EVOLUTIONARY BIOLOGY and CONSERVATION of DUNG BEETLES

Clarke H. Scholtz
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Dedication

This book is respectfully dedicated to Professor Gonzalo Halffter Salas of the Instituto de Ecología, México.

Professor Halffter has published a steady stream of papers on dung beetles since his first in 1952, with his most recent appearing just days before this book was set to print, and he has, without doubt, contributed more to the study of dung beetles than anyone else, living or dead. Virtually every research paper on dung beetles in most biological disciplines published over the past 57 years has quoted one or more of his numerous scientific papers.

We, as the authors of this book, trust that its contents have continued in the same vein and spirit as those set by Professor Halffter and we hope that it will, in some small measure, contribute to the field of dung beetle natural history that was exposed to us by Professor Halffter's numerous elegant studies.

PREFACE

In spite of their relatively small size as a group of insects, dung beetles have attracted an inordinate amount of scientific interest over the years, starting with the work of the French naturalist Jean-Henri Fabre around 100 years ago who wrote so eloquently about their behaviour. This was put onto a modern scientific footing with the works of Gonzalo Halffter in Mexico who published the first book (with Eric Matthews) on dung beetles (Halffter, G. and E.G. Matthews 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomologia Mexicana* 12-14:1-312). This was followed by Halffter and W. David Edmonds 1982 (*The nesting behavior of dung beetles: an ecological and evolutive approach.* Instituto de Ecologia, Mexico, D.F.). Ilkka Hanski and Yves Cambefort produced the next volume, an edited, multi-authored book in 1991 (*Dung beetle ecology*. Princeton University Press). All of these works are long out of print and generally unavailable.

Scientific interest in dung beetles continues to increase worldwide. This is probably because of the solid foundation of dung beetle natural history and ecology that was laid by the above works but also the beetles' increasingly appreciated value as indicators of habitat transformation, as well as growing concerns about their conservation status, mainly because of their value in ecosystem function, have certainly increased awareness and interest in them.

In the 18 years since Hanski and Cambefort's book appeared there has been a steady stream of research published on dung beetle phylogeny, biogeography, physiological ecology and conservation, fields that were not, or barely, treated in previous books. Although Hanski and Cambefort's approach to their book was "evolutionary" it was based mainly on an intuitive appreciation of breeding and feeding patterns amongst the groups since there had never been a comprehensive phylogenetic analysis of the major groups. Such analyses now exist which give us a tested and testable hypothetical platform on which to base evolutionary speculation.

Our research group and our collaborators have published widely in the fields covered by the book and these fields form the base from which we built the major sections.

The book consists of five major sections: (A) Evolution and ecological success of dung beetles; (B) Physiological and behavioural ecology of dung beetles; (C) Phylogeny of the Scarabaeinae; (D) Historical biogeography of the Scarabaeinae and its physical and biotic drivers; (E) Conservation of dung beetles. All have a phylogenetic basis, i.e. how evolution and relationships of the groups affect each of the aspects under discussion. Consequently, we believe that the sections are coherent. What we have chosen not to cover in the book is the "ecology" (i.e. population and community ecology) of dung beetles. This aspect was dealt with in Hanski and Cambefort, but with more recent developments in the field, and the evolution of "macro-ecology", a huge new discipline has emerged, and dung beetles have been included in such studies. These aspects, however, remain to be synthesised.

In retrospect, writing a book of this nature was never going to be easy. We enthusiastically set about writing some sections on aspects of research about which we knew very little so the chances that we wouldn't do them justice were good, but in view of the wealth of information currently available about various aspects of dung beetle evolutionary biology and conservation, we felt justified in attempting it. We, furthermore, attempted to balance the content of the book in such a way that the information contained would be of interest to both research specialists on dung beetle natural history but also to agriculturalists and conservationists as well as to interested lay groups. We are generally satisfied with the result and believe that we have managed to bring together various relevant aspects of the chosen disciplines. We trust that the reader will agree with us.

The authors

All three of the authors of the book were based in the Scarab Research Group in the Department of Zoology and Entomology at the University of Pretoria, South Africa during the planning and first stages of writing of the book. Ute Kryger has since returned to her native Germany after spending six years as a post-doctoral research fellow in the research group. Adrian Davis and Clarke Scholtz are still there; AD as a senior research fellow and CS as Professor of Entomology.

August, 2009

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Clarke Scholtz

For me, fast approaching the end of my professional research career, writing my sections of the book has been a somewhat sentimental journey of memories of discussions held, and papers read and others written jointly with some of the great scarabiologists of the last part of the last century and the first part of the 21st. Some are dead, others retired, and many still have years of productive research ahead of them. All of them have enriched my life tremendously, both intellectually and by shared fun in the lab and field, and also by correspondence. Many of the sections in this book revolve around aspects of dung beetle biology in which I have been intimately involved with some of these colleagues over the years and these interests are reflected in the choice of the topics discussed in this book. I am particularly grateful to the following with whom I could share a passion for dung beetles and their biology, in no particular order:

Erik Holm, my PhD supervisor in the 1970's and later colleague, to whom I am immensely grateful for many things, including irresponsible and exhilarating trips to war zones and motor cycle trips through the Namib Desert in pursuit of beetles, and who first exposed me to the wonderful world of *Pachysoma*.

Steven Chown, an ex-student and colleague who exposed me in hot places to the "grab-and-stab" techniques of the day used in research on scarab temperature physiology, interspersed with large quantities of cold beers to keep our temperatures down.

Henry Howden with whom I spent a wonderful 6 months in Ottawa in 1985; particularly memorable were the lunches of sandwiches and apples that Anne prepared for us, staring at the world map in Henry's office and talking about the wonderful scarabs that remain to be discovered in all sorts of magical places.

Bruce Gill, at the time a student in Henry Howden's lab, who was concerned about my conservative "upbringing" in South Africa so saw to it that I was exposed to all sorts of delinquent entertainment in the seedier parts of Ottawa and Hull.

Roy Crowson, the late, famously eccentric coleopterist from Glasgow, who opened my eyes to the fact that answers to the exasperating evolutionary questions posed by one beetle group are sometimes obvious when looked at in other groups. On a trip to South Africa in 1983 I asked him if he would like to pay a short visit to the famous Kruger National Park, home to large numbers of the "Big 5" and other large mammals, to which he retorted "only if we can see beetles!".

Stan Caveney of London, Canada, with whom I spent many nights in wonderful wild places in the 1980's, surrounded by potentially dangerous animals, studying activity and flight behaviour of different species. His boundless enthusiasm, energy and sense of humour kept us going even when confined for hours to our vehicle by prides of inquisitive lions.

Jonathan Browne, who came to study with me from Canada as a young student and eventually spent 10 years in South Africa. We visited wild places together many times, with Jonathan always hungry and complaining that I had brought too little food. One time he and another student carried a scavenged dead calf down a mountain to supplement our field rations. In spite of his eccentricity Jonathan's research productivity was exceptional, producing a number of detailed papers of wing structure in scarabs.

Geoff Monteith of Brisbane who, over the years, supplied me with an endless stream of Australian beetles for comparative studies and who introduced me to the wonderful world of *Cephalodesmius* in Tolloom Forest in 2004.

Daegan Inward, who, as a young student, took care of me during a 4-month stint in the Coleoptera Department of the Natural History Museum in London in 1997, and went on to produce the first comprehensive molecular phylogeny of the Scarabaeinae for his PhD and to whom the credit for the paper by Monaghan *et al*. (2007) is undoubtedly due.

Marcus Byrne, a South African colleague with a wonderful sense of humour and a passion for biology. Marcus also read through and contributed helpful comments on the bulk of the text of this book – we are extremely grateful for his time and diplomatic suggestions for changes to sections of the book he obviously felt were sub-standard. However, the quality or lack thereof of the book are entirely our responsibility.

Bill Bateman, an ex-colleague in the Department, who provided me with advice and literature on the principles of sexual selection.

Keith Philips, an ex-post-doc, who produced the first ever comprehensive phylogeny of the Scarabaeinae, and who convincingly demonstrated that rolling in scarabs is polyphyletic.

Marie Dacke, when as a young student, was asked by a South African colleague how she tolerated working with me replied in her lovely Swedish English that "Clarke enjoys me immensely!". We have continued to enjoy productive research collaboration over the past ten years, with Marie directing all the members of an often large group of project participants like a field general, for which she was affectionately christened "the General".

Eric Warrant who has had a long and productive association with dung beetles through his studies of eye design and vision. Eric also initiated and facilitated the dung beetle orientation research between ourselves, Marcus Byrne at Wits University in Johannesburg and the "Vision" group at Lund University. And although "The General" is now the principal project leader, Eric has remained an active participant at all levels of the research.

Peter Holter of Copenhagen who effectively solved the contentious riddle of what dung beetles eat, and how, using a very simple but elegant technique that he developed. We also spent several field trips together in wonderful places thinking up solutions to the world's problems over copious quantities of red wine.

Douglas Emlen, one of the crop of brilliant young scarab researchers who has produced some of the most elegant research on horn structures and mate selection in dung beetles and written some of the most eloquent papers ever on dung beetle biology. His willingness to discuss his data and to allow us to use copies of his beautiful illustrations for reproduction in this book, are greatly appreciated.

André Olwage painted the magnificent beetle illustrations used in this book as he has done so for many of my publications over the past 20 years. I am deeply indebted to him.

Finally, I have been supported and encouraged by my family over the years. Although my parents had doubts about a future chasing beetles all over the sub-continent, often on foot under dangerous conditions or in very old and unreliable vehicles, they supported me throughout, feeling, no doubt a little bit responsible for inculcating in me a passion for biology and the wild outdoors.

My sister, Lilian, typed and arranged the reference list and Appendix during her spare time, both particularly tedious processes. I am very grateful for the diligent and thorough product.

For 20-odd years Marianne tolerated my long absences on field trips and in foreign countries while I was working with colleagues on topics of interest – for this I will always be grateful. Anton spent many holidays at the beach without a father when he was young since the summer vacations always coincided with peak beetle activity so it is perhaps not surprising that, although he has tolerated and even participated in my eccentricity in his later years, he has chosen a quite different career path to mine.

Finally, I am particularly grateful to Jenny who came into my life at quite a late stage but provided me with a partner who not only tolerates my eccentricities but shares my passion for the outdoors and the small things that make ecosystems function. No doubt we will continue to pursue these interests into our dotage on our magnificent and isolated Karoo farm.

I am also very grateful to my HOD, Sue Nicolson, and the University of Pretoria for supporting me and my research over the years and to Sue for tolerating my long absences from the Department while I was writing my sections of the book, hidden away in an old house in Namaqualand.

Clarke Scholtz, Adrian Davis and Ute Kryger

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Innocent Pikirayi, of the Department of Anthropology and Archaeology at this University who provided us with information on human colonization of Madagascar, and the origin of cattle there.

Alberto Ballerio, Federico Ocampo, Brett Ratcliffe, Bruce Gill, Fernando Vaz-de-Mello and Giuseppe Carpaneto have kept us informed of new literature, provided us with data and advice on dung beetles or allowed us to use their photographs (Federico Ocampo, Fig. 9.2). Lena Stenseng of Copenhagen took the photographs used in Figs 4.1 and 9.1 – we thank her for that.

At the time of writing this book our Scarab Research Group at the University of Pretoria consisted of the following people, all of whom contributed in many ways to the final product: Angelika Switala, Carmen Jacobs, Catherine Sole, Christian Deschodt, Cornel du Toit, Jackie Brown, Power Tshikae, Rentia Tukker, Suko Mlambo and Werner Strümpher. Special mention, however, is due to Carmen Jacobs who was constantly on stand-by to trace hard-to-get literature and was responsible for producing the tables and figures used in the text. Rentia Tukker was also very involved in the final stages of proof-reading and reference-checking. We are deeply indebted to them.

Mervyn Mansell, although not directly involved in dung beetles and their research, has been associated with us for many years, both as a professional colleague and great friend of Clarke's and who has been an inspiration to all of us for the scientific standards he sets and for his wisdom and kindness. Mervyn also read and commented on all the sections of the book, a time-consuming and unrewarding task. His comments are greatly appreciated but the quality, or lack thereof, of the contents of the book remain our responsibility.

Finally, we thank Lyubomir Penev and his production team at Pensoft Book Publishers for, firstly, agreeing to publish the book, and then for producing it.

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INTRODUCTION

Under natural conditions an invertebrate dung community is hugely complex, often consisting of thousands of individuals of hundreds of species, all of which depend ultimately on the same resource, the highly desirable and nutritious dung; and virtually all types of dung are attractive to potential dung colonisers, although different types of dung generally attract different suites of invertebrates. In spite of specific differences in the invertebrate groups that might be attracted to the dung, and which in turn are determined by the geographical location of the area where the dung is produced and the environmental conditions to which it is exposed, the same major invertebrate groups predominate in all dung types in all regions. A typical dung community is usually made up of dung feeders, many of which are beetles, of which most in turn are “dung beetles”, the subject of this book, but flies are often also extremely numerous and compete aggressively for the rich resource. Various predatory beetles, in turn, are attracted to the abundance of prey provided by the dung beetles and fly maggots in the dung. Then, the flying beetles provide transport from one dung source to another for thousands of tiny flightless mites, some of which feed on the dung whilst others are predatory on fly eggs in the dung. Ants are also usually present, waiting around the periphery of the dung for beetles to tunnel into it and open up passageways for them to access and feed on fly eggs and maggots. And then, when most of the moist and nutritious dung has been fed on, removed or buried, the dry scraps that remain are colonised by termites which feed on the cellulose and lignin that were unusable for the earlier colonists.

In view of the nutritious but patchy and ephemeral nature of dung as food for beetles it is highly desirable, and, under favourable conditions it is usually quickly colonised, often by huge numbers of beetles of many different species that live and feed in dung, and which are often loosely and collectively called “dung beetles”. In tropical regions these mostly belong to by far the largest group, and, what in this book will be considered “true” dung beetles, i.e. members of the family Scarabaeidae and more specifically, of the subfamily Scarabaeinae. In temperate regions, this niche is often filled by some members of the closely related sister-group to the Scarabaeinae, the Aphodiinae or by those belonging to the more distantly related family Geotrupidae. Furthermore, in both tropical and temperate regions, morphologically and behaviourally similar, but completely unrelated groups such as the Hydrophilidae may also be found in wet dung. These all feed on the dung itself (Holter 2004) but many others are attracted to the dung where they prey on other insects such as fly larvae in the dung (Histeridae and Staphylinidae being amongst the most common).

Although dung beetles represent a relatively small group of insects (roughly 5000 species are known worldwide) and appear to live similar lives in an apparently homogenous environment, the complexity of their morphological, ecological and behavioural attributes is actually astonishing. Most of them are associated with moist herbivore dung and they have evolved an array of mechanisms to utilize not only this resource, but also other sources of dung, as well as numerous other non-dung food sources under a multitude of different environmental conditions. Adults and larvae split the resource further by feeding on different fractions of the food. Their evolutionary success is enhanced by well developed brood care, which permits a smaller energetic investment in reproduction than would otherwise be the case, and, ultimately, results in low juvenile mortality. Consequently, only small numbers of offspring are produced per breeding episode, but these are adequate to produce sufficiently high numbers of individuals to maintain healthy populations of the species. Because of this combination of factors, some dung beetle species have the lowest fecundity recorded for any insect group.

What Is Dung?

Dung is the general and loosely used term for the complex physical, chemical and microbial mix in the excreted food remains, the nature of which is largely determined by the original food, of a multitude of animals. The animals that produce the dung which is of interest to dung beetles fall into numerous taxonomic and feeding categories; vertebrate, invertebrate, omnivore, carnivore or herbivore, although the majority of dung beetles worldwide probably feed on mammalian herbivore dung. However, even this is not as simple as it appears with grazing and browsing mammals often producing very different dung types, and then a further complexity is whether the herbivore is a ruminant, producing fine-textured dung, or a non-ruminant producing coarse dung. Then, there is the question of whether the dung was excreted in a mass or in pellet-form, and whether the dung was produced from high quality spring, or poor quality autumn graze, or something in between (Edwards 1991). All of these characteristics affect the nature of the dung insect communities that colonise the dung.

Furthermore, adult dung beetles consume (and provide for their larvae), different fractions of the dung – adults filter out the highly nutritious liquid components consisting of a suspension of tiny dung fragments, microbes and sloughed gut epithelial cells from the host animal (Holter *et al.* 2002), while the larvae masticate the larger fibrous fragments which consist mainly of cellulose (Halffter and Matthews 1966). Also, some dung beetles have different preferences for adult and larval food. This may have to do with the physical nature of the dung (for example *Circellium bacchus* in South Africa prefer elephant dung for adult food and buffalo dung for rolling brood balls, quite possibly the difference being merely physical – the fibrous elephant dung is possibly more difficult to roll than the more pliable buffalo dung, which again has to do with the diet of the hosts in the area (a small area of south-eastern Africa) where they occur. The elephants in this area browse mostly fibrous woody plants, while the buffalo are exclusively grazers (Kryger *et al.* 2006a). Alternatively, there may be real differences in adult and larval food preferences such as in the African *Anachalcos*, where adults appear to prefer carrion for their own food but provision larval burrows with dung.

Very few studies have been undertaken on the nutritional quality of dung. This is largely because until recently it was not known precisely what part of the dung the beetles actually fed on nor what the nutritional value of that particular fraction is. Holter and co-workers, in a series of papers on dung beetle feeding (Holter 2000; Holter *et al.* 2002; Holter and Scholtz 2005; Holter and Scholtz 2007) determined that adults of all the species, representing all of the African tribes, that they studied feed on tiny particles in the liquid fraction of dung which is highly nutritious (see Chapter 6 for details).

Dung also has several common physical attributes that affect dung beetle attraction and colonisation – its occurrence is patchy, as determined by the distribution of its producer, and it is ephemeral, because it may very quickly be disturbed or removed from suitable habitat or it may be transformed into an unusable state by the elements. The former two characteristics determine the difficulty with which it can be located and utilized, while the latter determines the potential competition for the resource with other dung feeders.

