras que las otras tres lo hacen muy poco o nada. El perfeccionamiento en el sistema de nidificación desarrollado por los Coprini, representa un aumento tanto en la protección de los estados inmaduros como en el alimento acumulado para la larva.

En la subfamilia Geotrupinae se presentan varias formas de separar el huevo del contacto directo con el material alimenticio. Así, en Gromphas, el huevo sólo es rodeado y aislado por una cubierta de arcilla, mientras que el material alimenticio queda simplemente empacado en la galería. En Phanaeus (y en Deltochilum dentro de los Scarabaeei) tanto el huevo como el alimento son rodeados por una cubierta de arcilla, pero el huevo está en un compartimiento separado del alimento por una delgada capa de arcilla. Otros métodos utilizados para lograr el aislamiento del huevo son cementarlo en forma vertical en una cámara (Onthophagus), o suspenderlo del techo de la cámara (Scarabaeei), o bien cubrir la pared interna de la cámara del huevo con una secreción negra, que se supone pueda tener propiedades antibióticas (Copris y muchos Scarabaeei). El propósito aparente de todos estos procesos es aislar el huevo del contacto directo con el alimento, posiblemente para evitar el desarrollo de hongos, así como para favorecer el aireamiento.

Los métodos para proteger el alimento larvario en las tribus de Scarabaeeidae no Scarabaeinae muestran dos grandes adquisiciones a partir de una base primitiva en la cual el alimento larvario es simplemente empacado al final de una galeria (comportamiento del grupo I). El primer refinamiento aparece cuando la pared de la galería es tapizada por una sustancia cementante antes de empaquetar el alimento. Esto se ha observado en las especies europeas de Onthophagus. Esta sustancia cementante forma posiblemente una cubierta parcialmente impermeable en torno al
alimento y al huevo, a los que protege temporalmente de la desecación o de la inundación. Un proceso más elaborado, que envuelve un comportamiento diferente, consiste en el uso de arcilla para fabricar una cubierta protectora en torno al alimento y al huevo, estableciendo al mismo tiempo una capa de aire entre esta cubierta y las paredes de la galería. El aislamiento proporcionado por las capas de arcilla y aire, da una buena protección contra los cambios de humedad y contra el desarrollo de mohos. Desde el punto de vista evolutivo presupone la aparición de un complejo modelado cuyo producto final es la bola-nido cubierta de arcilla. El proceso comprende, en primer término, la formación cuidadosa de un ovoide de alimento en el fondo de la galería (fig. 38, A y B); una capa de tierra es colocada alrededor del ovoide y presionada contra él. La compresión de la tierra reduce el volumen que ocupa creando la capa de aire (fig. 38, C. grupo II). El escarabajo recorre todo el ovoide, no solamente comprimiendo la tierra, sino también modelando y alisando la superficie. Este proceso comprende como etapa preliminar el empaque del alimento, en forma similar a como se efectúa en la nidificación primitiva del grupo I, por lo cual suponemos que el comportamiento en la nidificación característico del grupo II ha derivado del grupo I. En efecto, en el género *Dichotomius*, en el cual conocemos bien la nidificación de dos especies, una de ellas —*Dichotomius carolinas* (Linneo) — únicamente empaque el alimento larval, mientras que la otra —*Dichotomius torulosus* Eschscholtz— modela una bola-nido cubierta de una capa de arcilla, en la forma como antes se ha descrito.

Sabemos que protegen sus bolas-nido con capa protectora de arcilla, y por lo tanto incluimos en el grupo II, los siguientes géneros: parte de *Dichotomius*, *Phanaeus*, *Bolbites*, *Oxysternon*, y probablemente *Helicocoris*.

Una tendencia evolutiva totalmente distinta se encuentra en los géneros *Onitis* y *Copris*, aunque el primero alcanza únicamente las primeras etapas. En estos dos géneros, en un principio, los escarabajos remueven una capa de tierra en torno a la masa de excremento recién enterrada, pero esta tierra no es presionada contra el alimento para formar una costra, sino por el contrario es fuertemente apretada contra las paredes de la galería, que así se transforma en amplia cámara. Resultado de este proceso, únicamente una capa de aire rodea el alimento. En el caso de *Onitis*, los escarabajos entierran una gran masa de excremento, en la que colocan cinco huevos sin hacer ovoides independientes. No se sabe cuanto tiempo permanecen en las mismas etapas de construcción de la gran masa, pero se sabe que el primer huevo se deposita la segunda después de E, hasta que la instalación de un nido de ovoides se completa, y que este método de nidificación se mantiene asegurado únicamente en parte la competencia

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Una tendencia evolutiva totalmente distinta se encuentra en los géneros *Onitis* y *Copris*, aunque el primero alcanza únicamente las primeras etapas. En estos dos géneros, en un principio, los escarabajos remueven una capa de tierra en torno a la masa de excremento recién enterrada, pero esta tierra no es presionada contra el alimento para formar una costra, sino por el contrario es fuertemente apretada contra las paredes de la galería, que así se transforma en amplia cámara. Resultado de este proceso, únicamente una capa de aire rodea el alimento. En el caso de *Onitis*, los escarabajos entierran una gran masa de excremento, en la que colocan cinco huevos sin hacer ovoides independientes. No se sabe cuanto tiempo permanecen en las mismas etapas de construcción de la gran masa, pero se sabe que el primer huevo se deposita la segunda después de E, hasta que la instalación de un nido de ovoides se completa, y que este método de nidificación se mantiene asegurado únicamente en parte la competencia

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 tiempo permanece la hembra con las larvas en desarrollo. Copris sigue las mismas etapas iniciales (fig. 38, C grupo III), pero separa una porción de la gran masa inicial y la modela en forma de ovoide después de
que el primer huevo ha sido puesto en ella (fig. 38, D), corta una se­
la masa original ha quedado dividida en un pequeño nú­
hembra temporariamente tras el primer huevo hasta que la masa original ha quedado dividida en un pequeño número de ovoides separados, cada uno conteniendo un huevo. Se supone que este método tiene sobre el de Onitis la ventaja de que cada larva tiene asegurada una cantidad adecuada de alimento, eliminando por otra
parte la competencia interlarvaria.

Hay que hacer notar que la etapa inicial en la que se remueve la
capa de tierra alrededor del alimento (fig. 38, C) difiere de la equiva-
ente en el grupo II, ya que la tierra no es presionada contra el alimento
 para crear una capa protectora, sino apretada en sentido opuesto (o posiblemente es el alimento el que es presionado para separarlo del contacto con el suelo), con el resultado final ya antes enunciado de que únicamente una capa de aire rodea al alimento.

Hemos mantenido a Onitis en el grupo I, a pesar de que por lo an­
tes dicho puede apreciarse que su comportamiento ocupa un lugar de
ión entre este grupo y el III. Se considera que el comportamiento
de este último grupo ha derivado de la base que representa el grupo I
directamente, por una línea evolutiva separada e independiente de la que
handa lugar al grupo II (fig. 39).

La característica fundamental del grupo III es que la hembra perma-
ace bajo tierra junto con las bolas-nido, y las cuida hasta que las larvas
han completado su metamorfosis. La presencia continua de la hembra
substituye la cubierta de arcilla que hemos visto en el grupo II, dando
una efectiva protección a la progenie, si juzgamos por la escasa
ladad que se registra durante el desarrollo, lo que a su vez se refleja en la
reducción del ovario.

El grupo III, o grupo con cuidados maternales a la larva, incluye
los géneros Copris y Synapsis, y probablemente también a Catharsius,
todos ellos pertenecientes a la subtrib Coprina.

En general, la adquisición de una nidificación eficiente, caracteris­
tica básica de la subfamilia, ha reducido la mortalidad larval y por con­
secuencia la producción de huevos. Esto, a su vez, se ha reflejado en la
reducción del sistema reproductivo de la hembra a un solo ovario, con
un solo ovario, en el lado izquierdo del escarabajo. Este fenómeno, general en la subfamilia, es uno de sus caracteres anatómicos con mayor significado evolutivo y taxonomico.

La tribu Scarabaeini (los escarabajos rodadores) se separa en forma radical de los tres grupos de nidificación precedentes, ya que ningún miembro de esta tribu empaña el alimento en una galería previamente construida. Incluso en aquellos casos aberrantes en los que no se prepara una bola, el fragmento de alimento es enterrado intacto, excavando directamente por debajo y no como sucede en las otras tribus arrastrando el alimento en fragmentos a una galería previamente preparada. La bola-nido, en todos los casos observados, es hecha remodelando una bola inicial y en algunos casos cubriéndola con una capa de arcilla. En esta última circunstancia, el procedimiento —en conjunto— es totalmente diferente del seguido por los Coprini del grupo II, aunque el producto final puede ser similar.

Por las razones antes mencionadas, y muy especialmente por el hábito único de rodaje de la bola no conocido de ninguna otra tribu, se considera que los Scarabaeini representan una línea evolutiva diferente, denominada GRUPO IV, que se separa del tronco común y básico a los otros tres grupos, muy temprano en la evolución de los Scarabaeinae.

La nidificación de los Scarabaeini se mantiene dentro de lineamientos muy homogéneos; sin embargo, existen algunas divergencias notables. Así, algunos Scarabaeini han abandonado la fabricación de bolas y adquirido —en parte— hábitos semejantes a los de los Coprini (algunos Canthochilus, Canthon y Canthonidia), e incluso es posible que en algunas especies (de los generos Canthon y Eurysternus) se presenten cuidados maternales semejantes a los descritos en Copris. Estas formas de nidificación "aberrantes", limitadas a los trópicos de América, están poco estudiadas y necesitan cuidadosas observaciones de campo; es necesario profundizar en sus mecanismos, que parecen representar un proceso de convergencia.

Las profundas diferencias que encontramos entre los Scarabaeini y las otras tribus, no sólo en la nidificación sino también en la alimentación del adulto, tienen un gran significado ecológico, ya que reducen la competencia de un modo radical. La manufactura y transporte de una bola de alimento permite a los Scarabaeini coexistir, con un mínimo de competencia, en las mismas áreas habitadas por otras tribus que entierran el excremento directamente por debajo de la fuente de alimento.

Al respecto, hay indicios de que los mismas presiones físicas del proceso de formación de la bola, aunque la forma final no sea una "bola" sino un fragmento o incluso el alimento en un suelo directamente por debajo, podría ser una explicación de cómo los Scarabaeini: Eucrania independientes, que se parecen a los Scarabaeini, pueden haber descendido del grupo Scarabaeini.

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bajo. Este fenómeno, que tiene una base fisiológica con mayor o menor grado de desarrollo, se separa en forma sistemática con mayor o menor grado de desarrollo. Ya que ningún otro animal de la galería previamente mencionada se prepara para el contacto, excavando diferentes en los que no se prepara el macho, arrastrando las tribus arrastrando el pedazo de estiércol con forma original adecuada, aunque el producto de este proceso de formación de la bola típica de los Scarabaeini, ya que aquí se aprovecha un fragmento de excremento con forma original adecuada, aunque el rodaje es mucho más imperfecto, la convergencia es notable, y los resultados finales son los mismos: disminuir o incluso evitar la agregación y la competencia intraespecífica.

Dos grupos, considerados hasta ahora como subtribus de Scarabaeini: Eucraniina y Eurysternina, parecen representar líneas evolutivas independientes. Del primero sabemos en forma definitiva, y del segundo hay indicios, del desarrollo de formas de transporte del alimento que no pueden haber derivado del rodaje de la bola típica de los Scarabaeini.

Los requerimientos adicionales de la coprofagia —protección del excremento contra la desecación y destrucción— así como las características físicas del propio excremento, han sido las influencias dominantes no sólo en el desarrollo de una complicada nidificación, sino también en el comportamiento alimenticio de los escarabajos adultos. Los mismos factores ambientales que requieren que el nido sea protegido de la desecación, y de las fluctuaciones violentas de temperatura, obligan al adulto a proteger su propio alimento cavando túneles en los que acumulan "salchichas" de excremento, o en los Scarabaeini, preparando y rodando bolas que entierras más tarde. En ambos casos la protección del alimento del adulto es semejante a las formas más primitivas de nidificación de los dos troncos evolutivos.

En algunos casos, descritos por vez primera en este trabajo, el comportamiento alimenticio del adulto pierde sus características, simplificándose a un nivel afodinoide. Es decir, no hay protección del alimento. La explicación de estos ejemplos es siempre ecológica. En todos ellos existe mucho alimento, o provisión continua del mismo, en condiciones muy estables de humedad y temperatura. Se trata de escarabajos adaptados a horneríceros o bien a cuevas.

La coprofagia no solamente ha afectado profundamente el comportamiento en la subfamilia, también ha sido la causa de profundas modificaciones morfológicas, especialmente en el adulto. Así, las piezas bucales de los imagos difieren totalmente de las de un coleóptero típico, mostrando una adaptación notable a un alimento bland y pastoso.
En este aspecto, como en muchos otros morfológicos y de comportamiento, la evolución de los Scarabaeinae ha ido mucho más allá de la de los Geotrupinae, cuyas piezas bucales están poco modificadas en relación con el tipo general.

Por otra parte, en los Aphodiinae más avanzados, las piezas bucales muestran modificaciones semejantes, ocurridas en un proceso de evolución paralela bajo las mismas presiones selectivas.