Although dung is often patchy and usually only suitable for dung beetle colonization for a short time, this may vary from cattle pastures where it may be almost contiguous, presenting an almost continuously available source of food of different ages and conditions, to the situation where herds of naturally grazing mammals which typically would aggregate for a while, produce a large amount of dung in a limited area over a short time, and then move off some distance to fresh, unsoiled pastures. At the other end of the extreme might be the dung of a small solitary animal in dense bush, which would be very limited in quantity, difficult to locate, and subject to desiccation within a short space of time. However, not only does the quantity and condition of the dung determine the potential colonizers, but so does the type of dung produced, and whether it is from an omnivore and strongly odiferous, or less odiferous from non-ruminant or ruminant herbivores, and whether the latter produced lumps of dung or pellets. Then there is the question of the age of the dung and whether it is needed for adult food, in which case it is usually only attractive when very fresh, or for larval food where older dung is sometimes preferred (for example the African oniticelline, *Tragiscus*).

The reproductive performance of some dung beetles is distinctly affected by the type and quality of the dung. *Oniticellus egregius* produce much larger numbers of broods from horse dung than from cattle dung (Davis 1989a). *Onthophagus binodis* produce more broods on dung from cattle feeding on young spring grass than from cattle dung produced on older late summer grass, but *Onitis alexis* brood production appears little affected by variation in dung quality (Doube 1991).

As mentioned above, thousands of individuals of dozens of species might be attracted to the same dung source over a short space of time, implying that they have very similar ecological requirements. Although, as would be expected, the resulting competition for the dung is fierce, the different species actually have very different preferences and partition the resource according to a clear hierarchy in their ability to compete for dung (Doube 1990). These are briefly mentioned here in order of their competitive dominance. First there are the large rollers and fast-burying tunnellers, which are small or large but aggressive beetles that quickly remove dung from the source. Small rollers are also often strong competitors. Some large and small species are slow-burying tunnellers. Ones that build shallow nests and nest within the dung are poor competitors and most likely to be disturbed by other groups. Finally, there are kleptoparasites which use the dung buried by other species. These and numerous other behavioural mechanisms developed by the different species over millennia to facilitate this co-existence make the study of dung beetle evolutionary biology particularly fascinating.

About The Book

There are various components to bear in mind when discussing the evolutionary biology of dung beetles, and these form the basis of this book. There are the beetles themselves, including their origins, evolutionary radiations and relationships, as well as how each of those has been historically, or is currently affected by the environmental conditions under which the beetles live. There is the food source on which the adult beetles feed, and in which the larvae live and feed, and the fierce competition amongst individuals of a species as well as between different species for this scarce resource. For most species this is the dung of a multitude of mainly herbivorous mammals, but many exceptions are known which vary from detritus in some species, to carnivore dung, carrion, fungus and even prey which they kill themselves, in others. Then, there is the complex reproductive and nest building behaviour and how the beetles manipulate the dung during nesting and how they care for their brood. Finally, there are various extraneous threats to dung beetle species and communities, most of which are as a result of human development.

This book is divided into five sections: (A) the evolution and ecological success of dung beetles as a whole; (B) how and which strategies dung beetles have evolved to overcome environmental pressures (C) the evolution of relationships amongst the major groups; (D) biogeography of the major groups; and (E) the major environmental threats to dung beetle species and communities.

Section A

EVOLUTION AND ECOLOGICAL SUCCESS OF DUNG BEETLES

Clarke H. Scholtz

CHAPTER 1
THE ORIGIN OF DUNG BEETLES

Various approaches to the question of the origin of dung beetles may provide evidence to support proposed hypotheses of the evolution of the various dung faunas and their ecological adaptations. One is the fossil history of the major dung beetle groups and that of their close relatives, another is the current distribution of extant genera, and a third is the evolution of feeding preferences.

1.1 THE FOSSIL RECORD

The question of whether ancestral dung beetles evolved/radiated in response to large quantities of reptile dung during the late Cretaceous (70 – 80 million years ago (mya)) as proposed by e.g. Chin and Gill (1996) and Krell (2006) or later, during the Tertiary (within the last 65 million years (my)), in concert with the rapidly evolving mammal diversity (Halffter and Matthews 1966; Cambefort 1991a; Scholtz and Chown 1995), is moot. However, there is no doubt that modern dung beetles have radiated in response to large quantities of mammal dung, so the central question should rather be one of what the ancestral dung beetles looked like, and what they are likely to have fed on that pre-adapted them for the explosive radiation that followed the radiation of mammals.

The fossil record, unfortunately, tells us very little about the possible origin of dung beetles (reviewed by Krell 2000 and 2006), and most of the hypotheses that consider this event use circumstantial evidence of supposed feeding signs or fossilised dung balls. The formation of balls into which eggs are laid as provisions for the larvae, is probably an apomorphic state for all dung beetles, so must have been present in the ancestral species. The oldest supposed scarabaeine dung beetle fossil is *Prionocephale deplanate* from the Upper Cretaceous of the Lanxi formation, Zhejiang, China (92 – 83.5 mya, Krell 2006) (Table 1.1). The fossil is apparently similar in general shape to a modern scarabaeine, but Krell expresses doubt that a species with the facies of a modern dung beetle was present during this time since he states, but does not discuss, that

Table 1.1. The dung beetle fossil record and the putative ages of various lineages based on molecular data.

Period / Epoch	mya	Fossils	Molecular dating
Pleistocene	1.8	*Onthophagus*[1] *Choeridium*[1+] *Phanaeus*[1]; *Copris*[1]; *Onthophagus*[1] Dung balls[3]	
Pliocene	5	*Copris*[1] Dung balls[3]	*Pachysoma*[8]
Miocene	24	*Onthophagus*[1]; *Scelocopris*[1+] *Oniticellus*[1] *Heliocopris*[1] *Gymnopleurus*[1] *Anachalcos*; *Copris*; *Metacatharsius*[1] Dung balls[3]	*Epirinus*[4]; *Scarabaeini*[7] *Nesosisyphus*[10] Canthonini of Madagascar[6] *Helictopleurus*[5]
Oligocene	38	*Onthophagus*[1]; *Ateuchites*[1+] Dung balls[3]	3rd Major lineage split[4] 2nd Major lineage split[4]
Eocene	44		1st Major lineage split[4] Minimum age of origin of dung beetles[9]
Palaeocene K/T Boundary Cretaceous	54 65 71 80 90	Dinosaur coprolites[2] *Prionocephale deplanate*[1]	Origin of Dung beetles[4] Maximum age of origin of dung beetles[9]

+ = *extinct.*

1. Krell (2006) 2. Chin and Gill (1996) 3. Halffter and Matthews (1966) 4. Sole and Scholtz (2009) 5. Wirta et al. (2008) 6. Orsini et al. (2007) 7. Forgie et al. (2006) 8. Sole et al. (2005) 9. Monaghan et al. (2007) 10. Davis et al. (2008b).

other similar-age fossils "have a different body shape than extant dung beetles". Chin and Gill (1996) claimed that a coprolite of an herbivorous dinosaur from the Upper Cretaceous with burrows backfilled with sediment, and, in the surrounding sediment, burrows backfilled with fecal material, were evidence of dung beetle activity such as that caused by several extant taxa. Dung balls, on the other hand, appear to fossilise well and many well preserved fossils have been recorded, especially from South America (Genise *et al.* 2000). Genise and collaborators have defined the fossil complexes in which dung beetle nests and balls predominate as *Coprinisphaera* ichnofacies. Genise *et al.* (2000) claim the oldest possible dung beetle traces to be in paleosols from the Del Palacio Member of the Asencio Formation of Uruguay, but there is contention about whether the formation is of Late Cretaceous or Early Tertiary origin. They claim, however, that there are unequivocal traces of dung beetles from the Palaeocene but unfortunately do not elaborate on the nature of the traces. They also claim traces of Eocene origin in Argentina and Antarctica, but again without elaborating. Consequently, the oldest reliably described fossil dung balls are from the Lower to Middle Oligocene of Patagonia (Frenguelli 1938, 1939, cited in Halffter and Matthews 1966). (See Table1.1).

According to Halffter and Matthews (1966) these fossils are undoubtedly those of dung balls, or rather the clay shell around the balls. Some show the very characteristic adult emergence holes, and these are filled with the same sediments as those in which the balls were found. Intact balls from which adults apparently did not emerge are generally hollow, indicating that the original organic matter of the food and larval remains decayed without sediments being able to penetrate and fossilize. The balls vary in size but all are spherical. Those from the earliest deposits are 29.0 – 39.0 mm in diameter, with 6.0 – 7.0 mm thick walls, an internal space of about 20 mm and an emergence hole of about 10 mm. Frenguelli (1939, cited by Halffter and Matthews 1966) recorded finding huge numbers of dung balls from various *lagerstätten* from Upper Oligocene to Pliocene age in Argentina. These vary in size from 35.5 to 59.0 mm in diameter and were attributed to extant South American genera, although there is no evidence to support this other than that this is roughly the size of balls made by the living members of these genera. However, two balls recorded from the Upper Pleistocene were 82.0 mm and 87.0 mm in diameter respectively, and are larger than any dung balls made by extant South American beetles, although they are roughly the size of those made by members of the living Afro-Oriental genus *Heliocopris*. This period also coincides with mammal gigantism in South America and the balls were most likely made by an extinct species that depended on large quantities of dung produced by some member of the mega-fauna (Halffter and Matthews 1966).

The environments that prevailed when fossilization of the *Coprinisphaera* ichnofacies occurred were claimed by Genise *et al.* (2000) to have been typically moist to slightly dry and warm savanna or grassland with their attendant large mammal faunas. This agrees with what is generally proposed to have been ideal conditions for the evolution and radiation of dung beetles (Halffter and Matthews 1966; Cambefort 1991a; Scholtz and Chown 1995; Davis and Scholtz 2001). These are the general conditions that prevailed during the Tertiary, especially from the Miocene onwards, and still do to a large extent, in Africa, the continent with the largest diversity of mammalian herbivores and dung beetle species. However, additional explanation is required to explain the high species richness in Neotropical and SE-Asian tropical forests (Halffter 1991; Davis and Scholtz 2001). See Chapter 17.1.2.

In his catalogue of scarabaeoid fossils, Krell (2000) and in a later (2006) comprehensive review of the fossil record and its evidence of evolution of the Scarabaeoidea, Krell was only able to conclusively attribute 23 fossils to members of the Scarabaeinae, 20 of which can be attributed to extant genera, the other three to extinct ones. Besides *Prionocephale deplanate*, from the Cretaceous, mentioned above, all other fossil beetles and balls are from the Tertiary and Quaternary Periods. The oldest of the more recent "confirmed" beetle fossils are from the Oligocene around 30 mya, two species of the extant genus *Onthophagus*, and one from an extinct genus *Ateuchites* (Krell 2000). More than half of the fossils are from the Miocene, around 15 mya, but whether this reflects species richness at the time or conditions suitable for fossilization is not clear.

On the basis of the above we can confidently assume that beetles similar to, or representative of, living genera, and those that made dung balls similar to those of modern dung beetles were already present during the Oligocene Period, thus a minimum age of about 30 my (million years). Evidence for anything older than that appears highly speculative but obviously if "modern" dung beetles were already present during the Oligocene, their ancestors must have evolved long before that. The question, of course, is how much earlier?

The sister-group of the Scarabaeinae is generally assumed to be the Aphodiinae (Browne and Scholtz 1998; Philips *et al.* 2004b; Krell 2006), but phylogeny of the "Aphodiinae" and related groups such as Aegialiinae is unresolved with some authors considering the latter nested in the former (see Browne and Scholtz 1998), while others consider it a monophyletic group and sister to the Aphodiinae. Diet of many Aphodiinae, particularly of the genus *Aphodius*, is dung (*i.e.* they are soft-diet consumers like their sister dung beetles – Cambefort 1991a) and that of most Aegialiinae is humus or a "hard" diet. The oldest recorded aegialiine fossil is from the Lower Cretaceous (about 130 mya), whereas the oldest aphodiine fossil is known from the Upper Palaeocene (56 mya) (Krell 2006). However, in view of our poor state of knowledge of relationships within the Aphodiinae in the broadest sense, and even of the nature of the relationship between Aphodiinae and Scarabaeinae, the fossil record of these groups contributes little to improving our understanding of the possible age and evolution of Scarabaeinae.

1.2 DISTRIBUTION OF DUNG BEETLES

This aspect is dealt with exhaustively in Section D, on biogeography of dung beetles, but it is appropriate to here discuss some of the major indicators of areas of evolution and radiation of the faunas in a geographic and historical context.

In a discussion of the current distribution of the 12 recognised tribes of dung beetles [the validity of these will be discussed at length in later chapters of this book] it is difficult to avoid invoking the appealing but phylogenetically unacceptable terminology used so eloquently by Cambefort (1991b) of primitive, intermediate, and modern tribes. However, in view of recent phylogenetic studies (Philips *et al*. 2004b; Monaghan *et al*. 2007; Sole and Scholtz 2009) which convincingly demonstrate the polyphyletic nature of, particularly, the basal "tribes", we will continue to us these terms in a structural and behavioural sense, because of the reasonably well defined nature of the groups, rather than in a phylogenetic one.

The primitive roller and tunneller tribes, Canthonini and Dichotomiini, respectively, have widespread distribution on the continents that once made up the ancient continent of Gondwana, where dung beetles are hypothesised to have evolved. They are currently widespread in Africa, South America and Australia but most genera are endemic to a single continent. Intermediate tribes (rollers – Eucraniini, Eurysternini, Gymnopleurini and Scarabaeini; tunnellers – Onitini and Phanaeini) are younger, and have high generic continental endemicity, but some have spread onto neighbouring continents. The modern tribes (rollers – Sisyphini; tunnellers – Coprini, Oniticellini and Onthophagini) are most widespread at generic level in their distribution, in both the Old and the New World.

The Canthonini also occur on Madagascar, although the Dichotomiini are absent there, which immediately raises questions about the widespread Gondwana nature of the putative ancestral tunnelling lineage. Using a molecular clock, Orsini *et al.* (2007) place the origin of the Canthonini on Madagascar during the Miocene, a mere 13-odd mya and an order of magnitude younger than the postulated separation of Madagascar from Africa 160 mya. Hence it is necessary to invoke one, or possibly several, dispersal events, as hinted to by Orsini *et al*. (2007), of canthonine founders on Madagascar, as opposed to the more fanciful vicariance of the ancestral Afro-Madagascan lineage. If this is an acceptable explanation, and similar logic is applied, the reason why Dichotomiini do not occur on Madagascar is simply that they never successfully dispersed there from Africa. However, the presence of "related" canthonine and dichtomiine taxa on the major Gondwana continents implies that the ancestors of the present continental lineages must have existed before the major fragments had drifted too far for dispersal to take place. The "final" breaks [although shallow seas and isolated islands would have maintained contact for long after this], between Africa and South America occurred during the late Cretaceous, (around 80 mya), and between South America, Antarctica and Australia, during the Eocene (about 40 mya) (Axelrod and Raven 1978). The older age is from well before there is convincing fossil evidence of the existence of dung beetles but is possible, considering that there were probable contact points and dispersal opportunities between the continental fragments until well after that.

There are several indications that dung beetles are actually excellent dispersers. Some modern groups of dung beetles such as the genera *Copris*, *Sisyphus* and *Onthophagus* which are thought to have originated in Africa (Davis *et al.* 2002b; Monaghan *et al.* 2007) have dispersed quickly and over vast distances and are now widespread on several continents. The ancestor of the Sisyphini genus *Nesosisyphus*, with four species endemic to the Indian Ocean island of Mauritius, must have dispersed there, probably from Africa, over an unbelievable distance of several thousand kilometres, since the island is of volcanic origin and a mere 8my old. The endemic canthonine, *Nesovinsonia*, likewise, must originate from a trans-oceanic dispersal event.

Charles Darwin recorded in "*The voyage of the Beagle*" (1839) finding living "*Scarabaeus*" floating at sea about 40 km from the mouth of the Rio Plata in South America. The African species *Digitonthophagus gazella,* which was introduced into Australia in the 1970's, crossed 50 km of sea onto various off-shore islands from the mainland within a few years of introduction. The same species had dispersed naturally from a 1970's introduction into the south-eastern USA (Fincher *et al.* 1983) by 700 km after only 12 years (Kohlmann 1991), and, subsequently, at a rate of 43-808 km/yr over thousands of kilometres to Central America (Barbero and López-Guerrero 1992) and across the ocean to the western Caribbean and West Indian islands, where it is now present on at least nine of the latter (Ivie and Philips 2008).

1.3 THE ORIGIN OF DUNG FEEDING

Another indication of the possible age of dung beetles may be deduced from evidence of food and feeding. It is generally accepted that dung beetles evolved from detritus-feeding ancestors, and that they depended heavily on microbial organisms in the detritus for their main nutritional requirements (Cambefort 1991a; Scholtz and Chown 1995). A switch to feeding on small particles in microbially-enriched wet and partially decomposed detritus, to wet dung, is easily explained in view of the similarity of the substrates. So, the presence of dung balls similar to those formed by modern dung beetles from the Oligocene, 30 mya, implies the evolution of the beetles from ancestral humus-feeding lineages some time earlier. If, as discussed above, the sister-group to the Scarabaeinae is something akin to the Aphodiinae, and they, in turn, are sister to an aegialiine-like ancestor, a Late Cretaceous / Early Tertiary origin of the Scarabaeinae appears plausible. Rapid radiation of scarabaeine lineages was then facilitated during the Tertiary by the rapidly increasing and highly diversified dung resource provided by the explosive radiation of mammals.

There can be little doubt that the increasing availability of mammal dung, particularly in open tropical savanna and grassland habitats that favour herds of grazing herbivores, especially from the Miocene onwards, greatly facilitated dung beetle evolution and specialization. This new resource was apparently relatively free of competition from other invertebrate groups and still is, with scarabaeine dung beetles being the major consumers of fresh herbivore dung in all warmer areas of the world.

Cambefort (1991a) has discussed the evolution of dung feeding in adult Scarabaeoidea from a hard (*i.e.* detritus) to a soft (dung) diet. He considers all Scarabaeinae and some Aphodiinae to be "soft-diet" consumers. The hypothesised process is as follows. Detritus is made up of relatively large fragments of vegetable matter and as decomposition proceeds the fragments become smaller and more microbe-rich. If decomposition is taking place in a moist environment the detritus becomes pasty in consistency, and the substance becomes increasingly more microbe-rich, with the semi-liquid components eventually being the most nutritious. Some extant dung beetle genera (*Bdelyrus, Bdelyropsis* and *Paraphytus*) are thought to feed on a resource approaching this putative ancestral diet, all of which are tropical forest inhabitants (the first two Neotropical, the latter Afro-Oriental) where the right combination of factors prevail. A hypothesised switch to feeding on moist herbivore dung from an ancestral diet of this nature is easy to understand in view of the similarity of the two substrates, - dung being little else than fragments of cellulose, remnants of gut epithelium of the animal that voided it, and a broth of microbes. The adults of all "typical" dung feeders whose precise diets have been determined, feed exclusively on tiny fragments (less than 100μm in diameter) suspended in the liquid fraction of the dung which they filter from the source (Holter *et al.* 2002; Holter and Scholtz 2005; Holter and Scholtz 2007; see details in Chapter 6). In spite of the widely-held assumption that beetles triturate large particles in the mandibular molar lobes and then filter out and digest only the smallest particles (Miller 1961; Cambefort 1991a), there is no empirical evidence to suggest that such a process actually takes place (Holter 2000; Holter *et al.* 2002). Cambefort's (1991a) use as a model of the distantly-related Geotrupidae, which feed on humus and dung, as a possible example of the transition from a hard to a soft diet in dung beetles does not offer a satisfactory explanation in view of the recent study by Holter (2004) which indicated that the Geotrupidae, like the Scarabaeinae, actually feed on the liquid components already present in the food. Consequently, they are also exclusively soft diet consumers. Some members of the hypothesised sister-group of the Scarabaeinae, the Aphodiinae, also feed on dung fluids in much the same way that Scarabaeinae do (Holter 2000), but it is quite likely that they evolved this feeding strategy independently of, and possibly simultaneously to, the Scarabaeinae.

Consequently, as discussed in Chapter 2.1, the unexploited and increasing availability during the Tertiary of herbivorous mammal dung with a high proportion of highly nutritious liquid created niche space for the evolution of dung fluid feeders, and is one of the obvious reasons for the success of dung beetles. This large resource was utilised most successfully by the Scarabaeinae (with about 5000 species world wide), especially in tropical regions, but also by Geotrupidae (about 150 species), exclusively in temperate regions, and Aphodiinae (with about 1000 species of dung feeders), mostly also in cooler regions, although many species have successfully invaded tropical areas and co-exist with Scarabaeinae. Some temperate and tropical groups of another unrelated beetle family, Hydrophilidae, have also exploited the dung niche, and as with the Scarabaeoidea discussed above, its members feed on the same small dung particles in wet dung in much the same way as the latter (Holter 2004). So, clearly, almost identical food preferences and feeding patterns developed independently but in parallel to each other in various beetle groups, some of which are closely related to Scarabaeinae (Aphodiinae), others distantly related (Geotrupidae), and yet others, unrelated, (Hydrophilidae).

If humus-feeding and a dependence on microbes, especially fungi, was indeed the ancestral food of dung beetles (Cambefort 1991a; Scholtz and Chown 1995), the persistence of a fungal diet over millennia in the African dichotomiine genus *Coptorhina*, one of the most basal groups in various morphological (Zunino 1983; Philips *et al.* 2004b) and molecular (Monaghan *et al.* 2007) phylogenetic reconstructions, is an intriguing possibility. Many other groups belonging to various of the tribes are thought to depend on microbially-enriched humus for food (for example the tiny [< 3 mm long] Afrotemperate forest canthonines which are only ever collected in humus (Deschodt and Scholtz 2008); the Australian canthonine *Cephalodesmius* which collects fallen leaves on the forest floor and prepares a food source of masticated fungus-enriched humus (Monteith and Storey 1981); the Afro-Oriental dichotomiine *Paraphytus* (Cambefort and Walter 1985); various ant-nest-associated species such as the Neotropical oniticelline *Attavicinus monstrosus* (Halffter and Matthews 1966; Philips and Bell 2008); and the African onthophagine *Megaponerophilus* (Davis *et al.* 2008b). With the exception of *Paraphytus* and *Cephalodesmius,* and the small forest canthonines whose sister-group relationships are currently unclear, all of the others belong to modern groups and share probable sister-group relationships with dung-feeding species, so they have undoubtedly adapted secondarily to humus from dung-feeding. The only detritus-feeder in which possible dependence on fungi for its nutritional requirements is well-studied, is the south-west African scarabaeine *Pachysoma glentoni,* in which it was conclusively shown that the beetles eat the detritus itself and that all their nitrogen and carbohydrate needs are obtained from the detritus and not from fungi at all (Holter *et al*. 2009). This is the more unusual because *Pachysoma* is the most derived genus in the modern ball-rolling tribe Scarabaeini (Sole *et al*. 2005; Forgie *et al*. 2006). So, clearly, switches in feeding preferences of this nature have happened frequently and over short evolutionary time spans.

Above, we have alluded to the fact that it is generally agreed that dung beetles probably evolved from a detritus-feeding ancestor. Concomitant with the switch by adults from feeding on detritus, to feeding on dung, would have come the behavioural changes associated with the formation and provision of nests with brood masses or balls made from the same, but much more malleable, resource. The advantages of forming and breeding in nests are discussed in subsequent chapters.

CHAPTER 2

EVOLUTION OF FEEDING, COMPETITION, AND LIFE HISTORY STRATEGIES

2.1 FEEDING STRATEGIES

Dung beetle success can largely be attributed to the evolution of several morphological specializations and behavioural strategies that set them apart from their relatives, and to their ability to compete successfully for food amongst themselves. Some of these are the probably pre-adapted mouthparts (Halffter and Edmonds 1982 – also see Chapter 5.1) for feeding on wet dung derived from a wet detritus-feeding ancestor, exploitation of vacant niche space presented by the diversity and quantity of mammal dung available during the Tertiary, the evolution of food relocation strategies, subterranean nests, and brood care. These have resulted in high fitness based on low fecundity, but concomitant low mortality, during development.

The opening up of habitats that led to the establishment of grasslands and savannas, particularly from the Miocene onwards, and the evolution of mammalian herbivores that lived in large herds and produced large quantities of moist dung, created ideal conditions for the exploitation by, and evolution of, dung feeding insects. However, the openness of the habitat exposed the dung and insects attending it to relatively harsh and probably unpredictable climatic conditions that could lead to desiccation of, and nutrient leaching from, the dung, as well as to disturbance from other, competing dung-feeding insects, such as flies and other beetles. Exploitation of the dung under these conditions would necessitate behaviour that led to its rapid use before it dried out, or the evolution of strategies that contributed to protecting it from the elements so that it could be used over an extended period. Dung beetles overcame these hurdles by locating the dung quickly, and then moving it to a protected environment where it was less susceptible to climatic vagaries, and less vulnerable to competition for the dung, and where they would be better protected from predation – they buried it for later consumption, or to breed in it. The long lives of the females of some species is possibly as a result of the often extended periods they spend underground with their brood, safe from predation and inhospitable climatic conditions, and the manifold strategies that they developed to exploit the dung resource optimally led to the complex nesting and breeding behaviours that make dung beetles unique.

Although the presence of large numbers of herbivores provided dung beetles with a sufficiently dependable resource for numerous species to feed on, in some regions and at some times, dung would have been scarce or unavailable, which may have necessitated a shift to alternative food sources. The ability to feed on liquid food with high nutritional content pre-adapted beetles to feeding on liquids from other food sources such as carrion, rotting fruit and other forms of decomposing organic matter. However, at least one well documented reversal from a liquid to a hard diet has been documented in the Scarabaeini genus *Pachysoma* (Holter *et al.* 2009), which undoubtedly masticates the hard detritus it collects for food. It is closely related to the exclusively liquid-feeding members of the genus *Scarabaeus* (Forgie *et al.* 2006). (See Chapter 12.2.2).

Although it would appear that dung feeding is an autapomorphic state for all dung beetles and that alternative feeding strategies secondarily evolved from dung-feeding ancestors, it is not clear whether detritus-feeding in some primitive groups is a primary or secondary strategy. This is particularly so in the case of very small (<3 mm long) relictual southern African canthonine groups which make up a part of the litter fauna in Afrotemperate forest fragments, and which apparently don't feed on dung at all (Deschodt and Scholtz 2008). Whether they are very similar to, and possibly directly descended from, an ancient detritus-feeding lineage is unclear. The tropical forest genera *Bdelyrus*, *Bdelyropsis* and *Paraphytus* mentioned above, which apparently feed on well-rotted humus, also belong to putatively ancient lineages. Another basal genus whose feeding strategy is very different from modern groups is the African *Coptorhina*, an obligate basidiomycete mushroom feeder. Once again, whether this is a reversal to a dependence on fungi or a continuation of an ancient feeding pattern is not clear.

By far the greatest number of Scarabaeinae species feed on herbivore dung as adults and use the same resource for brood provision, almost exclusively in pre-formed brood masses. So, if dung beetles radiated in response to the availability of mammal dung, what of the large numbers of "dung beetles" that don't feed on dung but on humus, carrion or fungi, for instance? Some of these have obviously evolved from dung-feeding lineages and the current feeding pattern is merely a reflection of a change in diet. But many lineages, some of which are considered "primitive", probably don't feed on dung at all and possibly evolved from groups that may never have fed on dung.

2.1.1 Alternative food sources

2.1.1.1 Vertebrate carrion

Tropical forests possibly have the largest number of non-dung-feeding dung beetles, with fruit- and carrion-feeding species common, although many of them are apparently actually generalist feeders (Gill 1991; Hanski and Krikken 1991). The change from dung-feeding to vertebrate carrion, in particularly the larger Neotropical species, such as those of the genera *Coprophanaeus, Deltochilum* and *Canthon,* is postulated to have happened with a switch from the dung of Pleistocene mega-herbivores necessitated by the extinction of the latter (Halffter and Matthews 1966). A similar situation of feeding generalists has also been recorded for the dung beetle communities [predominated by *Onthophagus* species] of South-East Asian tropical forests, of which a characteristic feature is the substantial overlap in species composition with carrion communities (Hanski and Krikken 1991). Carrion-feeding is generally thought to be uncommon in Africa because of the abundance of large vertebrate scavengers and the short duration of exposure of most carcasses (Halffter and Matthews 1966). However, Braack (1986) recorded 44 species of Scarabaeinae [probably roughly one-third of the species there] attracted to approximately 50 kg antelope carcases in the Kruger National Park, South Africa. This was in spite of high densities of vertebrate scavengers such as vultures, hyenas and jackals, which compete fiercely for carrion. Most of the dung beetle species are, however, also known from dung, so whether they were opportunistically feeding on the carrion, or were attracted to the rumen contents, or both, is not clear. At least one of these, though, the large canthonine *Anachalcos convexus*, is known to prefer carrion as adults (personal observation) but has been recorded to breed in herbivore dung (Marcus Byrne, University of the Witwatersrand, South Africa, personal communication). Another unusual African carrion specialist is the coprine, *Metacatharsius opacus*, in the Kalahari Desert of southern Africa, an area of abundant scavengers and very low densities of carrion (Tshikae *et al.* 2008), but about whose biology very little is known.

2.1.1.2 Invertebrate carrion

Dung beetles that feed on invertebrate carrion are apparently quite common in various parts of the world although many of the reported cases are opportunistic events by generalist feeders (Halffter and Matthews 1966). However, feeding on millipedes represents an unusual case of necrophagy. Millipedes are often very numerous with large individuals of up to 30 cm common in tropical and savanna regions, of particularly Africa, and seemingly attract a particular guild of specialist feeders to their defensive secretions. The main chemical components of spirostreptid millipede (Diplopoda: Juliforma, orders Spirostreptida, Spirobolida and Julida) defensive secretions are 1,4 benzoquinones which are strongly repellent to potential vertebrate and invertebrate predators, and require sophisticated feeding strategies to avoid them (see Schmitt *et al.* 2004). However, in spite of these repellent secretions, many animals prey on millipedes, and many dung beetles feed on freshly dead millipedes. Brühl and Krell (2003) reported about 50 species of Scarabaeoidea feeding on spirostreptid millipede remains in the Côte d'Ivoire, many of which were members of *Onthophagus*. Schmitt *et al.* (2004), also working in Côte d'Ivoire, baited traps with spirostreptid millipede secretions and collected large numbers of specimens of seven species of *Onthophagus*. They reported that the main components of the defensive secretions were 2-methyl-1,4-benzoquinone (toluquinone) and 2-methoxy-3-methyl-1,4-benzoquinone with the former as an isolate, always more attractive to the dung beetles. The seven *Onthophagus* species were considered by Schmitt *et al.* (2004) to be millipede specialists that are strongly attracted to millipede defensive secretions, which places them at an advantage over general invertebrate carrion feeders that are attracted by the smell of decay which only follows some time after death of the millipede. Apparently the millipede specialists feed on the millipede tissues and sequester it for breeding, although the details of this are scant.

All of the species discussed above are small tunnellers, but one very unusual group of southern African ball-rollers, the subgenus *Sceliages* of the well-known genus *Scarabaeus*, with seven localised species, has exploited the abundance of large spirostreptid millipedes after rain. All of the species are obligate millipede-feeders (Forgie *et al.* 2002). Females disarticulate freshly-dead millipedes and use the internal tissues and gut contents to form balls, using a unique brood-construction strategy (see Chapter 4.1.5.2).

2.1.1.3 Predation

In an unusual strategy, possibly derived from feeding on invertebrate carrion, two Brazilian species of *Canthon*, *C. dives* and *C. virens,* have been reported to prey on live alates of *Atta* species of leaf-cutter ants (Halffter and Matthews 1966). The former dung beetle species has also been recorded on carrion, but the latter is thought to be an obligate ant predator (Hertel and Colli 1998). Hertel and Colli (1998) reported that *Atta laevigata* female alates (25.0 mm long) that landed after a short emergence flight were attacked by the much smaller *C. vi-*

rens (body length about 10.0 mm). The females had mostly shed their wings. The beetles mounted the ants and decapitated them by prising the head from the body with the clypeus and fore tibiae and then rolling the body away to be buried where they were fed on or bred in. Halffter and Matthews (1966) claimed that several brood balls were formed from the bodies of gravid female ants.

2.1.1.4 Association with land snails

The Neotropical genus *Zonocopris*, (with two species), is considered to be a "roller" (Vaz-de-Mello 2007a) and has one of the most unusual feeding associations yet recorded for a dung beetle. Both species appear to have an obligatory association with giant land snails (*Strophoceilus* and *Megalobulimus*) where the small beetles (< 5 mm) live on the snails' mantles and feed on mucous (Vaz-de-Mello 2007a). Although this association was described as early as 1867, and the first species described in 1868, the details of the relationship between the beetles and the snails remained unclear (Vaz-de-Mello 2007a), with various claims over the years that the beetles fed either on mucous or snail faeces. Vaz-de-Mello (2007a) kept specimens of *Z. gibbicollis* and snails in the laboratory for several months and recorded that the beetles mostly remained on the same snail, seldom moving to another, and that the beetles ate only mucous, although snail faeces were plentiful in the terraria where they were kept. The beetles mated frequently on the snails but no signs of immatures or nests were located in the terraria. The snails burrowed into the soil to quiesce during the cooler months and the beetles remained on the exposed parts of the mantle, apparently also with reduced activity. Breeding in these species, tantalizingly, however, still remains unknown.

2.1.1.5 Fungi

Fungi are thought to have been an integral component of the ancestral diet of dung beetles (Cambefort 1991a; Scholtz and Chown 1995), and to contribute significantly to the nutritional requirements of modern dung beetles irrespective of their diet, in view of the almost ubiquitous nature of many fungi. These are, by implication, very small particles of decomposition agents and those preying on them, which provide a rich broth of carbohydrates and proteins. The main fungi are possibly yeasts (Blastomycetes) and Hyphomycetes. However, there are dung beetle groups associated with large "solid" fungi in the form of mushrooms, puffballs and bracket fungi (Basidiomycetes). Most appear to be opportunistic associations (see Halffter and Matthews 1966), but an obligatory dependence on mushrooms and puffballs has been recorded in the African genus *Coptorhina* (Davis *et al*. 2008b; Frolov *et al*. 2008 – see details in Chapter 4.1.5.1). Adults collect pieces of the mushrooms, which they drag into underground burrows where they are moulded into soil-covered brood balls. Davis *et al*. 2008b also speculated that the closely-related genera *Frankenbergerius* and *Delopleurus* may feed similarly on fungi.

2.1.1.6 Detritus

It is generally agreed that dung beetles evolved from a detritus-feeding ancestor, but possibly with high dependence on micro-organisms in the detritus for most of the beetles' nutritional demands (Cambefort 1991a; Scholtz and Chown 1995). From Holter and colleagues' studies of feeding in adult dung beetles (e.g. Holter *et al*. 2002), it is clear that they feed mainly on a suspension of tiny solid particles suspended in a liquid base, and, consequently, that they do not depend on cellulose, the major component of detritus, at all. Some genera are intimately associated with "detritus", such as: those found in ants' nests (Halffter and Matthews 1966 listed 14 species of 10 genera in the New World from Attini nests); the Afro-Asian *Paraphytus* (Cambefort and Walter 1985 – which live beneath the bark of fallen forest trees); and the unusual Australian genus *Cephalodesmius* (Monteith and Storey 1981 – permanently bonded pairs live on the forest floor where they harvest fallen leaves which they mould into "compost" in the burrow, and on which the larvae are fed). However, in none of these examples has it been shown that the adults actually eat the detritus, and in all probability subsist, as do other dung beetles, on fluids associated with the decomposing detritus.

The south-west African desert species *Pachysoma glentoni*, on the other hand, is without doubt a detritus-feeder, collecting and masticating large, coarse plant pieces, and depending largely on cellulose for its nutritional requirements (Holter *et al*. 2009) (See Chapter 6.4). The detritus collected by this species consists largely of fallen flowers from surrounding bushes, but also various other plant parts. An analysis of the detritus showed that it is actually nutritionally rich, with carbon to nitrogen ratios (a measure of digestibility) as favourable to detritivores, as the high quality graze available to domestic livestock feeding on well-watered and -fertilized European pastures (Holter *et al*. 2009). This species is unique for several reasons (aspects of its ecology are dealt with in detail in several sections in the book), but of relevance here is that it is phylogenetically a "roller", which should feed on dung fluids and roll balls of dung as do its relatives, neither of which it actually does.