La larva de los Scarabaeinae, que come el excremento seco y por lo tanto más duro, no muestra modificaciones en sus piezas bucales, que son del tipo general en la familia Scarabaeidae. Si se compara el grado de modificación que la coprofagia ha impuesto en las piezas bucales a los adultos y a las larvas, puede deducirse no solamente que comen el excremento en estado físico distinto (más seco y duro la larva), sino también que lo utilizan de una manera diferente: los adultos ingieren líquidos y contenido coloidal, así como gran cantidad de microorganismos; las larvas por el contrario consumen el contenido sólido, con un elevado porcentaje de celulosa.

El tracto digestivo también muestra modificaciones debidas a la coprofagia, de distinta intensidad en los adultos y en las larvas. En el adulto el intestino es extraordinariamente largo y enrollado, aparentemente como una adaptación a la coprofagia microfágica del adulto. Este tipo de intestino se adapta fácilmente a la necro y saprofagia que muestran muchos adultos, y que no son hábitos alimenticios básicamente distintos de la coprofagia.

El intestino de la larva es más similar al tipo general que encontramos en los otros Scarabaeidae: incluso tiene una porción dilatada en el intestino posterior similar a la “cámara de fermentación” de las larvas fitófagas, en la cual la celulosa es desdoblada por la acción de microorganismos simbióticos. La existencia de esta cámara plantea la posibilidad de que contenga microorganismos capaces de digerir la celulosa, que forma una parte muy importante del excremento de los mamíferos herbívoros, especialmente cuando está seco.

Las modificaciones que muestran la cabeza y patas del adulto, y que le permiten cavar, no son exclusivas de los Scarabaeinae, ya que se encuentran en mayor o menor grado en muchos grupos de la familia Scarabaeidae, y representan una adaptación muy temprana a la vida en relación con el suelo y los detritos orgánicos.

Por el contrario, los Scarabaeni, si es que se presenta una adaptación a este grupo, es el temprano de este grupo, las piezas bucales de los escarabajos del tipo general en los herbáceos. Las primitivas coprofagos —mejor que ninguno de las estratías de los Scarabaeidae, son el de la evolución metastásica de los excrementos de los herbáceos. Las larvas y las distintas larvas de los escarabajos del tipo general del suelo y los detritos orgánicos. Muy poco se ha sabido en la distribución de los biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los distintos biomas herbívoros, y los dist
Por el contrario el alargamiento de las patas posteriores en la tribu Scarabaeini, si es un importante carácter exclusivo de esta tribu, que representa una adaptación vital al proceso biológico más importante de estos escarabajos: la manufactura y transporte de una bola de alimento. Cuando esta modificación de las patas posteriores llega a sus extremos (por ejemplo en algunas especies de Deltochilum) se convierte en una dificultad para cavar, y estas especies apenas ocultan sus bolas en el suelo entre la hojarasca.

Las larvas y pupas de la subfamilia Scarabaeinae muestran adaptaciones morfológicas a la vida en pequeños espacios esféricos cerrados.

En esta discusión se ha concentrado la atención en las adaptaciones del comportamiento y morfológicas que acompañan a la coprofagia, porque la coprofagia, y muy particularmente la coprofagia en los biomas herbáceos, es el tema dominante de la biología de los Scarabaeinae. En este grupo, las principales adquisiciones evolutivas aparecen cuando los escarabajos desarrollan nuevas formas de manipular y proteger el excremento de las características ambientales típicas de los biomas herbáceos. Las principales categorías taxonómicas de la subfamilia reflejan la evolución del comportamiento en la nidificación, que corresponde —mejor que ninguna otra característica— con las subdivisión filogénicas de los Scarabaeinae. Sin embargo, líneas evolutivas de importancia regional se han presentado en algunas faunas precisamente como resultado de la invasión de biomas no herbáceos. A estos fenómenos nos referiremos más adelante.

Muy poco se ha publicado sobre las relaciones entre los Scarabaeinae y los distintos biomas, con la posible excepción de Europa. de donde tenemos una idea más o menos exacta sobre los biotopos ocupados por la mayor parte de las especies. Respecto al resto del mundo, el presente trabajo contiene el primer intento de analizar este importante punto con algún detalle.

Nuestra idea sobre la importancia relativa del alimento o del biotopo en la distribución ecológica de los Scarabaeinae, es que no se puede ni se debe desligar el alimento de los otros factores del bioma. El alimento es un factor más, en estrecha relación con los microclimáticos, edáficos y vegetacionales, y de ninguna manera puede desligarse de ellos.

Se considera que en la ecología de los Scarabaeinae, por ejemplo en los biomas herbáceos, todos los factores: insolación, temperatura,
vegetación a base de gramíneas con pocos o ningún árbol, abundancia de grandes mamíferos, abundancia de excremento, coprofagia, hábitos de rodaje de los Scarabaeini, galerías de alimentación y nidos subterráneos de las otras tribus, etc., están relacionados y son interdependientes unos de otros. En determinadas condiciones un factor puede ser el determinante, pero nunca se presentará aislado.

Se han expuesto (véase sección 1) los argumentos que nos llevan a considerar los biomas herbáceos como el lugar de evolución de los Scarabaeinae. En el Cenozoico, los pastizales (con abundancia de estiércol y concentración del mismo en determinados lugares, con problemas específicos derivados de la fluctuación de temperatura y humedad) han sido el medio donde se han desarrollado las líneas evolutivas dominantes de Scarabaeinae. La abundancia de excremento, en unión de las condiciones ambientales muchas veces difíciles, da lugar a poderosas presiones selectivas, cuya acción se manifiesta en el desarrollo de las técnicas de enterramiento y rodaje, las últimas bajo condiciones de intensa competencia, así como en la evolución de la nidificación. Un estudio de la distribución ecológica y geográfica deja la impresión de que cada vez que una nueva radiación adaptativa aparecía en las principales áreas de pastizales, elementos de las radiaciones anteriores eran empujados a nichos marginales, o bien a otros biomas, principalmente forestales.

Los bosques, muy especialmente la selva tropical, han sido el medio adecuado para nuevas radiaciones al margen de las líneas principales de evolución. En estos biomas las presiones de selección son diferentes: la rápida desecación del excremento deja de tener importancia, mientras que la escasez de excremento de grandes mamíferos la adquiere extraordinaria. Así, se encuentran dentro de la selva tropical algunos procesos evolutivos que en cierta manera pueden considerarse como regresivos, como son la pérdida de la capacidad de enterrar la bola-nido y la bola destinada a la alimentación, observada en Deltochilum, y que nunca se encuentran en un Scarabaeini de pradera. Por otra parte, el nuevo factor limitante: la escasez de excremento, da lugar a muchas y diversas especializaciones tróficas, casi limitadas o exclusivas de la selva tropical.

La selva tropical ha servido de refugio a muchas formas, como sucede con los pequeños canthoninos y dichotominos, que sobreviven en nichos especializados de este bioma, fuera de la intensa competencia de los pastizales, donde el perfeccionamiento de las técnicas de nidificación se convierte en el factor determinante de la sobrevivencia. Pero a pesar de la gran ecológicamente el en los pastizales, hasta no efectuar bioma es especialmente y, de la escasez de excremento, se ha empleado —contadas ocasiones las principales áreas.

En contraste, en los trópicos, abundantes de insectos de Scarabaeinae, tanto en taxas, y la tendencia progresiva en los trópicos hacia los biomas abiertos, no forestales, por los Scarabaeinae, se ha sólo con poco menor se merece.

La colonización tróficas especiales en asociaciones muy de la pradera hacia un aumento de la.

La saprofagía al ataque a frutos que corresponde menos humificado.

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a pesar de la gran variedad de Scarabaeinae que viven en la selva tropical, ecológicamente el grupo no desempeña un papel tan significativo como en los pastizales. Sin embargo, no podemos dar un juicio definitivo hasta no efectuar más estudios ecológicos en la selva tropical. En este bioma es especialmente difícil la recolección y observación de Scaraba-
, y únicamente el uso de cebos dispuestos con un criterio ecológico puede dar una idea sobre la abundancia real. Este sistema de captura, se ha empleado —con excepción de los trabajos de los autores— en muy contadas ocasiones, y de ninguna manera de un modo general que cubra las principales áreas geográficas.

En contraste con los Geotrupini, que son predominantemente holár-
ticos, abundantes en los bosques templados, los Scarabaeinae son básic-
mente insectos de climas cálidos. Hay progresivamente menos Scaraba-
nae, tanto en taxa como en individuos, a medida que nos separamos de
los trópicos hacia los polos, y lo que es aún más importante, hay una
tendencia progresiva a estar cada vez más restringidos a los espacios
abiertos, no forestales, con mayor insolación. La invasión de los bosques
por los Scarabaeinae es por lo tanto un fenómeno tropical, que en grado
mucho menor se repite en los bosques templados.

La colonización de la selva tropical va acompañada de adaptaciones
tróficas especiales como son, una saprofagia secundaria, necrofagia, o
asociaciones muy especializadas, A su vez la invasión de los ecotonos
de la pradera hacia el desierto, o bien la desertización, va acompañada de
un aumento de la asociación con nidos. Consideramos estas adaptaciones.

La saprofagia secundaria envuelve en la mayor parte de los casos
el ataque a frutos maduros caídos, y se distingue de la saprofagia primaria,
que corresponde a la alimentación a base de detritos vegetales más o
menos humificados.

Ya se ha indicado (sección 2) que en cada caso en que se supone de
un género de Scarabaeinae que es primitivamente saprófago (Epilissus,
Odontoloma, Onthobius, Saphobius, Panelus, Aphengium y Bdelyrus)
faltan evidencias concluyentes. Por otra parte, diversos géneros encontrados
en la hojarasca de los bosques (Nesostrypheus, Canthochilum, Cantho-
ella, Opicanthon) han demostrado ser coprófagos cuando se han estudiado
correctamente.

Las especies saprófagas secundarias pertenecen a géneros coprófagos.
Así especies de Canthon, Deltochilum, Geocanthon, Peltecanthon, Mono-
plistes, Onthophagus y Canthidium y algunos otros, se han encontrado en frutos u otras partes de plantas superiores en fermentación; especies de Neocanthidium, Liatongus y Onthophagus en hongos. Los géneros antes mencionados son solamente aquellos que comprenden especies principal o exclusivamente saprófagas. Varios otros tienen especies que son ocasionalmente saprófagas.

Todos los ejemplos de Scarabaeinae parcial o totalmente estenotróficos, que se alimentan de frutos u otras partes de plantas superiores en fermentación, corresponden a la selva tropical. Como en el caso de la necrofagia, la adquisición de un nuevo régimen alimenticio es consecuencia de las características del bioma, especialmente la pobreza de excremento.

Ni la saprofagia, ni la necrofagia, están limitadas a un determinado grupo taxonómico. Se manifiestan de manera muy similar en muy diversos grupos, que llegan a estas especializaciones tróficas como resultado de una evolución paralela, respuesta a las mismas presiones selectivas.

La necrofagia es un fenómeno prácticamente exclusivo de la región Neotropical. Fuera de algunos Onthophagus de la India, los demás ejemplos de necrofagia no neotropical, corresponden a capturas totalmente ocasionales dentro de géneros coprófagos.

En la región Neotropical, existen numerosos casos de necrofagia en las tres tribus de Scarabaeinae que la habitan, pero especialmente en las dos dominantes: Scarabaeini y Coprini. Hasta el punto de que esta especialización trófica es una de las características distintivas y más importantes de la fauna neotropical de Scarabaeinae. No solamente los adultos utilizan los animales muertos (a veces con hábitos estrictamente estenotróficos), sino que también son empleados para la alimentación de la larva, fenómeno exclusivo de los Scarabaeinae neotropicales.

El desplazamiento, dentro de la región Neotropical, de la alimentación de los Scarabaeinae hacia la necrofagia, puede relacionarse con: a) La falta de grandes rebaños de mamíferos herbívoros desde la desaparición de las formas propias hasta la introducción de vacunos, ovinos y equinos por los europeos; b) El predominio de selva o formaciones boscosas, mayor que en cualquier otra región de la Tierra, con la sola excepción de Asia sudoriental; c) La escasez, en comparación con otros biomas y otras regiones, de grandes mamíferos dentro de la selva tropical sudamericana; d) La poca importancia de otros insectos necrófagos, como son los Silphi-dae, cuyo papel es extensivo en las regiones extratropicales. Entre los factores e'

La necrofagia, en la evolución filogenética, se ha desarrollado en paro ' o subtribus como el coprófago. La necrofagia se encuentra en las especies de estas adaptaciones tróficas son limitadas a la región neotropical, así como la saprofagia, especialmente la savana. La necrofagia en los géneros como Onthophagus, y ningún otro género tiene especies de este tipo (no se conocen ejemplos de Onthophagus, y no se conocen ejemplos de Onthophagus, ni de otros géneros de este tipo).

La mirmecofilia es más que la asociación con las hormigas, en particular las hormigas de la tribu Attini; e) La mirmecofilia es más que la asociación con las hormigas de la tribu Attini; y f) La mirmecofilia es más que la asociación con las hormigas de la tribu Attini.

En todos los casos, los Scarabaeinae que se alimentan de las formaciones boscosas de la selva tropical, son híbridos de los Scarabaeini y Coprini, y su alimentación de las hormigas (en forma de mirmecofilia) es ligado con este peculiar y distintivo hábito de la escasez, que se puede relacionar con los factores ambientales y las fuertes presiones selectivas, que estos factores desplazan a los Scarabaeinae hacia la necrofagia.
han encontrado varios géneros con adaptaciones específicas. Los géneros Scarabaeinae incluyen especies que se alimentan principalmente de excremento. Como en el caso de Silphidae, el excremento es consecuencia directa del comportamiento de las hormigas, que son un factor ecológico muy importante.