2.2 COMPETITION

Because most of the food that dung beetles depend on is ephemeral (dung, carrion, fungi, fruits) and patchily distributed, and many species depend on it in some form, competition is fierce, both between individuals of the same species which have identical ecological requirements, but also between different species with varying levels of overlapping requirements. There is also a host of other insect species such as flies and other beetles which also compete with the dung beetles for the resources. Bernon (1981) recorded between 742 – 1,585 beetles colonizing fresh cattle dung pats over a 24-hour period in central South Africa during summer. These consisted of 161 beetle species including Scarabaeinae (42%), Aphodiinae (35%), Hydrophilidae (9%), Staphylinidae (9%) and Histeridae (5%) as well as numerous mites, flies and other arthropods. Doube (1986), working at a location in coastal Natal, South Africa, recorded from dung a total of 146 species of scarabaeine dung beetles, 43 species of Aphodiinae, 92 species of Staphylinidae, 27 of Histeridae and 13 of Hydrophilidae as well as about 20 species of flies, 100-odd species of mites and a few species of ants. Davis *et al*. (1988), working in the same area as Doube (1986) recorded 134 species of non-scarabaeine beetles in cattle dung exposed for 12 hours. These consisted of 100 species of Staphylinidae, 21 Histeridae and 13 Hydrophilidae. One of us (Scholtz personal observation) counted about 7000 individuals of a roughly-estimated 120 species of dung beetles in a single pile (about 25 kg) of elephant dung in the Kruger National Park, South Africa and Anderson and Coe (1974) counted 16 000 dung beetles attracted to 1.5 l of elephant dung over a period of two hours in East Africa.

All of these complex interactions have moulded dung beetle feeding activity and nesting behaviour and to a large extent determine the ecological success of a particular strategy or species. However, how much of the dung beetle population structure that we see in dung communities is the “ghost of competition past” (Connell 1980) or the result of more recent environmental pressures is impossible to determine.

Competition extends to all facets of feeding and breeding; the food, its origin, age, place and timing of deposition, the vegetation type in which it lies, and the soil type on which it lies. Every species of dung beetle has particular preferences with regard to all of these. Intra- and interspecific competition for dung can take a number of forms such as: the fighting often seen in rollers, where beetles contest the possession of a ball; resource pre-emption, in which the first colonisers exclude others such as in *Heliocopris* where the first to arrive at a dung pat cover the whole resource with soil; and scramble competition, when high densities of dung beetles at a source result in most individuals being deprived of enough resource for breeding (introduced *Sisyphus* in Australia – Doube *et al.* 1991)

There is a clear hierarchy amongst dung beetle species in their ability to compete for dung, and Doube (1990) divided the southern African dung beetle fauna into seven functional groups (FG) on the basis of their competitive ability. These are, in order of their competitive dominance, large rollers (FG I, e.g. some Scarabaeini) and fast-burying tunnellers (FG III, e.g. some Coprini, Onitini and Onthophagini), which are small or large, but aggressive beetles that quickly remove dung from the source. Small rollers (FG II, e.g. some Sisyphini) are also often strong competitors. Functional groups IV and V are large (e.g. some Onitini) and small (e.g. some Onthophagini), respectively, and are slow-burying tunnellers. Those that build shallow nests (FG V, e.g. some Oniticellini) and nest within the dung (FG VI, e.g. some Oniticellini) are poor competitors and most likely to be disturbed by other groups. Members of Functional Group VI are kleptoparasites which use the dung buried by other species (e.g. some Onthophagini).

2.2.1 Interference competition between dung beetles and other insects

The dung community is made up of large numbers of invertebrates other than dung beetles, but of these, flies are probably the most important competitors with the beetles for dung. However, the competition is usually strongly asymmetric, with beetles suppressing flies in most instances. This was one of the main reasons for the introduction of dung beetles into Australia in the 1970's, where two species of flies had benefited from the increasing amount of cattle dung generated by the growing herds of cattle there, and the absence of a suitable dung beetle fauna to process the dung (Waterhouse 1974; Doube *et al.* 1991).

Ridsdill-Smith and Matthiessen (1988) demonstrated that interference competition caused by the activity of two introduced exotic dung beetles species, *Euoniticellus pallipes* and *Onthophagus binodis*, into south-western Australia, reduced the numbers of the nuisance fly *Musca vetustissima* to about 10% of the level prior to the introduction. Field experiments by Doube *et al.* (1988) in South Africa and Australia demonstrated that dung beetle interference, as well as the effect of predation and of parasitoids, reduced the populations of the dung flies *Haematobia thirouxi* (Africa) and *H. irritans* (Australia) by up to 98%. However, the Australian examples represent a native dung fauna mostly incapable of degrading the dung produced by introduced cattle and which led to a massive increase in a resource that did not have a co-evolved fauna. The interactions recorded between introduced flies and dung beetles is therefore unlike that in any natural situation, where there would be a multitude of complex interactions between numerous species of the dung community, and probably, more symmetrical interaction between flies and dung beetles.

In a case of interference competition between carrion-feeding beetles and blowflies, the males of *Canthon cyanellus*, a common Central American carrion-feeding roller, secrete a chemical substance from their seventh abdominal sternite onto the surface of their balls. The primary aim of this is thought to be to attract females over a short distance, but the secretion is also apparently repellent to *Calliphora* blow flies (Bellés and Favila 1984; Favila 1988; Ortiz-Domínguez *et al*. 2006).

2.2.2 Intra-specific competition

Most natural habitats consist of many species of dung beetles, making studies of the effects of intra-specific competition difficult. However, dung beetles introduced into Australia for the control of dung often occur in virtual single-species assemblages of up to thousands of individuals per dung pat, with the result that there are times when the beetles have the potential to remove more dung than is available to them, for example, when *Neosisyphus spinipes* are abundant (thousands per pat) only a small proportion of them succeed in making dung balls (Doube *et al*. 1991).

Ridsdill-Smith *et al.* (1982) found that under laboratory conditions, increasing the numbers of individuals of the tunneller, *Onthophagus binodis*, (which was also successfully introduced into Australia) per pat above a critical density, resulted in a progressive reduction in the level of dung burial and brood production. They found that brood production increased with beetle densities up to 20-30 beetles per litre of dung (producing up to about 100 brood balls per litre), but then decreased markedly until, at 320 beetles per litre of dung, fewer than five brood balls were formed.

2.2.3 Aggregation

Individual dung pats are often occupied by several species of dung beetles with different resource-use strategies (Kohlmann 1991). Sometimes very large numbers of a species are found in a pat, while others with similar resource-use strategies are apparently excluded. Kohlmannn (1991) recorded that at a site in Mexico, when the locally common, small (7.0 mm) dichotomiine species, *Ateu-*

chus carolinae, was present, they excluded other common species of *Onthophagus, Copris, Phanaeus* and *Dichotomius* from the pats. This varied from partial exclusion when numbers of *A. carolinae* were low, to total exclusion when numbers rose to 27 to 48 individuals per pat. The density of *A. carolinae* (three density classes: 0, 1-27 and 27-48 individuals per pat) had a highly significant effect on the numbers of other species (Fig. 2.1; F[2,20] = 8.72, $P<0.005$). However, it was not clear whether this apparent exclusion was due to pheromones, interference competition, lack of space due to large numbers of individuals, or to differences in diel activities.

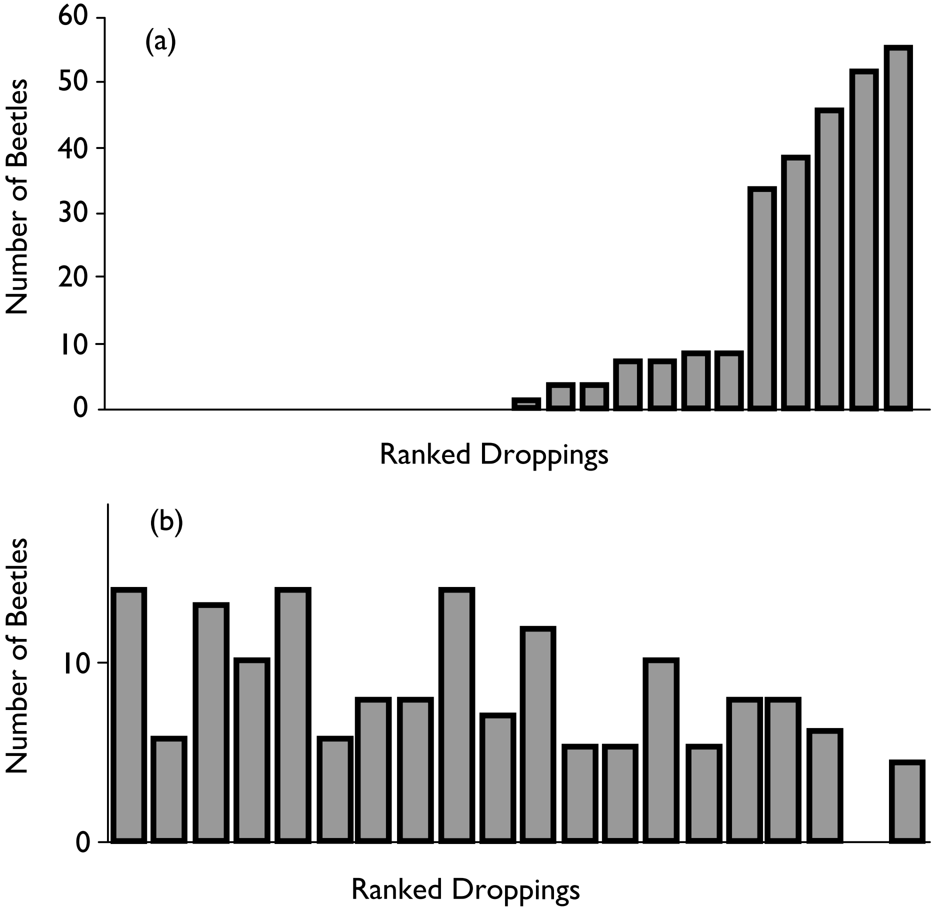


Fig. 2.1. (a) Number of individuals of *Ateuchus carolinae* in 27 similar-looking cattle pats in a forest-grassland ecotone in Teloloapan, Guerrero, Mexico; (b) number of individuals of other dung beetle specimens in the same pats. (Redrawn from Hanski and Cambefort 1991e).

Krell *et al.* (2003), in a study of dung beetle guilds in a forest-savanna mosaic in West Africa, proposed that spatial separation of the guilds was due to a trade-off between competitive superiority and energetic constraints. They studied dung beetle assemblages of fresh Cape buffalo (*Syncerus caffer*) dung in three adjacent habitats; savanna parkland, gallery forest, and river valley grassland. Savanna made up > 83%, forest 2.2% and grassland < 1% of the total area. They recorded clear differences in dung beetle guilds in the various habitats and at different times of the day (Fig. 2.2). By day, rollers and their kleptoparasites were dominant in the savanna, the largest habitat, but the former were present in very low numbers in the other habitats at any time, while the latter, surprisingly, in view of the absence of their hosts, dominated in the river valley grassland by day as well. Tunnellers dominated in the savanna at night and in the grassland by day. Endocoprids, most of which were members of the Aphodiinae, were most abundant in the grassland and forest by day, and the savanna at night, although their relative abundances were mostly low compared to the other guilds. However, they were much more abundant than the other guilds in both grassland and forest at night.

Krell *et al.* (2003) explained the results in terms of an aggregation model (Tokeshi 1999, in Krell *et al.* 2003) in which the competitively superior rollers aggregated in the dung in the savanna, and, together with their kleptoparasites predominated during the day. At night the rollers were virtually absent, and the competitively inferior tunnellers and dwellers could use the resource. The competitively most inferior dwellers aggregated in the grassland where all superior competitors were virtually absent. Furthermore, they hypothesised that the lower abundance of dung beetles in the forest than in the savanna, in spite of an abundance of dung, might be explained in terms of the sizes of the respective habitats, although they were unable to support this from their data. So, an alternative hypothesis proposed was that the beetles' physiological preferences might be responsible for the patterns, since soil and air temperatures differed significantly between open and closed habitats. Forming and rolling dung balls is energetically costly (Bartholomew and Heinrich 1978) and body temperature is likely to be optimised by external heating in open savanna on sunny days, with the result that rollers could be competitively inferior to forest species there. Furthermore, forests might present flight barriers to rollers that prefer open sunny places. Although grassland had adequate dung and suitable temperatures, the soil was shallow, making it unsuitable for both rollers and tunnellers, but suitable for dwellers, which exploited it very successfully in the absence of the much more superior competitors in the form of rollers and tunnellers.

Krell *et al.* (2003), consequently, concluded that significant differences in guild structure amongst dung beetles of different adjacent habitats may be de-

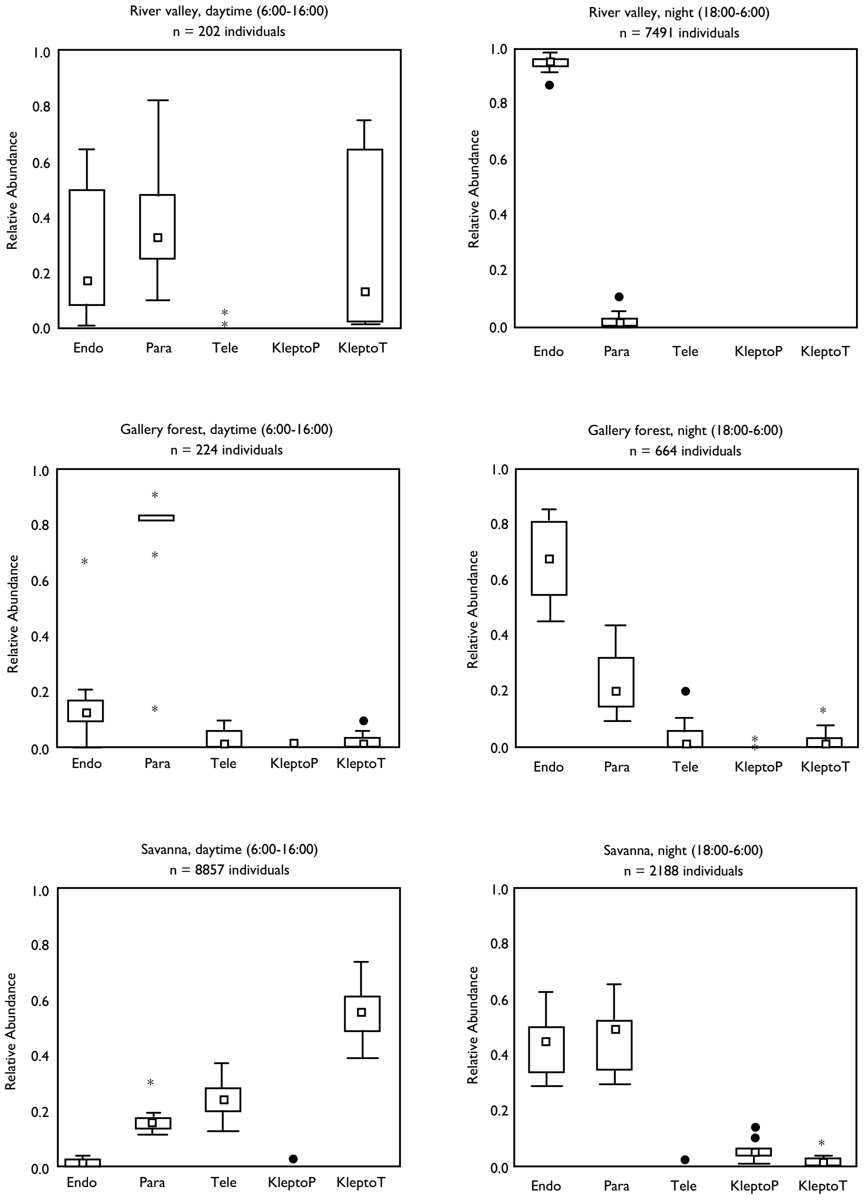


Fig. 2.2. Guild structure of coprocenoses in three habitats (savanna, gallery forest, grassland or river valley) at daytime and at night. Box-Whisker-Plots from medians (□) of relative abundance (percentages) of guilds, with 25%/75% quartiles (rectangle), minimum/maximum values (bar), outliers (o) and extremes (*). Endo=endocoprids, KleptoT= kleptoparasites of telecoprids. KleptoP=kleptoparasites of paracoprids. Tele= telecoprids. Para=paracoprids. (Redrawn from Krell *et al.* 2003).

termined by effects of the habitat itself. Furthermore, the spatial separation of competitively inferior guilds from more superior ones may be driven by energetic constraints that enable them to persist sympatrically, with the hierarchy of competitive superiority of dwellers < tunnellers < rollers determined by increasing energetic costs and decreasing ecological tolerance.

2.2.4 Competition among rollers

Rolling is thought to have evolved as a result of competition at the dung source, and is a strategy for quickly removing an adequate amount of dung for the individual's food and breeding requirements away from the focus of the competition. However, fighting amongst rollers at or near a dung source is a common and conspicuous occurrence, with the energy expended in fighting apparently compensated for by the theft of a ball rolled by another individual. Heinrich and Bartholomew (1979) have shown that the large, nocturnal ball-roller *Scarabaeus (Kheper) laevistriatus*' body temperature determines the speed at which it can form and roll a ball, and, coupled with size, also the degree of success during combat over a ball. The beetles generate and maintain high thoracic temperature endothermically during flight, and maintain it while forming and rolling balls. Individuals with the highest body temperatures are more successful at interference, as well as pre-emptive resource competition. (Table 2.1).

Interference competition also occurs between different species of rollers, and the larger species are, not surprisingly, more successful in these interactions than smaller species although the competition is usually limited to species of similar size because of the similarity of specific needs (see Table 2.2). Assuming that the difference in body size influences the degree of interspecific competition in a pair of species, we could expect that the most dominant species at a locality would be better spaced out in size than are species in a random selection of equally many species from the species pool (Hanski 1982, quoted by Cambefort

Table 2.1. Weight and thoracic temperature of *Scarabaeus (Kheper) laevistriatus* involved in contests over dung balls. (After Heinrich and Bartholomew 1979).

Body Weight (g)			Temperature °C			
	x	SE	n	x	SE	n
Winners	3.52	0.07	118	38.7	0.23	120
Losers	3.22	0.06	118	35.2	0.34	120
t-value	3.15			8.65		
P	0.001			0.001		

1991c). Cambefort (1991c) gave an example from West Africa to illustrate this observation and recorded that the sizes of the eight most dominant rollers were well spaced in size at 8, 17, 62, 130, 310, 540, 1165 and 1675 mg fresh mass. He concluded that because interspecific competition is a key interaction between rollers, these results strongly suggest that it affects the abundance relations and community structure of rollers. Young (1978) provided empirical evidence based on laboratory experiments that there is a linear competitive hierarchy amongst rollers, with larger species competitively dominant over smaller ones.