La necrofagia, en particular, es un factor evolutivo decisivo. Grupos enteros de esta familia tienen especies que son totalmente necrófagos. Varios géneros tienen especies exclusivamente necrófagas, como Canthon, Uroxys, Onthophagus, y muchos otros tienen especies necrocoprófagas. La mirmecofilia también aparece en un número apreciable de especies pertenecientes a diversos géneros, pero solamente un grupo supraspecífico —la subtribu Alloscelina de la tribu Scarabeini— es en su mayor parte o exclusivamente mirmecófilo.

En todos los casos en que se ha podido estudiar, la mirmecofilia de los Scarabaeinae trae consigo el consumo del detritus acumulado por las hormigas (en forma notable en las especies americanas asociadas con hormigas Attini); es por lo tanto una forma de saprofagia. Pero la mirmecofilia es más que una especialización alimenticia, ya que en ella influyen otros factores característicos del hormiguero como constancia del alimento, y estabilidad de humedad y temperatura. Estas características han modificado profundamente la nidificación de las especies más adaptadas a la mirmecofilia [v. gr. Liatongus monstrosus (Bates) y Onthophagus rufescens; Bates], que han perdido todo el complicado comportamiento ligado con este proceso. Lo que nos da una evidencia indirecta de hasta que punto la compleja nidificación de los Scarabaeinae es una respuesta a los factores ambientales que ocasionan la rápida desecación del alimento y las fuertes oscilaciones de temperatura y humedad. En el hormiguero, estos factores dejan de ser limitantes, y la nidificación desciende al nivel afdinoide.

A diferencia de la saprofagia y necrofagia, la mirmecofilia no parece ser una adaptación a las condiciones del bosque tropical. Por lo menos
en los casos de México que se han podido estudiar en detalle, representa una forma de sobrevivencia en condiciones más o menos áridas, con fuertes oscilaciones de temperatura, y largo periodo de secas. En el caso de Liatongus monstrosus, el hormiguero ha sido el refugio que ha permitido la permanencia de una especie relictica.

Otras dos adaptaciones, la depredación (sección 4) y la asociación con monos o ectocomensalismo (sección 5), están circunscritas a los trópicos americanos. En el último caso, las especies inodadas son los primeros Scarabaeinae en perder el contacto con el suelo, por lo menos en su estado adulto, ya que el estado larvario no se sabe si transcurre en una bola-nido dispuesta en las biocenosis arbóreas, o si acaso bajan a nidificar en el suelo, lo que parece poco probable.

La depredación en quizá la especialización alimenticia más notable (véase sección 4). Resumiendo, puede señalarse que durante el vuelo nupcial de Atta, Canthon virens Mannerheim ataca a machos y hembras. Si hay pocas hormigas, se concentrarán varios ejemplares sobre una misma hormiga; si hay muchas, cada Canthon ataca una hormiga. Si la hormiga es un macho, o una hembra no fecundada, el Canthon como su contenido. Si es hembra fecundada hace 2 o 3 bolas de nidificación con el contenido abdominal. El método de ataque utilizado por Canthon virens es el siguiente: se coloca encima de la hormiga, lo que consigue con mayor o menor dificultad, y con el clípeo —haciendo palanca— y algunas veces ayudándose con el borde externo dentado de las tibias que mueven de dentro hacia afuera —corta la cabeza de la hormiga. A continuación vacía el cuerpo, enterrando ligeramente el contenido y dejando los tegumentos limpios.

Otras adaptaciones de los Scarabaeinae al medio ambiente, que han causado divergencias radicales de los hábitos originales de vida en la pradera, son la colonización de nidos y cuevas.

Los nidos de vertebrados han sido un importante refugio de los Scarabaeinae en medios desérticos, pero también en las altas montañas, por lo menos en el México central. Las condiciones físicas relativamente constantes que prevalecen en los medios han permitido a muchas especies sobrevivir al proceso de desertización de la subregión convirtiéndose en nidícolas. Un fenómeno paralelo ha ocurrido en menor escala en Florida, evidentemente por diferentes razones ecológicas. Es significativo que en ambas áreas sean los mismos géneros los que estén inodados: Onthophagus y Copris, elementos de que (1964) ha designado la siguiente señal, que considera en los nidos de vertebrados como Onthophagini austriacus Onthophaginoidae verdaderamente Onthophagus. Las mismas adaptaciones pueden notarse en los Scarabaeinae y Onthophaginoidae, cuyos comportamientos son análogos a los de los de los nidos de vertebrados. Estos adaptaciones se pueden considerar como una adaptación a los biomas, especialmente en determinando adaptaciones al interior de los biomas, que entrarán de manera diferente en la historia de los Scarabaeinae.
En detalle, representa áridas, con fuerza seca. En el caso de un refugio que ha permitido
la asociación circunscritas a los nidos enodadas son los primeros vuelo, por lo menos en caso si transcurre en una pasional bajan a nidificar
mencionada más notable que durante el vuelo a machos y hembras sobre una misma hormiga. Si la hormiga como su contenido, la nida con el contenido del Onthophagus virens es el si-
ensemble — y algunas veces que mueven de den-
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la hormiga ambiente, que han
las altas montañas,

En México y Estados Unidos existen 10 especies conocidas de
Scarabaenae nidícolas, y 3 de Copris. El número de especies de Scaraba-
realmente cavernícolas se limita a dos, ambas del género On-

y Copris, elementos de la fauna original norteamericana, a la que Halffter
(1964) ha designado como Paleoamericana. Además es realmente intere-
sante señalar, que con excepción de algunas especies argentinas que viven
en los nidos de vizcacha (véase sección 7), todos los Scarabaenae aso-
ciados con nidos pertenecen a estos dos géneros, o al muy próximo de Onthophagini australiano Macropocoris. Copris y Onthophagius resaltan
cómo géneros muy antiguos y ampliamente distribuidos en el mundo. Además Onthophagius desarrolla una notable (posiblemente sin paralelo
en los Scarabaeinae) diversificación ecológica.

En México y Estados Unidos existen 10 especies conocidas de On-

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PARASITOLOGICAL AND ECONOMIC IMPORTANCE

31. SCARABAEINAE AS INTERMEDIATE HOSTS OF HELMINTHS

The role of Scarabaeinae as intermediate hosts of certain helminths is of more importance than is generally realized. The following examples give an idea — incomplete in our opinion — of the part played by these beetles in the life cycles of various parasitic worms, primarily Spiruroidea. Similar accounts have been published previously, notably in the Traité d’Helmintologie of Neveu-Lemaire (1936) — a classic source of information, which is simply repeated in later works, in the survey of Halfter (1959) and the monograph of Balthasar (1963), although in the latter work many data are omitted for some undetermined reason.

In the following account, the data which are mentioned without indication of source are from Neveu-Lemaire. Since this is a well known, classical textbook of parasitology, the data it contains may be considered to have been definitely incorporated into the literature. The taxonomic status of the helminths involved was verified in more recent works, such as Hyman (1951) and Lapage (1962).

One of the most striking facts which emerges from an analysis of the relationship between Scarabaeinae and helminths is the great variety of scarab species which can act as intermediate hosts of a given parasite in different geographical regions. For each species of helminth one or more of the scarabaeine species most common in the region will serve as host. We believe that the principal cause of the variation in intermediate hosts is the relatively restricted range of the scarabaeines in contrast to the very broad, nearly cosmopolitan ranges of the parasites.

Nevertheless, in spite of this great variation in hosts, which apparently does not follow any taxonomic lines (utilization of any special genus, subtribe, or tribe), the parasite must require some special conditions, since some very common species of scarabs are not cited as intermediate hosts. This may be due partly to an inadequate parasitological examination of Scarabaeinae, which has tended to concentrate on only a few well-studied species. Or it may be due to the fact that for a great many Spiruroidea, which from their taxonomic position could be found in Scarabaeinae, the intermediate host is not known. It may also be a real situation, due to the characteristics of the mouthparts and digestive system of the beetles. The works of Miller, cited further on, are of special interest in this regard.

The following is an incomplete account of the ways in which certain helminths utilize Scarabaeinae as intermediate hosts.

Raidletina cestoides (Cestoda, Cycloph) is an intermediate host of a certain wild galliform, and is found in the Ateuchus (cited as Ateuchus) and no Scarabaeinae are mentioned. The Aphodius Geotreptes seems to be the only species of these cestodes.

Rhabditis tritert (Cestoda, Cycloph) is found beneath the elytra and the species are not known. Various species of the genus tritert (according to Balthasar) are Ateuchus and two others of the same genus are known. There are many other species of these cestodes, which are not known to be found in Scarabaeinae.

Ascarops (= Ascaridae, Spiruroidea), a stomach worm, is found in the Aphodius Geotreptes, and hosts the scarabaeine species Ascaropsis nigriceps (as cited by Balthasar). The cestodes found in the Aphodius Geotreptes include the helminths mentioned above, and the cestodes Ascarops (cited as Ateuchus) are found in the Aphodius Geotreptes under the same conditions.

Spirura typhlonurus is an intermediate host of the scarabaeine species Onthophagus as a parasite, which is found in the Aphodius Geotreptes. It is also found in the Aphodius Geotreptes as a parasite of the scarabaeine species Onthophagus, but it is not a definitive host. We cannot tell whether it is a parasite of the scarabaeine species Onthophagus or an intermediate host.
IMPORTANCE OF HELMINTHS

The part played by these helminths, notably in the Traité classique source of works, in the survey of (1963), although in determined reason.

The following is an annotated list of the helminths known to infect coprophagous Scarabaeinae as intermediate hosts.

Raillietina cesticillus (Molin) and Hymenolepis carioca (Magalhaes) (Cestoda, Cyclophyllidea), parasites in the intestine of chickens and certain wild galliformes, have as an experimental intermediate host Ateuchus (cited as Choeridium) histeroides Weber. In Europe, however, no Scarabaeinae are cited as intermediate hosts; this role is played by Aphodius, Geotrupes, and other insects (Enigk and Sticinsky, 1959). The Aphodius seem to be of general importance in the transmission of these cestodes.

Rhabditis tretzeli Sachs (Nematoda, Ascaroidea) has been found beneath the elytra and in the folds of the intersegmental membrane of various species of Onthophagus. This seems to be a case of phoresy (according to Balthasar, 1963[1]:74). The same author cites this species and two others of the genus as occurring in Geotrupes and Aphodius, under the same conditions.

Ascarops (= Arduenna) strongylina (Rudolphi) (Nematoda, Spiruroidea), a stomach parasite of pig and wild boar, has as intermediate hosts the scarabaeines Onthophagus hecate (Pancer) and Paragymnopleurus sinuatus (Olivier), where it lives in the haemocoel. Recent citations of additional hosts are Trifonov (1963), who cites Caccobius schreberi (Linnaeus) and Sisyphus schaefferi (Linnaeus) as intermediate hosts in the Burgas district of Bulgaria, Balthasar (1963[1]:74) who adds Oniticellus to the above-mentioned genera, and, in America, Lahille (1930), who cites as intermediate hosts Phaneus (Phaneus) menelas Laporte (cited as Ph. splendidulus [Fabricius]).

Spirura rytipleurites (Deslongchamps) (Nematoda, Spiruroidea) has as definitive hosts cat, dog, fox, skunk, and hedgehog, in all of which it is found in the stomach. Beside cockroaches and various beetles, the scarabaeines Onthophagus sp. and Scarabaeus sacer Linnaeus serve as intermediate hosts.

1 In his monograph Balthasar does not indicate the source of the citations, hence we cannot tell whether they are original observations or, as seems more likely, literature data.
Spirocerca lupi (Rudolphi) (= S. sanguinolenta [Rudolphi]) (Nematoda, Spiruroidea), whose definitive hosts are dog, wolf, jackal, and fox, has various Scarabaeinae as intermediate hosts, as follows: Scarabaeus sacer Linnaeus, S. variolosus Fabricius, Gymnopleurus sturmi Mac Leay, Copris hispanus (Linnaeus), and Canthon sp., plus some other coprophagous insects and numerous amphibians, reptiles, birds, and mammals. Other records of scarabaeine hosts of this nematode, additional to those of Neveu-Lemaire cited above, are Paragymnopleurus sinuatus (Olivier) (Sado Ono, 1932, 1933, cited in Paulian, 1945:52), Phanaeus (Phanaeus) menelas Laporte (Martinez, 1959), and Sisyphus schaefferi (Linnaeus) (Balthasar, 1963[1]:75).

The following account of the life history of this nematode is taken from Neveu-Lemaire (1936:1216) and is very similar to that of other Spiruroidea found in Scarabaeinae.

The adult parasites are found in the definitive host in nodules located in the walls of the stomach and oesophagus, less frequently in the lymph nodes, lungs, bronchi, mediastinum, thoracic and abdominal cavities, and walls of the aorta. Larvae of the first three instars are found in Scarabaeinae; those of the third instar, when encapsulated, are found in the vertebrates which act as transport hosts.

The excrement of the definitive host contains eggs which are undergoing embryonic development; these eggs are ingested by the scarabs and hatch in the latter's digestive tract. The first-stage larva passes from the digestive tract to the body cavity, where the second-stage larva is also found. The latter does not undergo the second moult until it is encysted; the cyst results from the reaction of the host tissues, particularly the tracheal epithelium. The third-stage larva remains encysted until it passes to the definitive host. This explains the large number of animals — intermediates in the food chain from scarabs to canines — which carry the encysted third-stage larvae.

Physocelphalus sexalatus (Molin) (Nematoda, Spiruroidea) has as definitive hosts pig, wild boar, and peccary, less frequently donkey.

1 This is the only record of a Canthon (one of the dominant genera of the American coprofauna), and of the abundant subtribe Canthonina, serving as an intermediate host for a nematode. Aside from the inadequacy of the parasitological analysis, another reason for the absence of nematode records in Canthonina may have something to do with the microstructure of the triturating molar surface.
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1945:52), Phanaeus
and Sisyphus schaefferi

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hosts. The eggs, with developing embryos, are egested with the excrement; the Scarabaeinae become infected on eating this, whereupon the embryo develops into a larva which encysts in the body of the insect. The cycle is completed when the latter is eaten by the mammal host.

32. DESTRUCTION AND DISSEMINATION OF PARASITES

Aside from their importance as intermediate hosts for parasitic worms the role of Scarabaeinae in both the destruction and dissemination of parasites is probably equally important. The dispersal of many nematodes, protozoans, and bacteria which are parasites of man and domestic animals depends in the first place on the contamination of soil by excrement. Scarabaeinae are important both in causing the rapid disappearance of this excrement and in contributing to the dispersal of the infecting agents.

The following paragraph, taken from Hingston (1923:212), gives an idea of the magnitude of their role in India: "So far as I can estimate by rough observation, I believe that in certain active seasons of the year two-thirds of the excrement of this vast country must be carried by scarabs into the substance of the soil. Without their valuable aid the land would be an open sewer. Remember that it supports a teeming population of some 300 million souls. And, save for the few collected in the cities, the whole of this great multitude of people depends on the work of Nature's scavengers to clear its filth away.

I will not enter into numerical details, but, taking into account human ordure alone, I believe that in India during May and June as much as forty or fifty thousand tons of excrement must be carried by scarabs each day into the soil. And this does not include the dung of animals, which may easily double or treble this amount."

Various North American studies deal with the consumption and destruction of excrement by Scarabaeinae. Those with a parasitological orientation include that of L. O. Howard (1900:556), who cites the following Scarabaeinae among the fauna of human excrement in the United States: *Canthon pilularius* (Linnaeus) (cited as *C. laevis* Drury), *Onthophagus hecate* (Panzer), and *O. pennsylvanicus* Harold, and that of Wilson (1932), which deals with the relationship between coprophagous scarabs which feed on sheep dung in New Jersey and the transmission of worms.

But it is to detailed studies of the latter kind, and of the former in the southern United States, that all the Coleoptera of one species of *Canthon* (the genera of Scarabaeinae) by Miller clearly established traps situated in a burial pit. Miller buried 748 g of feces from four to six people, which weighed 18 to 102 mg; the excrement disappeared completely in a fact that human excrement in places where Scarabaeinae verify this report. Miller found that the is a radical difference in the surface between the dry season (when Scarabaeinae are scarabs depend on the year, the time, and the type of soil.

The burial and excrement by Scarabaeinae in the United States: *Canthon pilularius*, *Phanaeus vindex*, and *Phanaeus carolinus* (Linnaeus) have the idea of the quantity of excrement ingested (these experiments): the excreta were 80 mg and 55 mg; cons.
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OF PARASITES

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But it is to Miller and his collaborators that we owe the only
detailed studies of the relationships between Scarabaeinae and parasites,
and of the former’s role in causing the disappearance of human feces
in the southern United States. According to Miller (1954:372-388),
of all the Coleoptera collected in human fecal traps, 59% consisted of five
pecies of Canthon (in the broad sense), and seven species of five other
era of Scarabaeinae made up another 28%. Some more data given
by Miller clearly demonstrate the importance of Scarabaeinae: in three
aps situated in an area of 1,000 m², 361 scarabs were trapped; these
ured 748 g of feces in 24 hours, representing the daily defecation of
re to six people. In another instance, of 20 fecal deposits which
ighed 18 to 100 g, five disappeared in 2½ hours, and another five
disappeared completely or partially in seven hours. It is a widely observed
fact that human excrement remains on the surface much longer in those
aces where Scarabaeinae are scarce or absent. We have been able to
ify this repeatedly in Mexico, where even in the same locality there
is a radical difference in the time during which feces remain on the
urface between the rainy season (when scarabs are active) and they season (when the adults are not active).

According to Miller, the quantity of human feces which are buried
by scarabs depends on the species present in the region, the season of
the year, the time of day, the humidity, the propinquity of cow dung,
and the type of soil.

The burial and destruction of feces diminish the number of infective
orms of nematodes and other parasites. On the other hand, it is also
true that under certain conditions scarabs contribute to the parasites’
dispersal.

To determine what happens to enteric parasites consumed with
crement by Scarabaeinae, Miller, Chi-Rodríguez, and Nichols (1961)
formed a series of experiments with the following species in the
ited States: Canthon pilularius (Linnaeus) (cited as C. laevis Drury),
naeus vindex MacLeay, Ph. ignaeus MacLeay, and Dichotomius
olinus (Linnaeus) (cited as Pinomus). The following data give an
idea of the quantity of human excrement consumed by Canthon pilularius
(these experiments do not involve either rolling or burial, but simply
igestion): the excrement consumed in one hour varied between 36
 and 55 mg; consumption under natural conditions seems to be at least
50 mg and perhaps up to 150 mg per hour; the capacity of the alimentary tract of this species is calculated to be 100 mg of excrement.

Each scarab used in the experiments was given excrement contaminated with an artificially increased number of eggs and cysts. The parasites investigated were Ascaris lumbricoides, Necator americanus, Trichuris trichiura, Entamoeba coli, Endolimax nana, and Giardia lamblia. After an initial series of experiments it was concluded that Canthon destroys the eggs of all the helminths mentioned plus those of Taenia. Phanaeus and Dichotomius perhaps permit the passage of most Trichuris and a few eggs of Ascaris, but destroy or damage the majority of Necator and Ascaris eggs ingested.

In a second series of experiments the eggs of Necator were not found, and those of Ascaris only rarely, in the digestive tube and excrement of Canthon and Phanaeus. As for Dichotomius, all the specimens examined contained numerous eggs in the digestive tract; although these were devoid of the external albuminoid covering and many were broken, they could develop normally. These eggs were also found in the excrement of the scarab. The authors conclude that these observations indicate that practically all ingested Ascaris and hookworm eggs are regularly destroyed by Canthon and Phanaeus, but that many survive and are excreted by Canthon and Phanaeus [Dichotomius].

With regard to the part of the digestive tract in which the destruction takes place, Miller, Chi-Rodriguez, and Nichols (op. cit. 750) say: "Since eggs were not recovered in the pharynx or esophagus of Canthon and Phanaeus immediately after feeding, the mouth parts appeared to be responsible for egg destruction." This idea is further developed by Miller (1961) in a paper which appeared a month later, and which we will discuss below. As for the cysts of protozoans, especially Entamoeba coli, these authors conclude (op. cit. 752): "These results indicate that Canthon spp. destroyed almost all of the protozoan cysts which they ingested, while Phanaeus swallowed many in recognizable condition."

In summary, Miller, Chi-Rodriguez, and Nichols (op. cit. 753) come to the following conclusions: "The consistent absence or extreme rarity of eggs or cysts in the digestive tract and excrement of Canthon laevis and C. vigilans after the ingestion of amounts of feces that contained them in large numbers indicates that these species of beetles do not disseminate human hookworm, Ascaris or enteric protozoa through internal carriage and can be transport hosts with larvae from ingesting them.

"To the extent that hookworm eggs, these results indicate that the beetles' activities in the soil, particularly eggs in the soil at or near the surface, are not ordinarily found in the feces of man or his food, and do not constitute a likely source of contamination. Only the eggs of the smaller beetles, and those in the soil, constitute a likely source of the eggs in the experiments."

"To the extent that hookworm eggs, the net effect of the beetles' activities is to suppress the numbers of eggs, their infectivity of man, and their infectivity of the soil."

We have already seen that the potential of these in relation to the dissemination of eggs in Dichotomius is involved in the distribution of large areas of the mandible, consisting of parallel
of the alimentary tract; although these and many were broken, they were found in the excreta, and these observations indicate that many survive ingestion and could be excreted in viable condition. There is some evidence that Trichuris eggs can pass through both Phanaeus and Pinotus but not through Canthon."

"To the extent that dung beetles destroy ingested Ascaris and hookworm eggs, they diminish the number of these eggs in the soil. The beetles’ activities, however, also involve the transport of undigested eggs in the soil by their burrowing and burying activities, promote the soil at or near the site of stool deposition. Since the beetles ordinarily are found only outdoors and have no propensity to alight on man or his food, organisms carried externally on the beetles do not constitute a likely source of direct infection for human beings. While contaminated beetles may fly considerable distances, it is doubtful that the numbers of eggs disseminated in this way are of any epidemiological significance. Destruction of eggs by the beetles supplements the removal of Ascaris eggs from the surface of the soil and thus further reduces chances of man’s infection from this source. However, experimental evidence at hand indicates that the beetles, by distributing uningested eggs in the soil by their burrowing and burying activities, promote rather than suppress the development of hookworm larvae around the site where a stool is deposited. Thus, despite the destruction of ingested eggs, the net effect by beetle activity is to increase the potential hookworm infectivity of defecation areas."

We have already mentioned that the destruction of eggs and cysts is attributed to the mouth parts. Miller (1961) examined the microstructure of these in relation to chewing function, and explained the survival of eggs in Dichoromius by the characteristics of the molar surface, which is involved in the disintegration and grading of the food. The molar areas of the mandibles form an extremely efficient triturating surface consisting of parallel ridge lobes.
Each of the ridge lobes is a microscopic grinding, rubbing, or triturating instrument, here termed a "tritor". The tritors are specialized cuticular structures which extend at right angles to the direction in which the molar area moves. Their position and structural characteristics are perfectly fitted to their function. They combine strength and firmness with a degree of flexibility, collectively constitute the entire molar surface, and act as a multitude of stiff scrapers. Food squeezed into a thin film and rubbed between the two closely apposed molar areas is thoroughly triturated by thousands of these minute scrapers acting in unison against those of the opposite mandible. The efficiency of the grinding action is attested to by the destruction of particles as small as helminth eggs and perhaps even protozoan cysts. In this regard, the size of the tritors relative to such eggs and cysts is significant." (Miller, op. cit.: 736-737).

Dichotomius carolinus has fewer and larger tritors than Phanaeus or Canthon, hence its molar surface is less fine and less efficient.

In view of this destruction of parasite eggs, how is it that scarabs become infected with the Spiruroidea for which they act as intermediate hosts? According to Miller (op. cit.: 741):

"The eggs of spirurids for which dung beetles serve as hosts range from 30 by 11 to 59 by 34 microns, the shells are "thick" (3 microns), and each contains a larva when passed in the vertebrate host's feaces which does not hatch until ingested by the arthropod host. The eggs of cestodes known to undergo larval development in the beetles range from 60 by 45 to 88 microns in diameter, have thick envelopes surrounding the smaller onchospheres, and may be enclosed in the adult proglottid when passed by the vertebrate host (Sprehn, 1932). It seems doubtful that the size of these eggs would make them immune to the grinding action of dung beetle mandibles that destroys ascaris and hookworm eggs which are of similar or only slightly larger dimensions. They or the contained larvae must be adapted in some way to withstand mechanical destruction when ingested, perhaps by a resiliency of the walls different from that of the human parasite eggs, or by additional protective coverings around the egg mass. Probably many are, in fact, destroyed during ingestion, while others may be assisted to hatch by the grinding action of the mandibles. Since spirurid eggs are large among the arthropod parasites and harm the vertebrate host in the event of ingestion, the victor

The case for the destruction of spirurid eggs by the mandibles of scarabs calls for further investigation, especially in those of the Choristodera and Cerothriatae, which have been observed in Canthon in which spirurid infestation is a common condition of the gut. In Canthon, the mandibles of the beetle are of considerable size and have a few large teeth, which may be well adapted for the destruction of helminth eggs and cysts. In our opinion, the spirurid eggs which are large among the arthropod parasites and harm the vertebrate host in the event of ingestion, the victor

In Section 6 of the paper, phagin as endoparasites in occasional cases of occasional parasitism and not an habitual one.

34. In Section 6 of the paper, phagin as endoparasites in occasional cases of occasional parasitism and not an habitual one.

33. In Section 6 of the paper, phagin as endoparasites in occasional cases of occasional parasitism and not an habitual one.

32. In Section 6 of the paper, phagin as endoparasites in occasional cases of occasional parasitism and not an habitual one.

31. This is one of the interesting facts about the digestive system of dung beetles.
topic grinding, rubbing, triturating. The tritors are located at right angles to the mandibles. Their position and arrangement are significant to their function. They are utilized in the collection and rubbing of food materials. They act as a multitude of small, rubbing surfaces, evenly rubbing food against those surfaces. The tritor is a file-like structure. In unison against those surfaces, the tritors are thoroughly triturated. They are small as compared to the size of the tritor. The tritor is like a file, rubbing the surface of flexibility, collection, and rubbing as a multitude of small files. In unison, they act as a file against those surfaces. The size of the tritor is significant. (Miller, op. cit.)

Scarabs are often more efficient than Phanaeus and less efficient. How is it that scarabs act as intermediate hosts for such parasites as the hookworm? The occurrence of spirurids in the digestive tract of dung beetles, such as Scarabaeus, suggests that species of dung beetles, in the adult stage, may also differ in susceptibility to spirurid and cestode infection in accordance with the grinding efficiency of the mandibles. In the species that have been experimentally infected, mastication may be less efficient than in Canthom because the mandibles are small (Aphodius, Ataneius, Choeridium) or less specialized (Geotrupes). The occurrence of spirurids in the large dung beetles could also be the result of ingestion of eggs by these species during their larval stage. Mandibular action may be less efficient in the larva than in the adult.