Ybarrondo and Heinrich (1996) compared the typical ball-forming and – rolling strategy of *Scarabaeus (Kheper) nigroaeneus,* with that of a slightly smaller species, *Scarabaeus galenus*, foraging at the same piles of impala antelope (*Aepyceros melampus*) dung pellets in the Kruger National Park, South Africa. The latter dung beetle is phylogenetically a typical roller, although it falls alone on a clade of the phylogram (Forgie *et al*. 2006) and is behaviourally unlike most of its relatives. A pair of the beetles digs a burrow close to a dung pile and the males collect individual pellets, holding them off the ground in the hind legs and walking backwards to the burrow, where they are deposited. A pair of these

Table 2.2. Observations on interspecific interference competition in pairs of similar-sized dung beetles. (Adapted from Hanski and Cambefort 1991b).

Dominant (Subordinate) Species	**Length (mm)**	**Dung Type**	**Locality**
Gymnopleurus coerulescens	10	human	West Africa
(Sisyphus biarmatus)	9		
Scarabaeus (K) *lamarcki*	35	cattle	South Africa
(Pachylomera femoralis)	40		
Scarabaeus (K) *laevistriatus*	37	elephant	East Africa
(Scarabaeus (K) *platynotus)*	32		
Canthon septemmaculatus	10	carrion	Central America
(Canthon cyanellus)	8		
Paragymnopleurus maurus	14	human	SE Asia
(Sisyphus thoracicus)	6		
Copris lugubris	16	cattle	Central America
(Phanaeus tridens)	15		
Neosisyphus spinipes	9	cattle	South Africa
Neosisyphus infuscatus	8		
Canthon angustatus	11	human	South America
(Canthidium sp.)	7		
Oxysternon conspicillatus	26	human	South America
(Canthon angustatus)	11		

sequestered about 65 pellets (*ca* 1.0 x 1.2 cm each) in the time that it took a *S. nigroaeneus* to form a ball from 3-5 pellets. The authors did not determine the numbers of brood balls formed from this strategy but, by comparison, about 10 times more dung was collected by this method than by the typical roller method of its relative. Consequently, this strategy minimizes the effects of competition with congeners, reduces the time spent working on the ball and vulnerable to kleptoparasites (which were abundant at the site), and reduces desiccation.

2.2.5 Competition among dwellers

Because dwellers live and breed inside the dung source they are potentially subject to interference by the competitively superior tunnellers and rollers. However, they avoid this to a large extent by breeding during times when the other species are not active, or inside dung that is unsuitable for potential competitors. Most of the oniticelline dwellers are active during cool and dry periods (e.g. *Oniticellus planatus, O. formosus* – Davis 1989b) or when the dung is no longer attractive to other dung beetles (e.g. the African *Tragiscus dimidiatus* – Davis 1977).

Davis (1989b) studied colonization of experimental dung pats by two species of *Oniticellus*, *O. planatus* and *O. formosus*, in South Africa over an entire dry season and over 1.6 rainy seasons. Both species showed year-round activity although their patterns of abundance, colonization and residence in cattle dung varied seasonally. During the warm, rainy season (October - April), when there was extensive burial of dung by tunnellers, mean numbers of *O. planatus* were greatest in 3-day old sample pats, and those of *O. formosus* in 3- and 7-day old samples. During the cool, dry season, when there was little dung removal, mean numbers of both species were greatest in 14-day old sample pats. Monthly totals of both species were greatest in the dry season, although overall population density was low (Figs 2.3, 2.4). The inverse relationship shown by Davis (1989b) between dung removal and production of *Oniticellus* broods points to resource pre-emption by tunnellers, and to *Oniticellus* seeking breeding space removed from competition from tunnellers (Table 2.3).

2.2.6 Competition among tunnellers

Tunnellers usually dominate dung communities in terms of numbers of species and biomass of individuals, and in tropical regions the largest species may be orders of magnitude bigger than the smallest, with a full range of sizes in between. And, although they have the same fundamental requirements of food and suit-

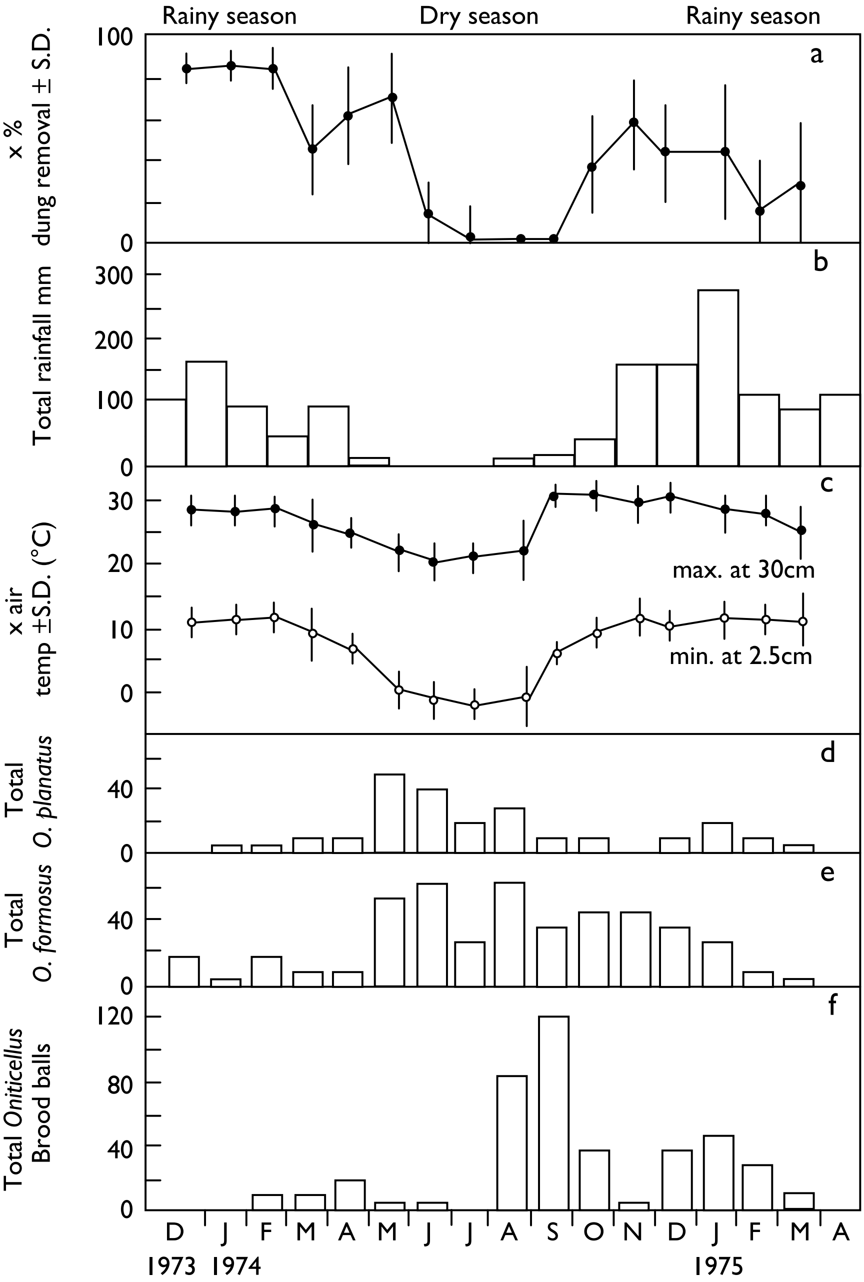


Fig. 2.3. Seasonal pattern of dung removal from 21 day old dung pads; and seasonal activity of *Oniticellus* spp. in South Africa. (Totals of beetles and broods are from 60 pads exposed during each 21 days sampling period. Temperature measurements are those recorded during sampling periods only). (Based on Davis 1989b).

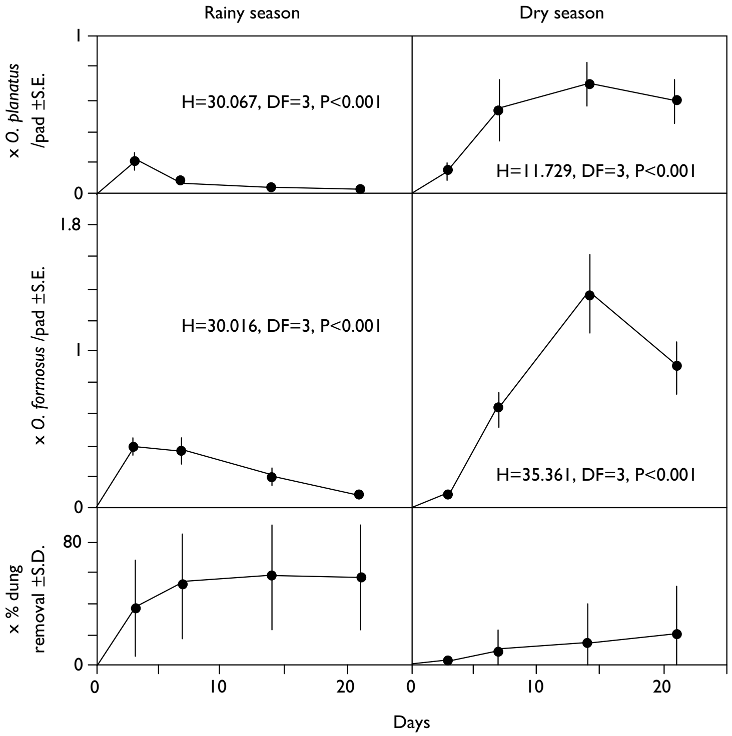


Fig. 2.4. Colonization patterns of *Oniticellus* spp. and dung removal from cattle pads at a site in South Africa during a single cool, dry season and 1.6 warm, rainy seasons. Results of Kruskal-Wallis tests on differences in frequency distribution of *Oniticellus* spp. with age of sample pads. (Based on Davis 1989b).

Table 2.3. Brood balls and brood chamber production by *Oniticellus* in relation to dung removal by other dung beetle groups from 1.5*l* cattle pads left in the field for 14 and 21 days (pooled data) at a site in South Africa. (Based on Davis 1989b).

Percentage dung removal classes	Total no. pads	Total no. brood chambers	Total no. brood balls	x no. (S.D.) broods/ chamber	x no. (S.D.) chambers/ pad*
0-20	196	56	275	4.9 (3.6)	0.29 (0.53) a
21-40	43	7	24	3.4 (3.4)	0.16 (0.37) ab
41-60	35	4	14	3.5 (2.4)	0.11 (0.32) ab
61-80	76	7	29	4.1 (3.5)	0.09 (0.29) b
81-100	113	2	2	1.0 (0)	0.02 (0.13) c

* Values followed by a different letter differed significantly ($p < 0.05$) (Kruskal-Wallis tests used as multiple range tests).

able soil in which to tunnel for successful breeding, they may potentially co-exist. Tunnellers also have the greatest diversity of nest architecture amongst the dung beetles, and some of this complexity may be attributed to competition for nest space. The largest species often have the deepest nests (e.g. *Heliocopris* species with nests deeper than 1 m below ground – Klemperer and Boulton 1976), but soil moisture (Edwards and Aschenborn 1987) and soil type (Hanski and Cambefort 1991b – see Fig. 2.5) also determine nesting patterns and success.

Doube *et al.* (1988) and Giller and Doube (1989) experimentally studied intra- and interspecific competition among 12 (eight Coprini, four Onitini) crepuscular / nocturnal tunnellers which co-exist in similar sandy soil regions of Natal, South Africa. They recorded two distinct patterns of dung burial. The coprines buried dung within 24 – 48 hours of arrival at the pat, while the onitines buried the dung over a period of 12 days. At high densities, *Catharsius tricornutus, Copris elphenor* and *Onitis alexis* removed 70-80% of the experimental pats. There was strong intraspecific competition for dung at densities of greater than two to four pairs of dung beetles per pat, and competition was asymmetric between the coprines and *O. alexis*. The former were apparently unaffected by the

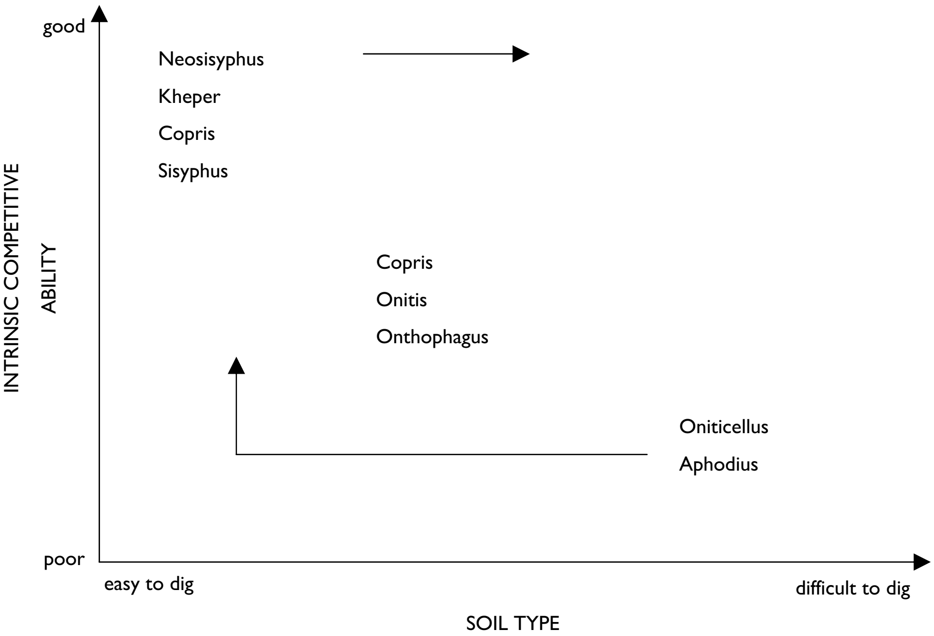


Fig. 2.5. Schematic illustration of assumed negative relationship between the intrinsic competitive ability and the sensitivity to the soil type in dung beetles. Many superior competitors are restricted to soils that are easy to dig, while inferior competitors find refuge in soils that are difficult to dig. (Adapted from Hanski and Cambefort 1991b).

presence of *O. alexis*, whilst the amount of dung buried by the latter was markedly reduced in the presence of two or three pairs of the coprines (Doube 1991).

2.3 LIFE-HISTORY STRATEGIES

Dung beetles have very low fecundity compared to most of their relatives and other similar-sized insects that live under roughly similar conditions. The reasons for some of this have been discussed above, and others will follow, but clearly provisioning of, and breeding in, a well-protected nest, and then caring for the brood, have contributed significantly to their success. However, even within the Scarabaeinae, there is a range of fecundities from extra-ordinarily low (one offspring per year), to a very moderate maximum of about 100 offspring per year. The lower end of the range is, without doubt, the lowest recorded for any insect.

A discussion of reproductive strategies is best approached for the dung beetles in terms of *r*- and *K*-selection theory which proposes that, in predictable environments, selection favours increased competitive ability, constant population size and more specialized use of resources (*K*-selection). Under unpredictable conditions, on the other hand, selection promotes high reproductive potential, variable population size and more generalized exploitation of resources (*r*-selection; MacArthur and Wilson 1967). We will also explore another template, so-called "adversity, or A- selection" (Greenslade 1983), which proposes that species which occupy predictably unfavourable conditions will be selected by "adversity".

r-Selected species are considered to be "generalists" while *K*- selected species are thought of as "specialists". A-selected species may have attributes of both *r*- and *K*-selected species, although they tend to be rather specialised. However, since these are relative concepts and a particular strategy is by definition relative to some other, and that they represent a continuum of tactics, all species are likely to have some attributes of each.

On the basis of the above, *r*-selected species could be considered ecologically efficient or successful in terms of the maintenance of high population numbers and efficient burial of dung. These were the attributes that proved most desirable in the species introduced into Australia for the control of cattle dung – reasonably wide habitat tolerance, rapid population build up, and efficient and fast dung burial (Hanski and Cambefort 1991a). Interestingly, the four species, three tunnellers and one roller that had the most desirable characteristics belong to four different tribes (*Digitonthophagus gazella* – Onthophagini; *Euoniticellus intermedius* – Oniticellini; *Onitis alexis* – Onitini and; *Neosisyphus spinipes* – Sisiphyni). All, however, share several similar attributes: they are quite small, and live only a single season; they process large amounts of dung relative to their size; produce relatively large numbers of progeny during several breeding episodes; and invest a minimum of time and effort in brood care. They are, thus, classical *r*-selected species. (Table 2.4).

At the other end of the continuum are the highly specialised *K*-selected species which are usually considerably larger than the above, live two or more years, bury only enough dung for a few progeny, breed mostly once per year, and invest heavily in maternal brood care. Several of the large ball-rollers fit this category (e.g. *Scarabaeus (Kheper) nigroaeneus* – Edwards 1988, and possibly *Scarabaeus (Kheper) aegyptiorum* and *S. (K.) platynotus* – Sato and Imamori 1988). However, the most extreme yet described is the flightless South African *Circellium bacchus* (Kryger *et al.* 2006a), in which a female cares for the single brood until the young adult emerges about 130 days after oviposition, under ideal conditions, or longer if the soil is dry, after which she leaves the nest. She then feeds for some time to replenish depleted energy reserves before being able to breed again. Thus, under ideal conditions, a female might breed twice per year, but once is probably more likely. Females live for at least three years, on average, in the field. The longevity of the females of species such as this may be as a result of the extended time spent underground brooding at very low metabolic levels, and where they are safe from predation and the vagaries of the environment. The longer lives and consequent extended reproductive life would then compensate for low fecundity.

Circellium bacchus' ecological characteristics are contrasted with those of the *r*-selected species discussed above in Table 2.4 for comparison between species at either end of the *r*-, *K*-continuum.

A-selected species occur in predictably unfavourable habitats (Greenslade 1983) and although no habitat is strictly "unfavourable" (otherwise the species would be unable to occupy it), certain habitats appear relatively unfavourable compared to others in which similar species occur. Such habitats occur in desert areas of south-western Africa, in which there are a number of very unusual dung beetles, such as members of the genera *Pachysoma, Dicranocara, Byrrhidium, Namakwanus*, and others. Members of the first genus are closely related to the quintessential roller genus, *Scarabaeus* and have been reasonably well studied (see Scholtz *et al.* 2004; Sole *et al.* 2005; Forgie *et al.* 2006) whilst the others have been considered to belong to the Canthonini (see Deschodt *et al.* 2007) but this has recently been contested (Sole and Scholtz 2009).