In our opinion there can be little doubt that the larval mandibles are far less efficient in grinding than the adult ones, being capable only of chopping up the food into relatively coarse particles (see Appendix I). The spirurids may thus infect the beetles principally during the latter's larval stages.

33. SCARABAEINAES AS HUMAN PARASITES

In Section 6 of this work we referred to the role of some Onthophagin as endoparasites of man in India. No doubt these only represent occasional parasitism, resulting from very unhygienic conditions, and not an habitual, or even frequent, type of association.

34. INFLUENCE IN THE CONTROL OF DIPTERA

On burying or dispersing excrement Scarabaeinaes modify the conditions of the medium used for the development of various Diptera, many of which are health hazards, even serious ones, for man and especially for domestic cattle. In much of the world Scarabaeinaes play an important part in the control of these flies under natural conditions. This is one of the important reasons for protecting these scarabs against
the indiscriminate application of insecticides, now so prevalent in some agricultural and grazing areas.

In some parts of the world, such as Australia and some islands, there are few or no native Scarabaeinae adapted to live in pastures. This fact was unimportant when there were no large herds of herbivorous mammals in these areas, but after the introduction of cattle by man a serious problem arose with the creation of conditions favorable for certain dung-breeding flies (native or introduced). In some places attempts were made to solve this problem by introducing Scarabaeinae.

Thus, in Puerto Rico, *Haematobia serrata* Desv., introduced during the early years of this century, is a serious problem in the drier parts of the island. According to Wolcott (1922), the rains which abound in most of the island render the excrement too humid for the development of this fly. In the south, however, which is generally drier, the fly breeds abundantly during the relatively wet season because, during the dry season, *Aphodius lividus* (Olivier) and *Ataenius stercorator* (Fabricius) are numerous and create unfavorable conditions for the fly.

Wolcott (op. cit.) reports that in order to try to control this pest, 146 specimens of *Boreocanthon* (cited as *Canthon*) *ebenos* (Say), *Canthon pilularius* (Linnaeus) (cited as *laevis* Drury), and *Ateuchus* (cited as *Choeridium*) *lecontei* (Harold) were introduced from Texas during the second decade of this century. Furthermore, about 100 *Nesocanthon* (cited as *Canthon*) *violaceus* (Olivier) were introduced from Santo Domingo, and eight specimens of *Dichotomius* (cited as *Pinotus*) *carolinus* (Linnaeus) were introduced from Illinois. After their release in the field no trace of these scarabs was ever seen again.

There is no doubt that for a program of introduction to be successful it is necessary to choose not only the species but also the area from which the specimens are to be taken, in order to introduce the proper ecotypes. None of the species released in Puerto Rico, except perhaps *Nesocanthon violaceus*, seem to have been selected with this in mind.

According to Howden and Cartwright (1963:26), *Onthophagus incensus* Say was taken to Hawaii by H. T. Osborn in 1923 from Mexico, to aid in the control of the horn fly *Siphona irritans* (Linnaeus). This species was recovered on the island of Hawaii in 1934 and on Oahu in 1940.

Copris incertus from Veracruz at the "Mexican Dung Bee" in a collection on 19 in Moloka'i on 22, 1930, it was deliberate up in collections on 1939 (apparently naturally recorded in 1939. In slower, it is not recorded in the Proceeding the above data were become extraordinarily islands of the Hawa 1958, cited in Thomas established on some it plays a part in the Thomas (1960) *Copris* into New Zealand also for the control of Johnston and Harker desired success, since and reproduce under no evidence of *Canthon humo at the same time that Onthophagus catta* introduced later, at

55.

The easily ob ticularly in pasture not been the subject by experimental ve Lindquist (1958) burying the dung.
Soil Conditioning by Scarabaeinae

The easily observable edaphic relationships of Scarabaeinae, particularly in pastures which maintain large herds of herbivores, have not been the subject of any really thorough quantitative studies supported by experimental verification.

Lindquist (1933) indicates that Scarabaeinae fertilize the soil by burying the dung, which they do not totally consume, by depositing...
their own excrement, which often remains in quantity in the burrows, and by overturning the soil when they bring it to the surface during the construction of their nests.

In this work Lindquist presents some quantitative data concerning the Coprini of Kansas. *Dichotomius carolinus* (Linnaeus) buries 6.2 to 130.5 g (averaging 48.5 g) of dung per nest (the nests may contain one or two individuals), and the quantity of soil excavated varies between 70.8 to 1,220.9 g (averaging 287.1 g). In September there is an average of 200 nests per acre, in which 21 lbs dry weight of dung is buried per acre and 126 lbs of earth are brought up (average values). It must be borne in mind that these quantities correspond to a limited period, and that the activity period of Scarabaeinae in Kansas includes the spring, summer, and early autumn. For *Copris...*(cited as *tullius* Olivier), Lindquist estimates the average amount of buried dung per nest as 7.26 g and soil excavated as 36.88 g; the density of nests per acre averages 180. For two species of *Phanaeus* considered together, Lindquist gives the following averages per nest: dung buried 9.62 g, soil excavated 93.4 g.

In these same pastures there are, in addition to the four species of Coprini mentioned, two species of *Onthophagus* — *O. pennsylvanicus* Harold and *hecate* (Panzer) — whose nests are found beneath 76% of the dung mounds, with an average of 11.2 dung deposits per mound (averaging 0.26 g per deposit). Finally, there are various species of *Canthon*, which are primarily responsible for the disappearance of dung from pastures in many parts of North America, and which are not considered by Lindquist.

We do not have any data on the number of nests made by each species during its active period, nor any on population density per unit of surface area. Therefore in spite of Lindquist’s data it is impossible to calculate the amount of dung buried and soil excavated per unit of time and space. However, these preliminary observations do confirm the fact that enormous quantities of dung are buried and even larger quantities of soil are excavated, and there is no doubt that scarabaeine activity has a significant conditioning and aerating effect on the soil.

In another work Lindquist (1935:8-9) points out that the species primarily responsible for the disappearance of dung in southwest Texas are *Canthon pilularius* (Linnaeus), *Phanaeus triangularis* (Say), and *Dichotomius carolinus* (Linnaeus). These scarabs destroy a large quantity of excrement, especially in the rainy season.

Teichert (1959) and Bornemisza (1966) consider Scarabaeidae in relation to the *Onthophagini*, and he indicates the quantities of dung of Scarabaeinae, quantitatively of *mopsus* Pallas to 300 g. This quantity are greatly exceeded by more than 500 g per nest. Thus in *C. pilularius* much more excrement is used.

Bornemisza (1966) points out that the excreta are incorporated in the soil after the pasture; in two tables excreta and compares the results, and indicates the very favorable for the production of soil. In another work (1967) he indicates the quantities of Scarabaeinae, quantitatively of *mopsus* Pallas to 300 g. This quantity are greatly exceeded by more than 500 g per nest. Thus in *C. pilularius* much more excrement is used.

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Teichert (1959) analyzes the relative importance of various Scarabaeidae in relation to the burial of dung in Central Europe. In a table he indicates the quantity of excrement buried per nest for eight species of Scarabaeinae, quantities which vary from 15.9 g in Gymnopleurus mopsus Pallas to 300 g for Copris lunaris (Linnaeus). These values are greatly exceeded by the Geotrupini: three species of the latter bury more than 500 g per nest and Geotrupes spiniger Mars. buries 725 g per nest. Thus in Central Europe the Geotrupini bury comparatively much more excrement per nest.

Bornemissza (1960) notes that in Australia, "On the majority of farms the excreta from grazing animals is the only return of nutrients to the pasture"; in two tables he analyzes the potential nutrient value of these excreta and compares them with various artificial fertilizers — with results very favorable for the dung.

"The extent of this return can be judged from the fact that domesticated animals in Australia void approximately 33 million tons of dung (dry weight) annually. However, this potential is not sufficiently exploited in Australia. Here, the dung remains on the surface, and becomes hard and dry. In this way much of its nutritive value is lost. This is due mainly to the absence of coprophagous insects which in many other countries (where domesticated animals are indigenous) bury the dung and hasten its decomposition."

With regard to the harmful effects of the prolonged presence of dung on the surface, Bornemissza says:

"In many ways the prolonged presence of dung has an effect on the pasture somewhat like a noxious weed ... the area covered by the pad is quite substantial ... Grass growth is prevented on the area covered, and a further loss results from the zone of rank growth around the pads which is not grazed by cattle for at least a year. Weed growth is also encouraged. In this way each pad causes the loss of an average area of 465 sq. in. As the average number of pads dropped by adult cattle per day is 10, a minimum of 365 sq. yd. of pasture or approximately 7.5 per cent of an acre is covered by dung from one cow annually. Taking the impalatable rank growth also into account, five cows would decrease the effective area of pasture by one acre over a period of one year ... the mechanical dispersion of cattle pads in pastures ... is of limited
value, unless carried out immediately after cattle have been removed from the paddock. Even so, the accumulation of organic debris on the surface cannot be prevented by harrowing alone and a rise in soil acidity can be expected."

Bornemissza calculates the annual loss to the Australian dairy industry due to the persistence of dung on the surface at £2,500,000. This sum is based on the estimate that 300,000 acres of land area are lost to grazing annually because of accumulated excrement. To the above-mentioned sum must be added the losses to the meat and wool industries.

Bornemissza (op. cit.: 56) believes that it is indispensable to introduce Scarabaeinae into Australia: "If these beetles become numerous in Australia, the following benefits could accrue:

- The rapid incorporation of dung into the soil during the warmer months of the year.
- Improved retention of volatile nitrogenous and other constituents of dung in the soil.
- Accelerated decomposition of the dung as a result of digestion by the beetle and its larvae.
- Reduced accessibility to sheep and cattle of the infective stages of parasitic worms.
- A reduction of breeding habitats for the buffalo fly, bush fly and house fly.
- An improvement in the friability, water permeability, and water holding capacity of the soil."

The conditions described by Bornemissza for Australia are repeated on many islands where there are no indigenous Scarabaeinae, or where they are few or absent in pastures. The introduction of cattle by man has undoubtedly created serious ecological problems, since the pastures (nearly all artificial) of these islands are receiving an influx of excrement which cannot be disposed of in the manner normal for pastures which have supported large herbivorous mammal herds in the past — that is, through the activity of Scarabaeinae. The result is an immobilization of quantities of nutrients and a consequent slowing down of the normal nutrient cycle in these biomes.

Bornemissza has pointed out the harmful effects of the persistence of dung on the surface and the advantages which may accrue from the introduction of Scarabaeinae to the world where there are distinct dry seasons, during this dry season the dung on the surface. But unlike passing through a period of dry seasons, causes by the absence of dung on the surface of the phenomencal is only self-imposed by biological activity, and not by the soil and insular pastures process.

The introduction of Scarabaeinae size from the vast extent of islands is thus highly necessary from ecological studies. In the determination what influence the fauna, particularly what influence seriously from the community.

The species which the uncertainty that they are the ecological factors of both the can be analyzed, and other the individual scarab productivity potential, the preferences, the places ecologically, to place, in order to bring of the area for survival in the area and wider areas. Thus we to even further, choose from precipitate introduction.

It must be borne in mind include various species according to their ecological behavior. For instance, the one or two species of L.
nal), plus an equivalent number of nocturnal forms, and two or three species of small size (including of course some Onthophagus). A similar composition is to be seen in most scarabaeine faunas established in areas with abundant excrement, and something of the sort must be achieved if it is desired to create a coprophagous fauna which will bring about the rapid removal of excrement. This will not be achieved with one or two species, or with an excess of either Coprini or Scarabaeini and the resulting competition due to similarities of behavior. We have emphasized that the burial in the vicinity of the dung source seen in Coprini, and the ball-rolling behavior typical of Scarabaeini, are types of behavior which materially reduce the competition between the species of the two tribes and hence permit the presence of more species in an area, and the faster utilization of the excrement. The presence of both diurnal and nocturnal forms, and perhaps also of species active at different times of day, probably also reduces competition, although to a lesser extent since the nests (of Coprini, etc.) accumulate in the proximity of the dung mound. All these factors must be taken into account on planning the introduction of a coprophagous fauna.

36. Forensic Medical Aspects

Some works (e.g. Pessoa and Lane, 1941) have greatly exaggerated the importance of Scarabaeinae in forensic medicine. Although we suppose that scarabaeines do come to large cadavers of the size of a human corpse (at least in the Neotropical region), we have no observations to confirm this. Such evidence as we have indicates a preference for small dead animals; the largest cadaver to which Scarabaeinae have definitely been recorded to come was that of a medium-sized dog. Furthermore, even if Scarabaeinae should be encountered with a human corpse, we know practically nothing about the sequence of arrival and the time remained with the cadaver in order to provide the necessary precise medico-legal information. Even when we finally obtain this information, which we are a long way from possessing, it will be of very limited usefulness because of the geographically limited distribution of the Scarabaeinae involved and the often profound differences in biology even between closely related species. In any case, there are now well established and far superior methods of determining the age of a cadaver.
37. SCARABAEINAE AS HUMAN FOOD

According to C. C. Ghosh (1924:403, cited in Arrow, 1931:89 and Paulian, 1943:351), in the Shan States of Burma there are extensive hunts by the human inhabitants for pupae of *Heliocopris bucephalus* (Fabricius) in the months of March to May. These pupae or "shwe-po" are considered to be a delicacy; they are found inside the hollow mud balls which are the remains of the original brood ball.
APPENDIX I

MORPHOLOGICAL ADAPTATIONS FOR COPROPHAGY IN THE ADULT AND LARVA

The morphological adaptations for coprophagy in the adult concern the mouthparts and digestive tract almost entirely. Other features of the body which are adaptations for digging, such as the flattened head, powerful legs and compact shape, and hidden abdominal spiracles, are shared by other laparosticts or other Scarabaeidae which are not coprophagous. In the larva of Scarabaeinae, there are several important external adaptations, not for coprophagy as such, but for living inside an enclosed spherical space. These adaptations have been discussed in Section 27. Internally, the larval adaptations for coprophagy are to be found only in the digestive tract.

Since the food of the larva and adult Scarabaeinae is basically the same, or even identical, in all known cases, it is surprising to find that there are important differences between larva and adult in both the mouthparts and digestive tract.

Larval mouthparts have been described for species of several common genera of Scarabaeinae and provide important taxonomic characters, but from the functional aspect they seem to be always basically the same, and are of the typical chewing type (fig. 40). The labrum epipharynx (Lbr) is fleshy and bears on its inner surface some spinelike projections, apparently for rasping, and some sensory hairs. The mandibles (Md) are powerful, with cutting scissorial lobes and crushing molar areas (ma). The tongue-like hypopharynx (Hp) is musculated and bears on its upper (anterior) surface some asymmetrical tooth-like sclerites (hypopharyngeal sclerites – hps – or oncyli); the maxillae (Mx) have toothed galeae (g) and laciniae (l) which are separate and apparently also have a chewing or crushing function. There is a minimum of sensory hairs on the mouthparts, these being mostly concentrated on the labium and the laciniae. The laciniae work closely with the tips of the mandibles on the inside, and the epipharynx applies against the mandibles on the outside. The relative positions of the parts when in place are indicated on the right side of fig. 40, which represents the head of a Phanaeus larva dissected for this study. The general effect of these mouthparts must be to chew and crush solid food, and produce relatively coarse particles for ingestion, a
Fig. 40. Lateral view of head of larva of Phanaeus sp., probably quadridens Say, showing natural positions of mouthparts in middle and on right side with left mouthparts removed. Middle parts also shown separately. Dotted lines in head indicate position of the subfamily. V-shaped individual parts are removed. (Lbr) is a complete head. Hips (hps) is a completely membranous part, which is toothed or felt with an insensible surface. The adult mouthparts are uniform, as far as we can see, for the subfamily. V-shaped individual parts are removed. The subfamily. V-shaped individual parts are removed.

We must consider the gut contents containing the food media. The fact that the adult mouthparts are uniform, as far as we can see, for the subfamily. V-shaped individual parts are removed. The subfamily. V-shaped individual parts are removed. The subfamily. V-shaped individual parts are removed. The subfamily. V-shaped individual parts are removed. The subfamily. V-shaped individual parts are removed.
supposition borne out by the nature of the gut contents of the larva dissected.

The adult mouthparts of all known Scarabaeinae are fundamentally uniform, as far as we know, and represent one of the basic characteristics of the subfamily. While following the usual mandibulate plan, the individual parts are remarkably modified (fig. 41). The labrum-epipharynx (Lbr) is a completely membranous flap very densely covered with sensory hairs. In close contact with the epipharynx are the scissorial (or incisor) lobes of the mandibles (Md), likewise membranous and densely covered with hairs. The molar areas (ma) of the mandibles, well separated from the scissorial lobes, each have a band of very fine ridges which work against each other. These ridges may be easily seen under the microscope and felt with an instrument. The microscopic structure of this molar surface was studied in some United States species of Canthon, Dichotomius, and Phanaeus by Miller (1961), who found it to consist of a close-set series of microscopic scrapers, capable of triturating food particles down to a few microns in size. The hypopharynx (Hp) is also membranous and bears anteriorly four membranous lobes, similar to the scissorial lobes of the mandibles but smaller. These are presumably modified hypopharyngeal sclerites (hps). The galea (g) and lacinia (l) of the maxilla (Mx) are likewise membranous, and densely covered with hairs. In sum, every part which is toothed or crushing in the larva is soft and sensory in the adult (except the molar areas of the mandibles) and evidently the mouthparts as a whole must have an extraordinary ability to taste, sort, and screen very small particles, down to the size of bacteria. The molar areas are then capable of finely grinding these very small particles. The resulting gut contents contain particles in suspension varying from less than two (Onthophagus) to 16 (Dichotomius) microns in diameter (Miller, 1961: 738).

We must conclude that although the larva and adult eat the same gross food, the portions of it that they utilize are very different, the adult feeding on the liquid and colloidal content (microorganisms and undigested food molecules) and the larva feeding mainly on the solid content (undigested food particles). This undoubtedly correlates with the fact that the adult feeds on more or less fresh dung and carrion, while the larva must feed on the same original supply of food for weeks or sometimes months on end, after which time the original biochemical content of the food must become greatly altered, probably with a great reduction in microbial content as the food partially dries out.

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The hidden mouthparts (epipharynx, mandibles, hypopharynx, laciniae, galeae) of many Scarabaeinae have not been examined, and we cannot be sure that some primitive forms do not retain more sclerotized parts. Among the other subfamilies of dung beetles, we find similar membranous adult mouthparts only in the coprophagous Aphodiinae, which have mouthparts remarkably similar to those of Scarabaeinae, with membranous and sensory labrum, mandible, hypopharynx, lacinia, and galea (Landin, 1961). Only the degree of modification appears to be less extreme. Since the more primitive Aphodiinae (e.g. Aegialia) have completely sclerotized mandibles, labrum, and maxillae (Landin, 1960), we must assume that the membranous mouthparts of coprophagous aphodiines such as Aphodius, Oxymus, etc. were independently evolved within the subfamily Aphodiinae in response to coprophagous habits. Similarity to Scarabaeinae is therefore convergent. Geotrupinae have far less membranous mouthparts in the few cases examined, and must therefore be considered to be less adapted for coprophagy than either of the other two subfamilies.

The digestive tract opens just behind the molar areas of the mandibles in both adult and larva (fig. 40) and again we find important differences between the two. There are very few studies of the digestive tract of scarabaeines, either larval or adult. The larval intestine of Scarabaeus is illustrated by von Lengerken (1954:281) from Fabre's description and sketch, but no new dissection seems to have been made to verify it. The larval intestine of Gymnopleurus geoffroyi Füessly and Sisyphus schaefferi (Linnaeus) was studied by Prasse (1957c), and that of Canthon pilularius (Linnaeus) by Rapp (1947) in relation to the gastric caeca. A larva of Phanaeus sp. probably quadridens Say was dissected for the present study (fig. 42) and one of Canthochilum n. sp. was studied by rendering the cuticle transparent so that the dung-filled intestine shone through (fig. 43). In all these species the larval intestine consists of a coiled tube of fairly large diameter. There are no gastric caeca on the mid gut, but Prasse describes a sort of “appendix” issuing from the hind gut of Gymnopleurus (fig. 44). The fore gut is very short, but both middle and hind guts are elongated. The Malpighian tubules are closely applied to the anterior portion of the hind gut of Phanaeus (fig. 42, Mt), but neither their number nor their point of insertion could be discerned. The degree of coiling of the mid and hind guts varies greatly in the different genera studied. The mid gut of Phanaeus (fig. 42) is far less coiled than that of the Scarabaeini studied (figs. 43 and 44) and is

Fig. 42. Larva of Phanaeus sp. of intestine, ma — mala, my — mycophorum.
Fig. 43. Larva of Canthon pilularius of intestine. Apparent dotted cross line. (Original. geoffroyi (Füessly).) ds — dorsal sac made.
of the digestive tract has been examined, and we find a greater sclerotization in the hypopharynx, labrum, and corona. We also find similar membranes in Aphodiinae, with membranous corona, lacinia, and galea. In comparison with Phanaeus and similar Aphodiinae, which appear to be less exophagous, the larvae of Aegialia have complex alimentary canals (Landin, 1960). We must therefore be inclined to the view that aphodiines have far less membranous digestive membranes than either of the other two groups.

In larval areas of the mandible we find important differences in the digestive tract; particularly in the larval intestine of Scarabaeinae, where the tubules have been made to verify the descriptions from Fabre's descriptions (1867). From Puesly's work (1867) we find that the larval intestine of Phanaeus (fig. 42) appears to be less exophagous than the larval intestine of Scarabaeinae. There are no gastric tubules or "appendix" issuing from the gut. The insect gut is very short.

Malpighian tubules are found only at the posterior end of the larval intestine of Phanaeus (fig. 43). The position of the tubules varies greatly, and is often obscured by the larval cuticle. The digestive system of Phanaeus (fig. 42) is far less complex than that of Canthochilum (fig. 43) and is similar to that of Gymnosoma (fig. 44). The larval intestine of Gymnosoma (fig. 44) is divided into three distinct regions: the midgut, hindgut, and dorsal sac. The midgut is long and narrow, while the hindgut is short and wide. The dorsal sac is made of fused loops of midgut. (From Prasse, 1957c)
therefore much shorter, being only half as long as the hind gut — possibly a primitive feature. That of Gymnoplectrus is not only extraordinarily coiled (fig. 44), but a portion of the mid gut which is bent in a U shape forms a sac (ds), since the walls between the two closely applied loops of the U have disappeared (Prasse, 1957c). This does not seem to occur in Canthochilum, which however was not dissected (fig. 43).

The entire intestine is 1.5 times as long as the body in the larva of Phanaeus sp., twice as long in Canthon pilularius (Linnaeus) (Rapp. 1947) and Canthochilum n. sp., and three times as long in Gymnoplectrus geoffroyi Füssly (Prasse, 1957c:1036, estimated from figure) and probably also Sisyphus schaefferi (Linnaeus). Since the larvae of phytophagous scarabs have an intestine which is 1.3-1.8 times as long as the body (Areekul, 1957), it seems likely that the shorter intestine represents a less specialized condition. Areekul's (1957:576) reasoning is the opposite of that adopted here. He believes the long, caecum-less intestine of Canthon is the most generalized of the family, apparently because of the position of the subfamily Scarabaeinae (= Coprinae) in Leng's Catalogue, where it comes first as the supposedly most generalized and therefore primitive group. Our belief is that, whereas the Scarabaeinae may be generalized in certain external features of the adult, the organs which have to do with feeding and digestion are highly specialized for coprophagy.

In many phytophagous scarabaeid larvae there is a dilated portion of the hind gut (the "fermentation chamber") in which bacterial fermentation of cellulose occurs. Since the scarabaeine larva similarly has an enlarged portion of the hind gut (figs. 42 and 43), the question arises as to whether this may also house bacteria to digest the cellulose in the dung of herbivorous mammals. We know of no investigations of this matter in the subfamily. The enlarged portion of the hind gut does at least serve to store large quantities of larval excrement, used for repairing the brood ball (Section 27).

The adult intestine has been examined in only two species: Phanaeus vindex MacLeay (Becton, 1930) and Canthon pilularius (Linnaeus) (Miller, 1961). The latter author also made comparisons with Dichatomitus carolinus (Linnaeus). The general aspect of the adult intestine may be seen in figs 45-47, which show no fundamental difference between even such remotely related genera as Phanaeus and Canthon. The intestine is simple, tubular, and of uniformly small diameter. There is no crop,
The hind gut — possibly not only extraordinarily long but bent in a U shape — is closely applied loops does not seem to occur (fig. 43).

The body in the larva of Phanaeus (Linnaeus) (Rapp. long in Gymnopleurus (fig. from figure)) and probably the larvae of phytotrophic times as long as the inner intestine represents apparently because of apparently because of caecum-less intestine (phaeinae) in Leng's Ca­nostae generalized and whereas the Scarabaeinae as the adult, the organs are quite highly specialized for the question arises as cellulose in the dung repair or repairing the brood dung does at least serve the foregut.

In two species: Phanaeus parallelus (Linnaeus) in the Scarabaeinae with Dichoto­mesia, the adult intestine may the problem of molar areas of mandibles: Mt — Malpighian tubules; oe — oesophagus; ph — pharynx; thv — thoracic ventriculus of mid gut. (Fig. 45 from Becton, 1930; figs. 46 y 47 from Miller, 1961)
gizzard, or caeca, and both cardiac and pyloric valves are simple folds. The fore gut is straight and short, while the mid gut is extremely long and coiled in nine rings in both species. The mid gut is densely covered with small crypts or papillae (represented by dots in the figures). These are not connected to the lumen of the intestine (Becton, 1930) and consist of epithelial replacement cells (Miller, 1961). There are four very long Malpighian tubules (Mt) in both species, and the simple hind gut is coiled twice. The entire digestive tract is eight times as long as the body in *Phanaeus vindex*, 10 times as long in *Canthon pilularius* and *Dichotomius carolinus*.

When feeding undisturbed, the beetle passes the finely comminuted, paste-like food steadily through the digestive tract, egesting it continuously as a coiled, dark brown strand wrapped in the peritrophic membrane.