The genus *Pachysoma* with 13 flightless species, each with fairly restricted distribution along a narrow 1500 km-long strip of coastal sand, from Cape Town near the tip of Africa, to well into the Namib Desert of Namibia is a fairly well-studied group of probably A-selected species. Some of the areas where they

Table 2.4. Ecological characteristics of four r-selected African species of dung beetles. These are contrasted with the extreme k-selected species, *Circellium bacchus*. (Data on r-selected species adapted from Hanski and Cambefort 1991a; data on *C. bacchus* from Kryger *et al.* 2006a).

Species **Native biome and Geographical distribution**	**Length (mm)**	**Approximate natural geographical range (millions of km²)**	**Development time from egg to adult (days)**	**Size and type of dung beetle (L=large; S=small; R=roller; T=tunneller)**	**Diel activity (D=diurnal; N=nocturnal)**	**Average longevity (days)**	**Mean lifetime fecundity**
Digitonthophagus gazella	11	15	30	ST	N	60?	90
Tropical savanna Africa, Asia							
Euoniticellus intermedius	9	12	28	ST	D	45	120
Tropical savanna Tropical-subtropical grasslands Africa, Mediterranean region							
Neosisyphus spinipes	9	1	52	SR	D	100	44
Tropical savanna Southern Africa							
Circellium bacchus	40	0.025	130	LR	D	1000	5
Dense scrub Southern Africa							

occur receive less than 50 mm of rain per year, but moisture is predictably available in the form of regular coastal fog that precipitates on plants and the sand (Sole *et al*. 2005). The *Pachysoma* species feed on dry rodent and hare pellets, as well as wind-blown detritus, with the more specialised species feeding only on the latter. The *Pachysoma* species provision a burrow with detritus and lay an egg in it. The nest is then abandoned and another constructed. This is probably repeated several times in a season, and although they probably only breed during one season, they may overwinter and live into a second.

The biology of the genera *Dicranocara, Byrrhidium* and *Namakwanus* is poorly understood, except that all species are flightless, and restricted to very small, localised and very dry areas of the Namib Desert where they live in the dung accumulations in rock shelters of the rock hyrax, *Procavia capensis* (Hyracoidea: Procaviidae). Rock hyraxes are found throughout much of sub-Saharan Africa, in rocky areas where shelter amongst the rocks is available. They are opportunistic plant feeders and eat a variety of grasses, forbs and shrubs, including some that are highly aromatic, and others known to be poisonous to other species (Skinner and Chimimba 2005). They are gregarious, living in colonies of up to 20 individuals in a tightly bonded social group. They have communal "toilets" or middens in which their dung pellets, from which most moisture has been resorbed before defaecation, accumulate over years. Consequently, the beetles probably occur in some of the most inhospitable areas imaginable for dung beetles. They are only active after the very irregular and low rainfall of the area. Breeding burrows are provisioned with dung fragments and an egg is laid, after which the burrow is abandoned and another dug, and the process repeated. Populations are very small, and even during favourable conditions for activity, very small numbers of adults are seen to be active (Deschodt *et al*. 2007).

CHAPTER 3
PRE-COPULATORY BEHAVIOUR, SEXUAL ATTRACTION, MATE SELECTION AND CO-OPERATIVE BREEDING

3.1 PRE-COPULATORY BEHAVIOUR

Adults of most dung beetle species emerge from the brood chamber physiologically immature and require a period of "maturation feeding" ("*Reifungsfrass*") before attaining sexual maturity. This period is short, often only about five days, in those [often smaller] species such as *Euoniticellus intermedius* which breed in dung masses and have relatively high reproductive output (Halffter and Edmonds 1982), or much longer in large species, where the amount of dung available for the maturing larva is the minimum required for larval development, such as the ball-roller *Circellium bacchus*, in which this period may be as long as several months (Kryger *et al*. 2006a). In a somewhat radical deviation from the usual pattern, different species of the very unusual Neotropical genus *Eurysternus* (with individuals of about 13.0 -14.0 mm in length), have maturation periods that vary between about 30 and 200 days on average (Huerta *et al*. 2003).

Female dung beetles will usually not react to males exhibiting sexual behaviour to attract females, nor begin nest construction until they are sexually mature. In some species, however, immature females will pair with a male and then feed on dung buried by him, or by the pair together, and she will then mature in a nest. This is well developed in *Phanaeus*, in which pairing often takes place before nesting begins. When nesting does begin, but before breeding commences, the female excavates the nest and the male provisions it. The pair then lives together in this "nuptial chamber" feeding and interacting until the female is sexually mature (Halffter *et al*. 1974), after which mating takes place and brood construction begins.

Eurysternus have some of the most bizarre pre-breeding bisexual interactions yet recorded for any dung beetle group. [Details of their breeding biology are discussed in Chapter 4]. Adults feed quietly at a dung source, often amongst aggressive rollers and tunnellers, during their maturation phase. After the period of maturation feeding females form balls in a nest close to the source. Under some conditions, and in some species, a pair then forms and mating takes place, and they provision what Huerta *et al.* (2003) call "provisional nests". These usually contain 6-7 balls but there may be as many as 14, in some of which the female oviposits, and then they, and the eggs or developing larvae in them, are devoured by the pair in a "nuptial feast" (Huerta *et al.* 2003), or the nest is abandoned. After the provisional nests have been abandoned (usually 2-3 per species), a nest is provisioned with another 7-8 (but as many as 21) balls in which the female oviposits. The female then remains with the brood for most of their development.

In the ball-roller, *Scarabaeus (Kheper) aegyptiorum*, sexually immature females usually roll and bury food balls on which they feed, but they are sometimes attracted to a male rolling a large ball (Sato and Immamori 1988). Because the male alone rolls and buries the ball with the female merely passively involved, all of the investment is the males'. Once underground, the female feeds on the ball ("nuptial ball") and the male leaves the chamber without mating having taken place. This is, consequently, more likely to be a chance event than an evolved system, since there is no advantage for the male in these cases because after feeding on the ball, and possibly others subsequently, the female will mature and in all probability mate with another male. Therefore the investment of the male offering a nuptial ball would be futile and could, at best, be considered a case of female parasitism of male food balls.

3.2 SEXUAL ATTRACTION

In all groups, the food resource acts as the long distance attractant for individuals of both sexes, and it is only there that pairing takes place. Short distance attraction between the sexes may involve pheromones secreted by abdominal glands, but appears to be mainly visual in ball rollers, at least, with a partially or completely finished ball with another individual astride, attractive to members of both sexes – of the same sex for attempted theft of the ball, and for the opposite sex, for pairing. Pair-bonding appears to be a simple process of brief head-to-head contact, maxillary palp palpation, and acceptance. Rejection of a potential mate appears to be quite infrequent.

Although the presence of abdominal glands in many groups is well documented (Pluot-Sigwalt 1991), their function in pheromone production is less certain and the use of an attractant chemical has only been documented in a few cases (see Burger *et al.* 2002 for references to the sex attractant chemicals in *Scarabaeus (Kheper))*. Males of some Scarabaeine species such as *Scarabaeus (Kheper) nigroaeneus* (Tribe 1975) and *S. (K.) aegyptiorum* (Sato and Imamori 1986) have a distinct ritual of scraping, with brushes on the hind legs, pheromone-impregnated waxy exudates from abdominal glands which volatilize as puffs of white vapour to which females are apparently attracted from a considerable distance. However, this is always done close to a food source or after the male has rolled a ball, so the pheromone appears merely to supplement the chemical cues produced by the food source and to combine them with visual cues presented by the ball.

In one of the better-studied roller species the Neotropical carrion-feeding canthonine, *Canthon cyanellus cyanellus*, the male attracts females over a short distance to the ball he is rolling by abdominal secretions, with which he impregnates the ball while he is rolling it (Favila 1988). The secretions also inhibit oviposition by the blow-fly, *Calliphora*. At close quarters epicuticular compounds appear to play an important role in the sexual recognition process in *C. c. cyanellus* (Ortiz-Domínguez *et al.* 2006).

The authors carried out a series of experiments in which dead beetles were offered to members of the opposite or same sex, either just killed (frozen and then warmed to room temperature); dead, but after having the cuticular compounds washed off in solvent; males impregnated with extract of female compounds; and females impregnated with male compounds. The results proved, with high statistical support, that cuticular compounds play an important role in sexual recognition in *Canthon c. cyanellus*, and that certain behaviours can be elicited or suppressed by removing or replacing cuticular compounds in cadavers, regardless of the sex of the cadaver used. This appears to be the only study undertaken so far that illustrates quite clearly the importance of these compounds in sexual communication, and there can be little doubt that similar situations may be found in other species.

3.3 MATE SELECTION

Sexual dimorphism is often pronounced in tunnellers but is virtually unknown in rollers. Contest between male rollers appears to be mostly about possession of a dung ball, whilst combat between males over access to females appears to be common amongst sexually dimorphic and male dimorphic tunnellers, although these traits are often unrelated to phylogeny (various papers by Emlen and coworkers, e.g. Emlen 2005a; - see Chapter 11 on "Sexual selection" for a detailed discussion of the subject). The major visible trait in male dimorphic beetles is the presence ("major males") or absence ("minor males") of horns, and the different morphs then typically have different reproductive behavioural strategies.

Most studies of sexual selection in dung beetles have dealt with the genus *Onthophagus*, which shows a wide array of horn types in males of many species. The horns may vary in shape and length and also in position, being either on the head or thorax, although their precise placement also varies considerably. Within a species, horn size may be positively allometric, with large males possessing large horns, while small males have rudimentary horns, or no discernible ones (e.g. *O. acuminatus* – Emlen 1997a), or not allometric (*O. binodis* – Cook 1990). Adult dung beetles usually exhibit continuous variation in body size as a result of differential food quantity available to the developing larvae. Emlen (1997a) also demonstrated that in *O. acuminatus*, a Central American species, males reared on low-quality diet had longer horns at any given body size than sibling males reared on high quality diet. Furthermore, males growing larger than a threshold body size develop long horns, whereas males that do not achieve this size grow only rudimentary horns, or no horns (Emlen 1997b). The horned and hornless males have different types of reproductive behaviour. Females of this species dig breeding burrows beneath a dung source and provision it with dung. Horned males guard the entrance to the burrow, fight off possible intruders, and mate with the female. By contrast, the hornless males avoid conflict and access the females by sneaking into guarded tunnels, or by digging new tunnels that intercept the guarded tunnels below ground.

In a series of experiments Emlen (1997a) tested whether females discriminated against either male morph, and whether body size and horn length affected the outcome of contest between males. Males of either morph were unequivocally accepted by females (Mann-Whitney test, $U_{14,7} = 44$, $P = 0.71$). Body size of males with the same horn lengths significantly affected male success at guarding tunnels (chi-square test: $\chi^2 = 6.40$, $P = 0.011$). In males of similar body size but different horn lengths, the latter was the major determinant of the outcome of a fight, and long-horn males were significantly more successful at combat than males with shorter horns (simple regression, $r = 0.696$, $F = 6.573$, $P = 0.037$).

Big horns, however, come at considerable physiological cost: firstly, that of smaller testes, less sperm production and consequently lower reproductive competition resulting in a trade-off between acquiring matings and investment in acquiring fertilizations (Simmons and Emlen 2006); secondly, that the production of horns significantly prolongs the development time, and in *O. taurus* (Hunt and Simmons, quoted by Emlen 1997a), results in increased larval mortality from soil-dwelling nematodes; and thirdly, is that allocation of developmental resources to horns in both *O. acuminatus* and *O.taurus* results in reduced allocation to other morphological traits, specifically eyes (Emlen 1997a).

So what maintains dimorphic males in a species when populations contain approximately equal numbers of horned and hornless males? One prerequisite is that the species experience a fitness trade-off across environments so that if they encounter several discrete environment types, or ecological, or behavioural situations, and these different environments favour different morphologies, then distinct morphological alternatives can evolve within a single population – each specialised for one of the different conditions (Emlen 1997a).

3.4 BISEXUAL CO-OPERATION

Co-operation between the sexes is widespread amongst burrowing and tunnelling groups, but is seldom consistently obligatory in any of them. If there is a general rule then it is that the groups with the more elaborate nesting behaviour have some co-operation between the sexes during some part of the process. Also, in some taxa with apparently well developed bisexual co-operation, mated females often successfully construct burrows and breed unaided by a male, although with reduced efficiency. See Chapter 4.1.2.

Selection for bisexual co-operation for food gathering, nesting, and brood ball preparation, has obviously been strong because of the frequency with which it is found amongst dung beetles across taxa. The co-operation apparently permits more rapid food relocation from the source, thus reducing exposure to competitors and to desiccation, and a pair of beetles working together are obviously more efficient than when working alone, which leads, ultimately, to more progeny. However, a caveat to this is, why then, do females of the most *r*-selected species work alone?

Co-operation undoubtedly increases labour efficiency and investment, and results in more resources available for progeny, hence higher brood productivity. Sato (1998) recorded that female *Scarabaeus* rollers founding nests alone produced as many brood balls as males (= pairs) but that the balls were smaller. Lindquist (1933) recorded that a pair of the tunnellers *Copris fricator* and *Phanaeus* sp. buried about 50% more dung (1:1.6 and 1:1.5 respectively) than a single female. Rasmussen (1994) recorded that pairs of *Phanaeus difformis* provisioned a breeding burrow at a faster rate (Mann-Whitney $U = 79.0$, $P = 0.001$), and sequestered more dung (Mann-Whitney $U = 86$, $P = 0.001$) than a female working alone, but there was no difference in number or average size of brood balls produced by single or paired females ($t = 0.86$, $P = 0.40$).

Most of the groups of rollers have fairly well developed bisexual co-operation during ball-formation, rolling and nesting, with males in Canthonini and Scarabaeini usually initiating ball formation, and doing most of the rolling and burying, whereas in the Gymnopleurini and Sisyphini it is sometimes the opposite or one of the pair "pushes" the ball, while the other "pulls" it (Halffter and Matthews 1966). Mated females of some Scarabaeini, however, are capable of forming and rolling balls unaided by males. Sato (1998) reported that in *Scarabaeus catenatus*, males founded nests in 69% of cases and females alone in 31%. Forgie *et al*. (2002) recorded that brood was found in all six nests of the millipede carrion-feeder *Scarabaeus (Sceliages) hippias* (which functions more as a tunneller than a roller), three weeks after they were dug and provisioned by females alone in the field. An unusual situation found in the typical dung feeding and ball rolling canthonine *Circellium bacchus*, is one in which females form, roll and bury brood balls unaided by males (Kryger *et al*. 2006a). The Australian canthonine *Cephalodesmius armiger* is the only dung beetle species recorded in which males and females co-operate throughout their lifetimes. Although this species is nominally (supposedly phylogenetically) a roller, it is functionally a tunneller where a permanently bonded pair dig and provision a burrow with a small amount of detritus, after which the female remains in the nest and "processes" the detritus into a dung-like compost from which brood balls are formed. The male continues for several months to forage and drag fallen leaves into the burrow where they are processed by the female and added progressively to the brood balls as the larvae develop (Monteith and Story 1981).

Amongst the tunnellers, the co-operation between the sexes usually takes the form of the female digging the nest burrow and constructing the brood balls, while the male's principal function is provisioning the nest. Bisexual co-operation is highly developed in most Onitini, Eurysternini, Phanaeini, Coprini, in some Oniticellini, and in the few cases for which we have empirical data for nesting efficiency, i.e. increased brood production, pairs are always more efficient than females working alone (*Copris* and *Phanaeus* - Lindquist 1933; *Phanaeus* - Halffter and Lopez 1977).

The male usually leaves the nest after mating, or both sexes leave, or the female remains with the brood for various periods. In *Heliocopris* the duration of the female's stay in the nest may be determined by outside environmental conditions. If conditions are favourable for another breeding event she may leave the nest of clay-covered brood soon after it is completed, or during unfavourable conditions, she may remain in the nest, sometimes until she dies, about the time of the progeny's emergence (Klemperer and Boulton 1976).

So, what about groups without bisexual co-operation? If co-operation between the sexes leads to increased brood provisioning and higher survival of progeny, why is it that the most highly derived and also the most fecund species are, almost without exception, single-sex (= female) nesters? The answer probably lies in the fact that the females of the *r*-selected species may mate with different males at each breeding episode, thus mate multiple times. These males, therefore, have no confidence of paternity, so would not be selected to provide any parental care. By contrast, males in bisexual relationships are assured of the paternity of the progeny in the nest, so it would be adaptive for them to contribute to parental care.

CHAPTER 4
NESTING AND BREEDING PATTERNS

4.1 NESTING

Nest-building and -provisioning are widespread but not common behaviours across the Coleoptera. The most well studied group outside of the Scarabaeinae are the Holarctic burying-beetles of the family Silphidae, where a pair of adult beetles buries a carcass of a small vertebrate such as a bird or rodent, and the female lays eggs adjacent to it. The developing larvae then feed on liquids oozing from the decomposing carcass. Various members of the Geotrupidae (*Geotrupes*, *Lethrus*) provision pre-constructed burrows with litter (*Geotrupes*) or green twigs and leaves (*Lethrus*). Eggs are laid in the nest and the larvae feed on the decomposing nest material. Larvae of the dung-feeding Aphodiinae are free-living inside the dung source.

Scarabaeinae are the only group of beetles that provision a burrow with dung, and in most cases, form a "sausage" with separate sections, ball or "pear", in which an egg is laid and in which the larva develops. From the basic state of burying one or several balls a multitude of specializations has occurred such as burying dung immediately below the dung source, forming brood balls inside the dung, or rolling it away and burying it at some distance from the dung source. In the nest the dung could be formed into single or multiple broods, coated with clay or not, and they could be abandoned or guarded and cared for for up to several months. It is in these respects that dung beetles have developed a multitude of strategies that are unique in the insect world, and which have undoubtedly contributed to their unequalled success.

The complexity of these processes would usually be considered an indication of evolutionary specialization, so simple nests and nesting behaviour could be considered primitive and highly complex nesting behaviour, derived, as has been proposed in the past (Halffter and Edmonds 1982). It is in fact quite the opposite, with some phylogenetically terminal taxa producing ill-defined brood masses and laying relatively large numbers of eggs with little parental care (e.g. Onitini, Onthophagini and some Oniticellini – Halffter and Edmonds 1982), and some basal taxa, such as the canthonine *Circellium bacchus*, with only a single breeding event per year in which only one well-formed brood ball is produced and there is a very high degree of maternal care (Kryger *et al.* 2006a).