There can be no doubt that the extraordinarily long and coiled, simple intestine is an adaptation not to coprophagy as such (since the larval intestine is not so long), but to the special type of microphagous coprophagy of the adult beetle. This type of intestine evidently serves also (secondarily) for microphagous necrophagy and saprophagy.
valves are simple folds. The hind gut is extremely long and densely covered with glands (see figs. in the figures). These glands (Becton, 1930) and con-tinuous. There are four very small and the simple hind gut is eight times as long as the foregut. Canthon pilularius and is the finely comminuted material, egesting it continuously through a peritrophic membrane, is ordinarily long and coiled. Canthon pilularius is extremely long and coiled. The gut is as such (since the normal type of microphagous scarabaeine serves mainly in coprophagy and saprophagy.

APPENDIX II

MODIFICATIONS OF THE FEMALE REPRODUCTIVE SYSTEM

One of the most unusual adaptations of Scarabaeinae is the extreme reduction of the ovary, which, in the cases examined, is reduced to a single ovariole on the left side, the right ovary having disappeared altogether. The Scarabaeinae are the only group of Coleoptera showing this degree of ovarian reduction (Robertson, 1961). This phenomenon, which is not related to coprophagy but to nidification behavior, was well studied by Heymons (1930) and Willimzik (1930) in some European species of the genera Scarabaeus, Onthophagus, and Copris. According to Robertson (1961), who made a survey of known ovariole numbers in the entire Coleoptera, a single ovary and ovariole are also seen in Sisyphus schaefferi (Linnaeus), Canthon rutilans Laporte var. cyanescens Dejean, Dichotomius carolinarus (Linnaeus), and D. anaglypticus (Mannerheim) (citing Heymons, 1929, and Williams, 1945). The only other data we have is a mention by Navajas (personal communication) that the female reproductive system of Canthon virescens Mannerheim is also reduced to a single ovary. The constancy of this phenomenon in genera as diverse as those cited above indicates that the condition may well be general throughout the subfamily.

Willimzik (op. cit.) also compared the female gonads of some Aphodius and Geotrupes. In the former genus, we see a normal insect ovarian apparatus, symmetrical and with seven ovarioles in each ovary (fig. 48). In Geotrupes, there are still two ovaries, but the number of ovarioles is reduced to six each, only one of which ripens at a time. In two species of Bolbocerini, the ovarioles are reduced to one per ovary, but there are still two ovaries (Robertson, 1961, citing Williams, 1945). In all the Scarabaeinae investigated, only one ovariole of the left ovary remains, but there are important differences between the genera.

The two species of Onthophagus investigated were O. fracticornis Preysasser and O. mwichicornis (Linnaeus), and both are identical in having the single ovariole relatively large and consisting of many follicles, up to 14, averaging 7-8, and a short germarium (fig. 49). In Scarabaeus sp. (Heymons, 1930), the ovariole has not more than three follicles and occupies a relatively smaller space (fig. 50), while in Copris lunaris (Linnaeus) and C. hispanicus (Fabricius) we see the maximum possible reduction — a single follicle (fig. 51).
There is a further reduction in the form and musculature of the female reproductive system. The primitive condition is seen in Aphodius fossor Mulsant, where the receptacle is modified to the shape of a sylvaticus Panzer of Onthophagus fracticornis Preyspler showing reduction to a single left ovariole. Fig. 50. Female reproductive system of Onthophagus to Copris hispanus (Linnaeus) showing extreme reduction to single follicle; a — anus; f — follicle; g — germarium; mid — right introductor muscle of bursa copulatrix; mrv — retractor muscle of vagina; mt — muscles to tergites; ov — combined oviduct and vagina; rs — receptaculum seminis; tp — tunica peritonealis or terminal filament; v — vagina. (Figs. 48, 49, and 51 from Willimzik, 1930; fig. 50 from Heymons, 1930)

Fig. 52. Seminal receptacles of Geotrupes sylvaticus (Ditto of Onthophagus fracticornis). dr — ductus receptaculi seminis; rs — receptaculum seminis.
There is a further indication of a possible evolutionary sequence in the form and musculature of the seminal receptacle. Here the most primitive condition is seen in *Geotrupes stercorarius* (Linnaeus) (fig. 52), where the receptacle is symmetrical and musculated on two sides. In *G. sylvaricus* Panzer the muscles are confined to one side (fig. 53). In *Aphodius fossor* Mulsant we begin to see the familiar C-shape, with the muscles extending between the ends of the C (fig. 54). Finally, through *Onthophagus* to *Copris* the seminal receptacle acquires the extreme U-shape (figs. 55 and 56) also seen in *Scarabaeus* (fig. 32). These muscles, by bending the receptacle in a bow, force sperm out through the ductus receptaculi (dr) and also aid in pumping sperm in, as we have seen (Section 22). The gland associated with the receptacle (gr) apparently secretes a fluid to lubricate the movement of sperm and it may also have a nutritional function (Heymons, 1930:570). The duct of this gland appears to move from the entrance to about the middle of the receptacle in the above sequence.

Fig. 52. Seminal receptacle of *Geotrupes stercorarius* (Linnaeus). Fig. 53. Ditto of *Geotrupes sylvaricus* Panzer. Fig. 54. Ditto of *Aphodius fossor* Mulsant. Fig. 55. Ditto of *Onthophagus fuscicornis* Freyssier. Fig. 56. Ditto of *Copris hispanus* (Linnaeus). dr — ductus receptaculi; gr — glandula receptaculi; mr — receptacle muscles; rs — receptaculum seminis. (From Willimzik, 1930)
Although the complicated musculature of the bursa and canalis copulatrix has been studied in detail only in Scarabaeus (Heymons, op. cit.), it seems likely that a similar apparatus occurs in the other scarabaeine genera, but not in Aphodius or Geotruper.

Other differences may be seen in the fact that Onthophagus and Geotruper have no terminal filament (or tunica peritonealis—tp) and the interesting point that only Scarabaeus has an investiture of glandular tissue surrounding the ductus receptaculi (Fig. 32, gr). Heymons (1930:571) believes this has something to do with the habit, exclusive to Scarabaeus, of gluing the egg suspended in the egg chamber (Section 20). His only mention of the genus Dichotomius (as Pinotus) notes that it also does not have a glandular ductus receptaculi.

While we apparently see two evolutionary sequences in the structure of the ovary and seminal receptacle, we must remember that the genera involved are not in a direct evolutionary line; furthermore the relative positions of Aphodius and Geotruper are reversed in the two sequences. What we may assume is that certain primitive conditions are retained in some of these genera, enabling us to reconstruct the probable evolution of the ovary and receptacle which culminates in what we see in Copris.

Willimzik (op. cit.) points out that the degree of reduction of the ovary (and consequently of fecundity) is directly related to the degree of brood care. At one extreme we have Aphodius, without brood care (Pflege) or provisioning (Fürsorge), and at the other Copris with perhaps the most highly developed brood care and provisioning seen in beetles, and consequently the greatest possible reduction in the ovary and in fecundity. At the same time, we must remember that in the American Copris remotus Leconte, Lindquist (1933) was able to obtain up to 41 eggs successively from a single female by repeatedly removing the completed ovoids from her. This would indicate that the single follicle (if the ovary is so reduced in C. remotus) is still capable of rapid and continuous egg production.

Among other insects, such an asymmetrical reduction in ovarian development is seen only in some viviparous chrysomelids, Diptera and aphids. The complexly muscculated bursa copulatrix, which acts to pump sperm in coordination with the seminal receptacle muscles (Section 22), appears to be unique to the Scarabaeinae (and, in different form, to social Hymenoptera) among insects. The relationship between this and the biology of the beetles is not clear. It has perhaps something to do with the storage and maintenance of live sperm for a very long time.

In order to indicate some of the recently described, and others the generic list has been made since the above-mentioned data have been complete account or the subfamily here.

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For all these reasons the group the genera included in one or in some cases it is like subgenera in the family or lowest alpha level of the Coprina, and

Generic synonymy is seen only in some viviparous chrysomelids, Diptera and aphids. The complexly muscculated bursa copulatrix, which acts to pump sperm in coordination with the seminal receptacle muscles (Section 22), appears to be unique to the Scarabaeinae (and, in different form, to social Hymenoptera) among insects. The relationship between this and the biology of the beetles is not clear. It has perhaps something to do with the storage and maintenance of live sperm for a very long time.
The bursa and canalis co- 
crabaeus (Heymons, op. 
that Onthophagus and 
the probable evolution 
cosmopolitan in reference to the 
APPENDIX III
THE TRIBES, SUBTRIBES, AND GENERA OF THE 
Subfamily Scarabaeinae
In order to indicate the positions of the genera which have been 
recently described, and to provide the reader with some understanding 
of the tribal and subtribal concepts adopted by the authors, the following 
generic list has been prepared. The last general catalogue of the sub-
family is that of Junk (Coleopterorum Catalogus, 1911). All more recent 
lists and revisions have been on a regional basis and there has been no 
complete account or catalogue for the subfamily as a whole since the 
above-mentioned date. 201 presently recognized genera are listed for 
the subfamily here.

In preparing the following list the authors were hampered by the 
very unequal state of present knowledge of the subfamily. While in 
some groups — those which have been revised by recent workers with 
modern concepts — knowledge is almost at the beta level, in certain 
others the generic concepts are very confused and no real progress has 
been made since the time of Harold, 100 years ago. In the first (beta) 
category we have the Omitcellini, Omitini, Gymnopleurina, some of the 
Scarabaeina, and the Madagascan and American Canthonina. The latter 
— the group of the subfamily in which the most work is being done 
at present — are in the process of revision and their classification is 
approximating a phylogenetic scheme. All of the American canthonine 
genera included in our list represent natural groups of species, although 
in some cases it is likely that their rank will be lowered to the level of 
subgenera in the future. At the other extreme, among groups at the 
lowest alpha level of study, we have the remaining Canthonina, some 
of the Coprina, and especially the Dichotomina.

For all these reasons, the list published here does not portray a 
convincing phylogenetic scheme, although an attempt has been made to 
group the genera according to their morphological and biological affinities.

Generic synonymies are not complete in most cases. Only those 
synonyms are listed which may cause trouble to the investigator through 
having been only relatively recently synonymized.

Since the Scarabaeinae are predominantly a tropical and warm-
temperate complex, the term “cosmopolitan” in reference to the distri-
bution of a group describes a range embracing the intertropical and warm-temperate areas of all zoogeographical regions. Only in the case of Onthophagus does the term cosmopolitan have a broader meaning, including the cold-temperate lands of the Northern Hemisphere as well.

Geographic distribution is indicated by regions, employing the following abbreviations: Palaear. — Palaearctic Region, Ethiop. — Ethiopian Region, Oriental — Oriental Region, Austr. — Australian Region, and Neot. — Neotropical Region. In some cases it was deemed preferable to delimit the range further (e.g. Mauritius), or to indicate it otherwise (e.g. America, Old World, or Gondwanan distribution).

Subfamily Scarabaeinae

(= Coprinae)

Tribe Onthophagini

(Cosmopolitan, markedly less abundant in the Western Hemisphere, especially South America.)


Mimentophagus Balthasar — Ethiop.
Macropocopris Arrow — Austr.
Caccobius Thomson — Palear., Oriental, Ethiop.
Mičichas Peringuey — Ethiop.
Cyobius Sharp — Oriental.
Anoctus Sharp — Oriental.
Caccephilus Jekel — Ethiop.
Phalops Erichson — Ethiop., Oriental.

Subtribe ONITICII

Australia; the secondly in the display all the
Scaptocnemis Peringuey
Drepanoplatynus Balthasar
Timiocellus Peringuey
Liaticellus Peringuey —
Oniticellus Serville, cellus Balthasar
for Australia.
Pseudoniticellus Krug.
Tragiscus Klug (= Subtribe DREPA
Drepanocerus Kirby
Subtribe HELICTI
Helicopleurus Orb.

(Principally Ethiopian is 13% Palaear.)

Chironitis Lansberge
Aptychonitis Janssens
Onitis Fabricius — Guinea.
Tropidonitis Janssens
Allonitis Janssens
Bubas Mulsant —
Megalonitis Janssens
The intertropical and intercontinental regions. Only in the case of the Ethiopian Region, employing the fol­lowing names, was it deemed preferable to indicate it otherwise (with the exception of Australia; the group is more abundant in the Ethiopian Region, secondly in the Oriental Region. The American representatives display all the characteristics of relict species).

Scaptocnemis Péringuey — Ethiop.
Drepanoplatynus Boucomont — Ethiop.
Tiniocellus Péringuey — Ethiop., Oriental.
Liatongus Reitter — Ethiop., Oriental, Western North America.
Oniticellus Serville, with the subgenera Euoniticellus Janssens, Paroniticellus Balthasar, and Oniticellus Serville — Cosmopolitan except for Australia.
Pseudoniticellus Kraatz — Oriental.
Tragiscus Klug (= Deronitis Arrow) — Ethiop.

Subtribe DREpanocerina (Ethiopian and Oriental).
Drepanocerus Kirby (= Cyptochirus Lesne) — Ethiop., Oriental.

Subtribe HELicopleurina (Malagasy).
Helicopleurus Orbigny — Madagascar.

Tribe Onitini
(Principally Ethiopian, with 75% of the species; the remainder [3 genera] is 13% Palearctic and 12% Oriental.)

Chironitis Lansberge — Palear., Ethiop., Oriental.
Aptychcnitis Janssens — Ethiop.
Onitis Fabricius — Palear., Ethiop., Oriental (with some species in New Guinea).
Tropidonitis Janssens — Ethiop.
Allonitis Janssens — Ethiop.
Bubas Mulsant — Mediterranean.
Megalonitis Janssens — Ethiop.
Tribe Coprini

Subtribe DICHOTOMINA (= Pinotina) (With a Gondwanan distribution, predominating in the west — the Neotropical and Ethiopian regions).

Deltochlorium Harold — Neotr.
Bdelyrus Harold — Neotr.
Bdelgropsis Pereira, Vulcano, and Martinez — Central America.
Pedaridium Harold — Neotr.
Aphengium Harold — Neotr.
Trichillum Harold — Neotr.
Uroxys Westwood 1 — Neotr.
Pseudouroxys Balthasar — Neotr.
Scatonomus Ericson — Neotr.
Onthocharis Westwood — Neotr.
Ateuchus Weber (= Choeridium Serville) — Neotr.
Hypocanthidium Balthasar — Neotr.

1 At present this genus includes, beside typically dichotomine species, some which appear to belong in the Coprina.

Canthidium Ericson
Neocanthidium Marx
Agamopus Bates —
Chalcocoris Burmeister
Holocephalus Hope
Dichotomius Hope
Isocoris Pereira and
Ontherus Ericson
Zonocoris Arrow
Macroderes Westwood
Sarophorus Ericson
Pinacotarsus Harold
Coptorhina Hope (=
Dolopleurus Ericsson
Stipocoris Pereira
Saprophorus Pereira
Xinidium Harold —
Paraphytus Harold
Cacchibionymus Burmeister
Aulonocnemis Klug
Disphysema Harold
Parachorius Harold
Paraphytus Harold
Onychothecus Bouvier
Pedaria Laporte —
Heteroclitopus Périn.

Subtribe PHANAeus
Phanaeus on the

Bolbites Harold —
Gromphas Brullé —
Ocrascatus Bates —
Canthidium Erichson — Neotr.
Neocanthidium Martínez, Halffter, and Pereira — Neotr.
Agamopus Bates — Neotr.
Chalcocopris Burmeister — Neotr.
Holocephalus Hope — Neotr.
Dichotomius Hope (= Pnotus Erichson) — Neotr.
Isocopris Pereira and Martínez — Neotr.
Ontherus Erichson — Neotr.
Zonocopris Arrow (= Plesiocanth (Gillet) — Neotr.
Macroderes Westwood — Ethiop.
Sarophorus Erichson — Ethiop.
Pinacotarsus Harold — Ethiop.
Coptorhina Hope (= Frankenbergerius Balthasar) — Ethiop.
Delophorus Erichson — Ethiop., Oriental.
Stipropodius Harold — Ethiop.
Saproeicus Pénguex — Ethiop.
Xinidium Harold — Ethiop.
Parapinotus Harold — Ethiop.
Caccobiomorphus Balthasar — Ethiop.
Aulonocnemis Klug — Ethiop., Oriental.
Disphysema Harold — Oriental.
Parachorius Harold — Oriental.
Paraphyius Harold — Ethiop., Oriental (including Japan).
Onychotracus Boucomont — Oriental.
Pedaria Laporte — Ethiop., Austr.
Heteroclitopus Pénguex — Ethiop., Austr.
Thyregis Blackburn — Austr.

Subtribe PHANAEINA (Neotropical, but with species of the subgenus Phanaeus on the Mexican Plateau and in the United States).

Bolbites Harold — Neotr.
Gromphas Brullé — Neotr.
Oruscatus Bates — Neotr.
Pteronyx Lansberge (a genus of doubtful position) — Neotr.

Phanaeus MacLeay, with the following subgenera: Coprophanaeus Oslosieff — Neotr., Metallophanaeus Oslosieff — Neotr., Megaphanaeus Oslosieff — Neotr., Sulcophanaeus Oslosieff — Neotr., and Phanaeus MacLeay — all America except the Antilles.

Teurocopris Oslosieff — Neotr.

Oxystermon Laporte — Neotr.

Tetracereia Klages (= Eurypodea Klages = Boucomontius Oslosieff) — Neotr.

Megatharsis Waterhouse — Neotr.

Homalotarsus Janssens — Neotr.

Dendropaemon Perty — Neotr.

Subtribe ENNEARABDINA (Argentina).

Ennearabdus Lansberge — Argentina.

Subtribe COPRINA (Cosmopolitan, with about 65% of the species Ethiopian).

Heliocopris Hope — Ethiop., Oriental.

Copridaspis Boucomont — Ethiop., Oriental.

Catharsius Hope, with the subgenera Metacatharsius Paulian — Ethiop., and Catharsius Hope — Ethiop., Oriental.

Synapsis Bates — Oriental, Palaear.

Microcopris Balthasar — Ethiop.

Pseudocopris Ferreira — Ethiop.

Copris Müller, with the subgenera Liocopris Waterhouse — Ethiop., Paracopris Balthasar — Ethiop., and Copris Müller — Cosmopolitan, except Australia.

1 Including Coptodactylina Paulian, which should not be separated as a distinct subtribe.

2 This genus appears to be a dichotomine, but has always been placed in the Coprina.
Coptodactyla Burmeister, with the subgenera Boucomontia Paulian and Coptodactyla Burmeister — Austr.
Arrowianella Paulian — Austr.
Pseudopedaria Felsche — Ethiop.
Scutimus Erichson — Neotr.
Palaeocoris Pierce (a fossil of uncertain position in the tribe) — California.

Tribe Scarabaeini

Subtribe EUCRANIINA (Neotropical).
Anomiopsoides Blackwelder (= Anomiopsis Burmeister) — Argentina.
Glyphoderus Westwood — Argentina.
Eucranium Brullé — Neotr.

Subtribe EURYSTERNINA (Neotropical).
Eurysternus Dalman — Neotr.

Subtribe SISYPHINA (Cosmopolitan).
Nesosisyphus Vinson — Mauritius.
Platyphymatia Waterhouse — Austr.

Subtribe GYMNOPLEURINA (O'd World).
Paragymnopleurus Shipp — Oriental, including the Celebes.
Allogymnopleurus Janssens — Ethio., Oriental.
Subtribe SCARABAEINA (Old World, especially the tropics).

*Pachysoma* MacLeay — Ethio.

*Neopachysoma* Ferreira — Ethio.

*Mnematium* MacLeay — Ethio.

*Neomnematium* Janssens — Ethio.


*Scarabaeus* Linnaeus, with the subgenera *Kheper* Janssens, and *Scarabaeolus* Balthasar, and *Scarabaeus* Linnaeus — Ethio., Palear., Oriental.

*Parascarabaeus* Balthasar — Oriental.

*Neateuchus* Gillet — Ethio.

*Madateuchus* Paulian — Madagascar.

*Drepanopodus* Janssens — Ethio.

*Pachylomera* Kirby — Ethio.

*Circellum* Latreille — Ethio.

*Scelaeus* Westwood — Ethio.

*Sebasteos* Westwood — Ethio.

*Ateuchites* Meunier (fossil) — Neotr.

Subtribe CANTHONINA (Gondwanan distribution).

*Eudineops* Burmeister — Argentina.

*Megathoposoma* Balthasar (= *Glauconia* Paulian) — Central America.

*Poltecanthus* Pereira — Neotr.

*Megathopa* Eschscholtz — Neotr.

*Malagoniella* Martinez, with the subgenera *Megathopomina* Martinez and *Malagoniella* Martinez — Neotr.

*Strebelepus* Lansberge — Neotr.

*Strebelopoides* Balthasar — Neotr.

*Canthonoides* Chapin — Antilles.

*Ipselissus* Olsoufieff (= *Ipselissus* Paulian) — Neotr.

Subtribe CANTHONINA (Gondwanan distribution).

*Canthotrypes* Petiver — Central America.

*Sinapisoma* Bouche — Central America.

*Pseudepilissus* Paulian — Palear., Oriental.

*Nesocanthon* Petiver — Central America.

*Anisoscanthon* Moss — Central America.

*Holocanthon* Moss — Central America.

*Trichocanthon* Vester — Central America.

*Teuta* Blaisdell — Central America.

*Canthonidia* Petiver — Central America.

*Canthomeecthus* Petiver — Neotr.

*Pseudepilissus* Paulian — Neotr.

*Vulcanocanthon* Petiver — Neotr.

*Goniochanton* Petiver — Neotr.

*Melanocanthon* Petiver — Neotr.

*Boreocanthon* Petiver — Neotr.

*Francmonrosia* Petiver — Neotr.

*Canthon* Hoffmannsegg — Neotr.

*Scybalocanthon* Petiver — Neotr.

*Deltochilum* Eschscholtz — Neotr.

*Canthochilum* Hoffmannsegg — Neotr.

*Geocanthon* Paulian — Neotr.

*Cryptocanthon* Petiver — Neotr.

*Scybalophagus* Petiver — Neotr.

*Canthotrypes* Petiver — Central America.

*Sinapisoma* Bouche — Central America.

*Pseudepilissus* Paulian — Palear., Oriental.

*Nesocanthon* Petiver — Central America.

*Anisoscanthon* Moss — Central America.

*Holocanthon* Moss — Central America.

*Trichocanthon* Vester — Central America.

*Teuta* Blaisdell — Central America.

*Canthonidia* Petiver — Central America.

*Canthomeecthus* Petiver — Neotr.

*Pseudepilissus* Paulian — Neotr.

*Vulcanocanthon* Petiver — Neotr.

*Goniochanton* Petiver — Neotr.

*Melanocanthon* Petiver — Neotr.

*Boreocanthon* Petiver — Neotr.

*Francmonrosia* Petiver — Neotr.

*Canthon* Hoffmannsegg — Neotr.

*Scybalocanthon* Petiver — Neotr.

*Deltochilum* Eschscholtz — Neotr.

*Canthochilum* Hoffmannsegg — Neotr.

*Geocanthon* Paulian — Neotr.

*Cryptocanthon* Petiver — Neotr.
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Ethiop., Palear...

Central America.

pomima Martinez

Scybalophagus Martinez — Neotr.
Canthotyphes Paulian — Neotr.
Sinapisoma Bucomont — Neotr.
Pseudopilus Martinez — Neotr.
Nesoconthone Pereira and Martinez — Antilles.
Xenocanthone Martinez — Neotr.
Anisocanthon Martinez and Pereira — Neotr.
Holocanthon Martinez and Pereira — Neotr.
Trichocanthon Pereira and Martinez — Neotr.
Tetraechma Blanchard — Argentina.
Canthonidia Paulian — Neotr.
Canthoaeocnus Pereira and Martinez — Neotr.
Pseudocanthon Bates — Neotr.
Vulcanocanthon Pereira and Martinez — Neotr.
Goniocanthon Pereira and Martinez — Neotr.
Melanocanthon Halffter — North America.
Boreocanthon Halffter — North America.
Francmonrosia Pereira and Martinez — Neotr.
Canthon Hoffmannsegg — America.
Scybalocanthon Martinez — Neotr.
Deltochilum Eschscholtz, with the subgenera Aganhyboma Kolbe, Calphy-
boma Kolbe, Euhygoma Kolbe, Telhyboma Kolbe, Hybomidium Shipp, Parahyboma Paulian, Rubrohyboma Paulian, Deltohyboma Lane, and Deltochilum Eschscholtz — Neotr.
Deltepilussus Pereira — Neotr.
Glaphyrocanthon Martinez — Neotr.
Opiocanthon Paulian — Antilles.
Paracanthon Balthasar (= Paracanthon Paulian) — Neotr.
Canthochilum Chapin — Antilles.
Geocanthon Pereira and Martinez — Neotr.
Cryptocanthon Balthasar — Neotr.
Anachalcos Hope — Ethiop.
Gyronotus Lansberge — Ethiop.
Eurhidi um Harold (= Elasso canthon Kolbe) — Ethiop.
Epirhinus Reiche — Ethiop.
Aphengoe cus Per inguey — Ethiop.
Odontoloma Boheman — Ethiop.
Epilissus Reiche — Madagascar, South Africa, Austr.
Aporoclamys Olsoufieff — Madagascar.
Arachnodes Westwood, with the subgenera Pseudarachnodes Lebis and Arachnodes Westwood — Madagascar.
Epactoides Olsoufieff, with the subgenera Alci antus Olsoufieff and Epactoides Olsoufieff — Madagascar.
Nanos Westwood — Madagascar.
Sphaerocanthon Olsoufieff — Madagascar.
Nesovinsonia Martinez and Pereira — Mauritius.
Phacosomoides Martinez and Pereira — Mauritius.
Phacosomus Boucmon nt — Oriental.
Cassohzs Sharp — Oriental
Pycnepanelus Arrow — Oriental.
Panelus Lewis — Oriental, Japan, Austr., Ethiop.
Monoplistes Lansberge — Austr.
Tennoplectron Westwood — Austr.
Tesserodon Hope — Austr.
Savages' nella Paulian — Austr.
Cephalodesmius Westwood — Austr.
Canthonosoma MacLeay — Austr.
Aulacopris White — Austr.
Coproecus Reiche — Austr.
Heteroateuchus Paulian — Austr.
Ignamibia Heller — Austr.
Labroma Sharp — Austr.
Mentophilus Laporte — Austr.
Onthobius Reiche — New Caledonia.
Saphobius Sharp — New Zealand.

Subtribe ALLOSCI

Alloscelus Boucmonnt
Megaponerophilus
Afreharoldius Jans
Freyus Balthasar
Haroldius Boucmonnt
Ponerotrogus Silver
Subtribe ALLOSCELINA (Ethiopian and Oriental).

*Alloscelus* Boucomont — Ethiop.
*Megaponerophilus* Janssens — Ethiop.
*Afriharoldius* Janssens — Ethiop.
*Freyus* Balthasar — Ethiop.
*Haroldius* Boucomont — Oriental.
*Poneotrogus* Silvestri — Oriental.
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