There have been various attempts to define nesting and breeding patterns (Halffter and Edmonds 1982; Cambefort and Hanski 1991) in dung beetles, but there are as many exceptions as there are patterns. Cambefort and Hanski (1991) admitted that these are not well-defined and do not contain any useful phylogenetic information since patterns transcend taxa, and virtually all of the aspects involved are undoubtedly driven by the ecological requirements of the species, or imposed by the environment. In spite of the lack of phylogenetic information, for convenience, the tribes are usually separated into a basal dichotomy of either rollers (telecoprids), or tunnellers (paracoprids), with dwellers (endocoprids) being a subdivision of tunnellers, and kleptoparasites being derived mainly from tunnellers.

The tribes Canthonini, Scarabaeini, Eucraniini, Sisyphini, Gymnopleurini and Eurysternini are considered to be rollers, and the Dichotomiini, Coprini, Onitini, Phanaeini, Onthophagini and Oniticellini, tunnellers. Some Oniticellini are dwellers and various Onthophagini and Dichotomiini are kleptoparasites. However, the system immediately breaks down without much critical analysis since Eucraniini do not "roll" in the classical sense of head down and pushing backwards while controlling the ball with middle and hind legs, but "carry" dung pellets in their fore legs. Furthermore, the Eurysternini do not roll balls above ground, but do so underground, and were thought to be rollers that have reverted to a form of tunnelling. Recent phylogenetic analyses, however, (Philips *et al.* 2004b; Philips *et al.* 2002; Ocampo and Hawks 2006; Monaghan *et al.* 2007) have indicated that the Eucraniini probably evolved from a tunnelling, dichotomiine-like ancestor, as did the Eurysternini (Philips *et al.* 2004b; Ocampo and Hawks 2006; Monaghan *et al.* 2007). Various "tunnellers" such as *Heliocopris* in Africa (personal observation, A.L.V. Davis), *Dichotomius* and *Phanaeus* in the New World (Halffter and Matthews 1966), *Phalops* in Africa (Cambefort 1991b) and *Onthophagus* in SE Asia (unpublished thesis, A.J. Davis) have been recorded rolling balls, albeit mostly pre-formed or crude ones. On the other hand, some rollers such as the African *Scarabaeus catenatus* (Sato 1998) and *Pachylomera femoralis* (personal observation, C.H. Scholtz) switch from tunnelling to rolling and back, sometimes within a single feeding or breeding event. Then there are groups that are undoubtedly phylogenetically related to true rollers, such as *Canthon obliquus*, a Baja California endemic closely related to a very large number of typical roller species (Halffter and Halffter 1989), which drags dung fragments held in the hind legs, and the South-West African genus *Pachysoma* (sister to the quintessential roller genus, *Scarabaeus*), which similarly hold food fragments in the form of small dung pellets and detritus in setal brushes on the hind legs and drag them forwards. Even within *Scarabaeus*, the obligate millipede feeding subgenus *Sceliages*, is functionally a tunneller, pushing millipede fragments with the fore legs and head into a burrow near to the dead millipede or some distance from it (Forgie *et al.* 2002).

Consequently, it would appear that nesting behaviour has been mediated more by environmental conditions than phylogeny, hence the ability of certain taxa that phylogenetically belong to groups that mainly utilize one nesting type to switch, apparently over short evolutionary time spans, to an alternative nesting strategy.

In spite of the imprecision of the "types" of nesting patterns, the traditional classification system has become entrenched in the literature, (Halffter and Edmonds 1982, Cambefort and Hanski 1991), so for clarity we discuss these types below, and provide examples of some obvious exceptions that have been recorded since Cambefort and Hanski (1991).

4.1.1 Nesting in rollers

Rolling is thought to be a strategy that evolved to avoid the focus of competition at the dung source because suitable dung is ephemeral and often in short supply. However, rolling a ball places several limitations on the beetles because it requires a fairly open substrate so as not to impede rolling and usually a sunny position to warm the beetles because of rolling's high energetic demand. There is also a limit to the size of the ball that the beetle can manipulate and roll, and consequently, the amount of food available for the brood is restricted. Therefore the number of progeny produced per breeding episode is limited.

Rollers may roll balls for various reasons: these may be for food for the beetle itself, of either sex (food ball); they may be rolled by a male and then shared with a female (nuptial ball); or they may be initiated by one of either sex, or by a pair and be destined for larval food (brood ball). Food balls may be smaller than nuptial and brood balls, or they may be of similar size. Brood balls may be divided further into more balls or "pears" in which eggs are laid, they may be coated with clay after oviposition or not coated, and they might be abandoned by the female or she might remain with the brood until her progeny emerges.

Five typical nesting patterns have been described for rollers (based on Halffter and Edmonds 1982 and expanded by Cambefort and Hanski 1991), but as pointed out above, and elsewhere in this text, there are several exceptions to these (for example Forgie *et al.* 2002; Kryger *et al.* 2006a).

Type1. Mating occurs at the food source (carrion, in the only typical example, the Neotropical *Megathoposoma*), after which the female rolls the ball away to be buried. The male then plays no further part in the process. Breeding in the African millipede specialist, *Sceliages*, may eventually be considered to be of this general type, since, in the only published record to date, females apparently nested unaided by males. However, at no stage is a ball rolled above-ground (Forgie *et al.* 2002) so this type should perhaps be placed with the "exceptions" listed below.

Type 2. This is the more typical pattern amongst rollers. It is one in which there is usually some participation by both sexes, although the male is the more active partner. The ball is formed at the source by the male and the female is then attracted to him and the incipient ball by vision, and, as reported in some cases, by pheromones, although pheromones are likely to play a more important part than has been recorded to date. The ball is rolled away and buried some distance from the source, after which mating takes place and the male abandons the nest. The female remodels the ball into one or two pears and lays an egg in each and then she too abandons the nest. This type of nesting is common in some Canthonini, Gymnopleurini, Scarabaeini and Sisyphini, although some *Neosisyphus* abandon the ball at the soil surface or attach it to some above-ground object such as a twig or grass clump. Fecundity amongst these latter species may be high.

Type 3. This type is similar to the previous one except that females may undertake the whole process unaided by a male, or when aided by a male who executes most of the above-ground labour, she remodels the ball into one to four pears after mating and then remains with the brood until the offspring emerge. This has been described for several species of *Scarabaeus* subgenus *Kheper*, and fecundity may be very low, with, in some cases, only one offspring produced per female per year (Edwards 1984). Possibly as a counter to the necessarily low fecundity that results from the limited amount of dung sequestered by rollers, some East African species roll very large balls (*S. catenatus, S. platynotus*) from which up to four pears are formed (Sato and Imamori 1987, Sato 1997). The brood is then also cared for until offspring emergence.

Type 4. The male and female together roll several balls to a nest and after mating the male may stay in the nest with the female until the progeny emerge (some carrion-feeding *Canthon*). With some expansion of the definition of this type, the Australian *Cephalodesmius* may be included, although as pointed out elsewhere in this text, it is not strictly a roller.

Type 5. Rolling has been lost. Examples are the Eurysternini, but as pointed out elsewhere, there is now a substantial body of phylogenetic evidence to support the hypothesis that they evolved from a dichotomiine-like ancestor, so were never part of a rolling lineage (Ocampo and Hawks 2006; Monaghan *et al.* 2007). Other examples generally considered to belong to this type are some *Canthon* (Halffter and Halffter 1989) and some *Scarabaeus* species (Ybarrondo and Heinrich 1996) that collect and carry dung pellets to a burrow.

Exceptions to the behaviour manifested in these five types may be, for example: the southern African *Pachysoma* which move forwards dragging dry dung pellets and detritus that are held in the back legs (Scholtz *et al.* 2004); the southern African *Circellium* in which females roll balls and prepare nests unaided by males (although they may be considered a slightly aberrant Type 3; Kryger *et al.* 2006a); and the Argentine Eucraniini which were also traditionally considered to be aberrant rollers but, as with the Eurysternini, have recently been shown to have evolved from a tunnelling ancestor (Ocampo and Hawks 2006; Monaghan *et al.* 2007). The example of *Pachysoma* (which is closely related to the quintessential roller *Scarabaeus*) perhaps best illustrates how flexibly these behavioural types actually respond to environmental pressure, and how phylogenetically suspect conclusions may be that use similar behavioural patterns as evidence to support presumed shared ancestry.

4.1.1.1 Small size as a constraint on the ability to roll balls

Because forming a ball necessitates a malleable material, ball-rollers are somewhat restricted in their choice of food, thus limiting them considerably compared to tunnellers. A further restriction, although not one that has previously been seriously considered, is the constraint of size – very small beetles are probably physically limited in their ability to form and roll balls, and this is confirmed by the fact that most species recorded to actually form and roll balls, have a body length longer than an average of about 7.0 – 8.0 mm. A large majority of Canthonini in the major zoogeographical areas are much smaller still than this arbitrary size, with another 50% of those only half this size, which would probably effectively preclude them from rolling. In the Afrotropical region 33 of about 40 genera have a body size smaller than the above average figure, about 23 of 30 in Australasia, and roughly 17 of 27 in the Neotropics. The smallest average body length recorded for a canthonine [and Scarabaeinae] is the South African *Outenikwanus*, with an average body length of only 1.9 mm (range 1.6-2.1 mm) (Scholtz and Howden 1987a) and it is one of nine African genera smaller than 4.0 mm. All of these are forest or montane relict genera with very small numbers of species and most are flightless.

Species of the Neotropical *Canthochilum*, on average about 5.0-6.0 mm long, are claimed by Halffter and Edmonds (1982) to be "poor rollers", with *C. oakleyi* from Puerto Rico, albeit one of the larger species in the genus at about 7.5 mm, apparently unable to roll (Halffter and Halffter 1989). The genus is one of those small groups that has characters of "Canthonini" and "Dichotomiini" (Matthews 1966, quoted by Halffter and Halffter 1989) and it has been compared to various small dichotomiines because of its general body shape, and its poor rolling ability. Other Neotropical taxa that fall into this category are *Agamopus* and *Cryptocanthon* (Halffter and Halffter 1989), and *Zonocopris* (see Vaz-de-Mello 2007a), all of which are smaller than 5.0 mm, and doubtfully rollers.

4.1.2 Nesting in tunnellers and dwellers

Burrowing differs fundamentally from telecoprid behaviour in that tunnellers excavate burrows before dung is collected with which to provision them. Rollers first collect the dung and then bury it somewhere appropriate. Tunnelling has some obvious advantages over rolling – the burrow is close to the source so more dung can be collected over a shorter time. This may lead to higher fecundity because of lower energy-resource investment per offspring, and predation is also likely to be less severe because less time is spent by the adults in exposed situations. However, interference competition is often fierce around a dung source and space for nests under the dung is often crowded.

Besides the obvious differences between nesting in rollers and tunnellers, there are some subtler differences. One is that male rollers are usually the most active contributor to dung acquisition and nest preparation, while in tunnellers the roles are reversed, with the females taking the more active part in burrow construction and forming the brood balls. Furthermore, male rollers rarely participate in brood care while some male tunnellers do.

Because of the limited nest space below the dung source, competition is fierce among tunnellers, and different species partition it accordingly. Although there are few empirical data to support such a supposition, it is quite likely that spacing beneath the dung may be further facilitated by the use of territorial pheromones which mark areas already occupied by the same or other species. Usually the smaller species make shallow nests, while larger species burrow deeper. The small species usually form several brood masses and do not care for the brood, and, they breed several times during their relatively short lifetimes, hence have high fecundity. In contrast, larger species produce fewer brood balls and maternal care is well developed in at least some of them. Consequently, the females spend long periods underground caring for the brood, which increases offspring survival, and may contribute to increased longevity of the females because of their long periods at low metabolic rates, and reduced predation underground. Because of the lower numbers of offspring produced per breeding episode, increased female longevity and breeding spread over more than one season increases lifetime fecundity.

The following types of nesting patterns have been proposed (Halffter and Edmonds 1982).

Type 1. In this type there is a single shallow brood mass produced by the female alone. Nests are abandoned after eggs are laid and the process is repeated several times, which results in high fecundity. Examples are small species of Dichotomiini, Onitini, Oniticellini and Onthophagini.

Type 2. Nests of this compound type are also shallow and contain several cylindrical brood "sausages" or ovoids. There may be limited sexual co-operation but there is no maternal care. Most Onthophagini probably nest in this way but some small species of the other tribes mentioned under Type 1 also construct nests of this type. Fecundity is also high.

Type 3. This type of nest lies at the soil / dung interface, with half in the soil and the other half in the dung. There is female brood care. This type is only known only from African *Oniticellus*.

Type 4. These are typical endocoprid nests, with virtually the entire nest built within the confines of a large dung source, such as that produced by cattle or elephants. Some species of *Oniticellus* show this nesting pattern.

Type 5. Nests of this type consist of a few shallow, adjoining brood masses, with maternal care. It has been recorded in the African oniticelline *Cyptochirus*.

Type 6. In this type the nest is deep and consists of several brood balls lying in a tunnel or in cavities branching from a central tunnel. The broods may be separated by soil or not. Maternal care is rare. This type of nesting has been recorded in Coprini, Dichotomiini, Onitini and Oniticellini.

Type 7. Nests of this type are also deep and usually only contain a few balls which are separated from each other. There may be sexual cooperation or maternal care. In Coprini there is male-female cooperation and extensive maternal care; in Dichotomiiini maternal care is present in some species and absent in others; and in the Phanaeini, although the pair or the female may remain in the nest, there is no maternal care.

4.1.3 Kleptocoprids

Many small species, belonging mostly to the Onthophagini, have dispensed with the behaviour of sequestering their own supplies of dung in which to breed, and have become nest parasites of both rolling and tunnelling species. Being smaller than their host, their larvae are able to complete their life-cycles more quickly and at less energetic cost than their hosts. The smallest species, often less than about 5 mm long, are kleptoparasites of rollers and belong exclusively to the Onthophagini. Some larger species of Onthophagini and Dichotomiini (*Pedaria*) parasitize large tunnellers such as *Copris* and *Heliocopris*. Cambefort (1984, according to Cambefort and Hanski 1991) recorded up to 37 individuals of six species in one ball rolled by a large *Neosisyphus* species and 109 Scarabaeinae of five species as well as two species of Aphodiinae in one *Heliocopris* nest. Although there are no data on the effects of competition between the kleptocoprids themselves, based on densities such as these, there can be little doubt that they have to contend with both intra- and interspecific competition in much the same way as those species that compete for, and acquire, their own brood supplies.

To this may be added the special breeding patterns recorded for the small (< 7.00 mm long) Neotropical dichotomiine genera, *Pedaridium* and *Trichillum*, which do not sequester dung nor do the larvae develop in a pre-formed brood mass. Females lay eggs at regular intervals in a dung mass (cow, sloth or tapir dung, or kleptoparasitically in that sequestered by larger dung beetles) and larvae feed inside the mass as in the case of the Aphodiinae (Verdú and Galante 2001). Some species pupate in the dung mass, others in the soil beneath the dung, but no pupal chamber is formed. Although this breeding pattern superficially appears to represent the ancestral one, it is functionally identical to that of typical kleptoparasites in which eggs are laid in a dung mass provided by another, larger individual, and the larvae live inside it. *Pedaridium* larvae stridulate, possibly to warn others of their proximity to avoid contact and competition or cannibalism. Larvae are typical of those living in the confines of a ball – they have the enlarged "hump" and the anal lobes that function as plastering trowels, so although they have lost the typical dung-ball-inhabiting behaviour, they have retained all the functional morphological attributes of their relatives. (See Verdú and Galante 2001).

4.1.4 Rolling vs tunnelling

Clearly different nesting tactics must result in adequate fitness for the survival of the species involved, but it is difficult to compare payoffs of different species and their strategies. It is generally assumed (Halffter and Matthews 1966; Cambefort and Hanski 1991) that tunnellers produce larger broods than rollers, but that they are subject to a greater amount of interference competition near the dung source. Rollers avoid this to some extent by rolling a ball away from the source of dung and the focus of other beetles. However, Sato (1998), in a study of the "roller" *Scarabaeus catenatus*, which uses both rolling and tunnelling tactics, found that these beetles use alternative tactics under different conditions. He considered the selective advantage of the tactics, the fitness payoffs, and the kind of strategy that maintained the co-existence of the tactics.

Scarabaeus catenatus is a "true" roller belonging to a genus of obligate rollers. It is a large, diurnal, East African species which forms three types of nests; food, brood and nuptial-food nests, classified according to their use (Sato 1997). Food nests are made by individuals of either sex, and buried dung is consumed by the beetle itself. Nuptial-food nests may be started by an individual of either sex, but it is joined by another of the opposite sex, and after the dung is buried it is fed on by both individuals. Brood nests may also be founded by either sex but pairing and co-operation take place during nest building. The female makes one to four brood balls from the dung and lays an egg in each. The male remains in the nest with the female until after oviposition (about four days after dung burial), after which he leaves. The female remains with the brood for 2-9 months, until the offspring emerge.

Sato (1998) reported that 69% of brood nest founders were male and 31% female, and that the founders tunnelled more often than rolled (75% against 25%). The proportions did not differ significantly between the sexes ($G = 0.764$, d.f. = 1; $0.3 < P < 0.5$). In contrast to this, a large proportion (86%) of food nest founders rolled, and only 14% tunnelled. The proportions differed significantly between brood nest and food nest founders ($G = 64.101$ adjusted by Williams' correction, d.f. = 1; $P < 0.001$).

Sato (1998) considered the rolling effort to include the time taken to cut a chunk of dung, form, roll and bury it, whereas tunnelling effort included the dung-processing time as well as the time taken for multiple trips between the source and the burrow. He found that tunnelling took significantly longer (80 ± 31.5 min. $N = 38$) than rolling (51.7 ± 17.4 min. $N = 9$) (Mann-Whitney *U*-test: $U_{cal} = 74.0$, $P < 0.001$). Sato found no correlation between beetle size and whether they rolled or tunnelled.

Beetles often investigated nests being built by other individuals. If there was a single individual of the opposite sex in the burrow the beetles usually paired, but the intruder was usually repulsed by a single individual of the same sex, or by one of the same sex of a pair. The frequency of intrusion into brood nests depended on the nest-building tactic, and Sato found that significantly more males than females intruded into nests, and this happened significantly more often in tunnelled than rolled nests.

Fights over nests were common, particularly between males, and the proportion of those usurped by intruders in tunnellers was higher (49%) than for rollers (25%). Conflict between females, on the other hand, was less common, and usurpation of females from tunnelled burrows was about 10% and in burrows resulting from rolling, 0%.

Consequently, Sato (1998) estimated that the two nesting tactics have equal fitness payoffs for males. The tunnelling tactic results in more brood balls because the beetles can move a larger amount of dung over a shorter distance because of repeated forays between the burrow and the dung source. However, it involves substantially increased risk from intruders because of the longer time taken to build and provision the nest, and the proximity to the dung source. Rolling, on the other hand, results in a single brood ball, but at considerably less risk. Consequently, males face a trade-off between brood size and nest defence success (Sato 1998). For females, however, the two tactics have unequal fitness payoffs. Because of the low intensity of females fighting over nests, the rolling tactic has no advantages over tunnelling, since the latter results in more brood at lower cost.

Why two strategies and what maintains them? One must assume that the two tactics result in similar reproductive success in males. If most males use the tunnelling tactic, then a male that employs the rolling tactic will gain higher reproductive success because of avoiding costly fights over a nest, and the proportion of rollers in the population will increase. Alternatively, if most males are rollers, then a tunneller gains reproductive advantage over them because of increased brood production and little conflict. When the reproductive success of one tactic becomes equal to the other, the increase in proportion of the one tactic over the other will cease.

In this study females adopted the tunnelling tactic in the same proportion to the rolling tactic, as did males (75:25), yet tunnelling offers a clear advantage over rolling. Sato (1998) offers two possible hypotheses to explain this: (1) females that are physiologically capable of producing only one egg may opt for the rolling tactic; (2) tunnelling, because of increased energy usage to burrow and forage repeatedly, may require more energy and consequently result in lower viability. Finally, it may merely result from the fact that females maintain the tactic because it is highly favourable to males (Sato 1998).

4.1.5 Nesting in the different groups

(for a very detailed treatment of the subject see Halffter and Edmonds 1982).

4.1.5.1 Tunnellers

Dichotomiini

Although this tribe is poorly-defined, we will use the classical understanding of it since most of its constituent members have broadly similar nesting patterns. That is, most are tunnellers making nests of four of the six types proposed by Halffter and Edmonds (1982), and elaborated slightly by Cambefort and Hanski (1991). None of these, however, is unique to the tribe. These are:

- Those with one nest containing a single shallow brood mass (Type 1). There is no co-operation between the sexes and females nest repeatedly. There is no maternal care. These are usually small species, and the pattern is very similar in some Onitini, Onthophagini and Oniticellini;
- Compound nests with several to many cylindrical or spherical brood masses (Type 2). Limited bisexual co-operation may occur but there is no maternal care. Also found in some Onitini, Onthophagini and Oniticellini.
- Those with several spherical brood masses arranged in single or branched tunnels, with or without separation between them (Type 6). Limited bisexual co-operation may occur but there is no maternal care. Also found in some Coprini, Onitini, Onthophagini and Oniticellini;
- Nests with very few brood balls that are physically separated from each other (Type 7). Sexual co-operation and, usually, maternal care occur. Also recorded in Phanaeini and Coprini.

Phanaeini

Phanaeini are probably monophyletic and evolved from a dichotomiine-like ancestor (Philips *et al.* 2004a; Philips *et al.* 2004b). All species make nests with a few, physically separated, brood balls (Type 7). Sexes co-operate, and, although one or both of them may remain in the nest, there is no maternal care.

The brood balls are covered with a thick clay layer and each in a separate nest chamber is the norm. There is considerable bisexual co-operation in nest-building and ball formation, but no brood care. Some Coprini (e.g. *Catharsius*) also exhibit this nesting pattern.

Coprini

Although doubtfully monophyletic as presently constituted, Coprini have only two different nesting patterns (Cambefort and Hanski's 1991, Types 6 and 7). Type 6 nesters have several round brood masses in one or several branched tunnels, and usually no maternal care, whereas Type 7 nesters have a few brood balls in a chamber and there is extensive maternal care. These types are shared with Dichotomiini, Onitini and Oniticellini (Type 6), and Dichotomiini and Phanaeini (Type 7).

In most Coprini the brood balls are covered with a thin clay layer and they are grouped together in a chamber. There is extensive bisexual co-operation and prolonged maternal care.

Onitini

Onitini are probably monophyletic. They share Types 1, 2 and 6 with other tribes such as Onthophagini, some Oniticellini and Dichotomiini.

Onthophagini

Although this is the tribe with the greatest number of species (mainly in the genus *Onthophagus*), they only make two nest types, i.e. 1 and 2, with Type 2 being the commonest. Maternal care is absent and fecundity is high in both of these types.

Oniticellini

Although the tribe appears monophyletic in Philips *et al.*'s (2004b) phylogeny, there is some evidence to suggest that they are nested within the Onthophagini (Monaghan *et al.* 2007). Although it is a relatively small tribe, its members have the highest number of nest types (6), with all but Type 7 found in the tribe. Types 3, 4 and 5 are only found in Oniticellini. Type 3 nesters place the brood mass at the soil/dung interface; Type 4 nests are placed inside the dung pat (thus the endocoprid or "dwelling" nest type); and Type 5 nests consist of a few more or less coalescent shallow brood masses. Maternal care occurs in all studied taxa, and in the only recorded cases in dung beetles, there is possible communication between the larvae, which stridulate inside the balls, and the brooding female in *Tragiscus dimidiatus* (Davis 1977).

Davis (1977), in a study of endocoprid breeding in Oniticellini, concluded that strong environmental pressure probably drove the ancestral tunnellers back into the interior of the dung source, but this could only be done in the absence of tunnellers and rollers. This was made possible by: switching to drier dung, which was no longer attractive to other dung-feeding insects, or by restricting activity to drier or cooler periods of the seasonal cycle, because both tunnellers and rollers are dependent on high temperatures and soil moisture for breeding successfully. The obstacles presented by unfavourable climatic conditions are mitigated against inside the dung pat since micro-climatic conditions in the dung remain favourable for breeding – moisture is retained inside the dung source because of a surface crust that quickly forms and retards desiccation, and temperatures remain high enough for breeding, even under cool conditions, because of absorption of solar heat and metabolic heat produced by micro-organisms. However, exposure to danger as a result of life histories restricted to the soil surface may be a reason both for the only recorded instances of parasitism on the Scarabaeinae by other insects, and for the number of protective devices developed by *O. egregius* (Davis 1989a). Larvae of *O. formosus* are parasitized by a bombyliid fly and by a small pteromalid wasp, although the latter may be a hyperparasite of the fly larvae (Davis 1989a).

4.1.5.2 Rollers

As mentioned above, several groups of "rollers" do not roll, nor do they belong phylogenetically to groups of rollers. We have therefore added several more patterns to the types defined by Cambefort and Hanski (1991).

Canthonini

As presently constituted, this is a large, cosmopolitan, basal group but is undoubtedly polyphyletic. Although considered to be "rollers", as many as 50% of the genera worldwide have not been seen to roll, and may, in fact be too small to do so (see Chapter 4.1.1.1). Nesting behaviour in a few of the large or common species has been studied but it is unknown in most species.

Megathoposoma candezei is the only species thought to illustrate Type 1 nesting, where copulation occurs at the food source, the female makes the ball, rolls and buries it, all unaided by the male. Many species of Canthonini are "true" rollers and share Type 2 nesting with most Scarabaeini, Gymnopleurini and Sisyphini. There is bisexual co-operation in ball-forming and rolling, with the male the most active partner during the above-ground activities. Mating takes place after the ball is buried and the male leaves the burrow. The female then remodels the ball, or splits it into two brood pears. After oviposition the female abandons the nest and may repeat the process again up to several times.

Cambefort and Hanski (1991) attributed this type of nesting to *Circellium bacchus*, based on earlier reports, but it has subsequently been shown (Kryger *et al.* 2006a; Le Roux *et al.* 2008) that this species is quite different to any other. Females form, roll and bury the ball, followed by a male, but completely unaided by him. The male is buried with the ball after which mating takes place and he abandons the nest. The female then cleans the ball of debris adhering to it from the rolling process, and re-forms the ball. An egg is laid in a cavity at the top of the ball. The female then remains in the nest with the ball and emerges with the young adult 4 – 5 months later. Under ideal conditions the female, who lives several years, may breed twice in a year but once appears to be the norm (Kryger *et al.* 2006a).

Although the very unusual flightless Australian forest species, *Cephalodesmius armiger*, is taxonomically classified as a canthonine and is nominally a "roller" it behaves as a tunneller. It is also the only known group in which permanently bonded pairs live together throughout their adult lives. They make a burrow in the forest floor, and males collect and drag fallen leaves backwards into the nest where the female grinds them with her fore legs and head into compost (Monteith and Story 1981) from which brood balls are made. The compost is then progressively added to the brood balls as the larvae grow.

Some, mainly carrion-feeding Neotropical species of *Canthon*, illustrate Type 4 nests in which males and females roll several balls together to a nest in which they both care for the developing brood until the emergence of the progeny. This may be repeated several times over one season.

Cambefort and Hanski (1991) considered some New World *Canthon* to have lost the ability (Type 5) to form balls but to use round dung pellets as a substitute. *Canthon obliquus* drags such pellets forwards (Halffter and Halffter 1989). Some small African desert-adapted species (e.g. *Dicronacara*), push pellets and dung fragments backwards but this is probably more a function of size of the beetle than anything else.

Eurysternini

Eurysternini have traditionally been treated as rollers because they roll near-perfect balls (all species studied except *E. foedus* which breeds in an unformed brood mass – Huerta *et al.* 2003), albeit in a shallow nest, that have lost the above-ground rolling behaviour (Type 5, Cambefort and Hanski 1991). However, as mentioned above, they apparently evolved from a dichotomiine-like ancestor (*i.e.* a tunneller, Philips *et al.* 2004b; Monaghan *et al.* 2007), so it is more likely that they never had the ability to roll. They are best considered to be "endocoprids" as in the Oniticellini, but the selective pressure for the evolution of the pattern in the Oniticellini is very likely to have been quite different to that in the Eurysternini since the latter are a tropical group living under a completely different set of environmental conditions to most Oniticellini (a largely savanna group). As with the latter, however, they utilize drier dung that appears to have become largely unattractive to tunnellers and rollers. Halffter *et al.* (1980) speculated on why *Eurysternus* dung balls lying in very superficial nests are not stolen by other dung beetles active at the same time, a very common occurrence amongst them, and concluded that the balls may be impregnated with chemicals repellent to other insects, something that has subsequently been demonstrated in the Neotropical ball-roller *Canthon cyanellus cyanellus* (Favila

1988, 1993). Oniticellines, on the other hand, are active when few other dung beetle groups are.

Eurysternus nesting and breeding behaviours are complex and there is a high degree of maternal care in most species (none in *E. jessopi* - Halffter *et al.* 1980; Huerta *et al.* 2003; Huerta *et al.* 2005). There is a long maturation feeding period of 30 – 200 days in different species. Some of the species excavate "provisional nests" just below or adjacent to the dung mass and roll several (6 – 7 on average, but up to 55 in some species) well-formed balls. These are attended by a pair of beetles and the female may oviposit in some of them. After some period the male and female devour some of the balls and eggs, and also often developing larvae, in a frenzied "nuptial feast" which may last up to 90 days, or they may abandon the nests. This may be repeated several times before "definitive" nests are prepared, again with several brood balls (usually about 7-8) which the female then broods, sometimes attended by the male (Huerta *et al.* 2003; Huerta *et al.* 2005). The female remains with the brood until late in the development of the larvae and then abandons the nest.

The most intriguing aspect of *Eurysternus* breeding biology is the activity of developing provisional nests, obviously at great energetic cost, and then indulging in a nuptial feast in which the dung balls and developing immatures are devoured in an infanticidal frenzy. Halffter and colleagues have hypothesised that females whose oocytes continue to develop during nesting are most likely to develop provisional nests and indulge in nuptial feeding, or to abandon the brood. Once vitellogenesis has ceased, females enter a definitive nesting phase and the infanticidal and brood abandonment behaviour stops. This may explain the mechanism, but the selective pressure to behave in this fashion and the possible ecological advantages of this bizarre behaviour continue to elude us.

Scarabaeini

This tribe represents the quintessential ball rollers revered by the ancient Egyptians and studied in detail by Jean-Henri Fabre, the French naturalist who wrote so eloquently about them 100-odd years ago. The tribe is clearly monophyletic but feeding specializations and food relocation behaviour are apparently polyphyletic (Forgie *et al.* 2006).

Although the more usual nesting pattern in Scarabaeini is the formation of a ball at the food source as well as rolling and burying the ball, all performed by the male, usually without assistance from the female, there are several exceptions. Copulation is in a simple chamber constructed by the male after which he abandons the nest. The female then remodels the ball and may:

- Care for a single uncoated brood ball for the full duration of immature development (e.g. *Scarabaeus* (*Kheper*) *nigroaeneus* in southern Africa – Edwards 1988;
- Coat the rolled ball in clay, leave it for a few days then prepare two to four broods from the original ball rolled, not coat them, then brood them (many *Scarabaeus* (*Kheper*) species e.g. *S. aegyptiorum* – Sato and Imamori 1986; *S. platynotus* Sato and Imamori 1987, both in East Africa);
- Form 1 – 3 balls in a pre-constructed nest chamber, coat them in clay, and brood them (*Scarabaeus (Sceliages) hippias* in South Africa - Forgie *et al.* 2002);
- Collect dry dung pellets and detritus in the hind legs, drag them into a previously excavated burrow, lay an egg, then abandon the nest (*Pachysoma* species in south-western Africa – Scholtz *et al.* 2004).

Cambefort and Hanski (1991) considered the Scarabaeini to use only two nesting patterns, Types 2 and 3, equivalent to the first two types above. Type 2 is a general pattern shared with Canthonini, Gymnopleurini and Sisyphini, (as discussed above). Type 3 is considered a highly specialized form in which females of some *Scarabaeus* and *Scarabaeus (Kheper)* species may produce a single brood ball using a typical rolling strategy, or several balls in an alternative tunnelling strategy (Sato 1998). There is usually only one breeding episode per year.

Pachylomera femoralis has not been studied in detail but it appears to have a mixed reproductive strategy of rolling / tunnelling similar to that of some *Scarabaeus*.

Scarabaeus (Sceliages) species are all obligate millipede-feeders, using the internal tissues and gut contents of freshly-killed spirostreptid (Spirostreptida: Spirostreptidae) millipedes for food and breeding (Forgie *et al.* 2002). They represent a different pattern to any other described for scarabaeines. Mated females bury whole or large fragments of fresh millipede remains in a burrow constructed adjacent to, or at some distance from, the millipede. The millipede is pushed with head and fore legs up to and into the burrow. It is disarticulated underground, and the internal tissues and gut contents scraped out and used to provision the brood balls. Depending on the size of the millipede, from 1 – 3 brood balls are constructed, coated with a thick soil layer and brooded by the female.

Another highly unusual member of the tribe is the south-west African desert genus *Pachysoma* in which rolling has been abandoned completely in favour of dragging dry dung pellets and detritus held in the hind legs forward, to a pre-constructed burrow (Scholtz *et al.* 2004). Males provision a burrow and then wait at the entrance for a female to pass by. The burrow is loosely filled with detritus. Attraction appears to be pheromonal. Mating takes place and an egg is laid, after which it is abandoned by both parents.

The south-east African *Scarabaeus galenus* holds fresh round dung pellets between the hind legs, off the ground, and walks backwards into a pre-formed burrow where a number of these are squeezed together and a larger ball is formed (Ybarrondo and Heinrich 1996).

Eucraniini

Members of this near-endemic Argentine tribe have been considered "rollers" since earliest times, yet it has been known for as long that they carry dung pellets in their fore legs and run forwards on the middle and hind legs. The dung is carried to a pre-constructed burrow where it is squeezed into larger brood balls (Philips *et al*. 2002; Ocampo and Hawks 2006). Several recent phylogenies (Philips *et al*. 2002; Philips *et al*. 2004b; Ocampo and Hawks 2006; Monaghan *et al*. 2007) have provided unequivocal evidence that they have evolved from a dichotomiine-like tunnelling ancestor, so the highly specialized food relocation strategy is probably an adaptation to the availability of only small pellets in the arid environments in which they occur.

Gymnopleurini

This is a small tribe of morphologically and behaviourally similar rollers, all of which apparently produce nests of Type 2, as discussed above.

Sisyphini

All members of this tribe also produce Type 2 nests, except that in some *Neosisyphus*, brood balls are abandoned above ground, or attached to stems of plants near the dung source (Cambefort and Hanski 1991).

4.2 EGG-LAYING

Nest preparation and brood mass construction are precursors to the next step in the breeding process, egg-laying, so once the brood mass is completed and the female has mated, eggs are laid. However, because eggs probably represent the most vulnerable of the immature stages, there is considerable investment in preparation of special egg chambers and in oviposition itself. Energetic investment in eggs themselves is massive. They are very large relative to the body size of the female, hence physiologically expensive.

The eggs are either laid directly into the dung mass, or in a specially constructed egg chamber in the apex of the ball or pear, which is sealed off from the dung provision, or in something in between. The female may prepare one brood mass to receive a single egg. The different behavioural patterns of egg chamber preparation and egg placement are as diverse as the nesting patterns themselves and vary widely between different groups.

In the simplest form the female lays eggs in a chamber in the dung mass, and then in increasing levels of complexity, egg chambers are separated from the dung by being placed in the soil layer covering the brood ball, or placed in a specially constructed chamber of tightly compacted dung. The eggs are usually attached at one end to the floor of the chamber. This may prevent injury to the egg when balls are moved during brooding, but also exposes the minimum surface area of the egg to possible direct contact with micro-organisms.

Before a discussion of egg-laying behaviour is considered, however, some background on the physiology of egg-production is appropriate. The most striking features of the female reproductive system are that it is reduced to a single ovary which produces as few as one egg at a time, and at most a few sequentially, and the massive size of the eggs relative to the female. In *Pachysoma glentoni* (Fig. 4.1), the single mature egg fills about half of the female's abdomen. Halffter and Lopez (1977) attribute this reduction in reproductive system "… to the high degree of complexity and efficiency of the nidification behaviour…". Clearly the large parental investment in constructing a suitable nest in equitable surroundings and protected from predators, as well as securing sufficient food for the development of the larvae, and preparing the brood for survival if abandoned, or caring for the brood for up to many months, have contributed to the high reproductive success of dung beetles.

In the simplest type yet recorded, that in the dichotomiine genera *Pedaridium* and *Trichillum*, females lay eggs directly into a dung mass without preparation of an egg chamber or elaboration of the brood mass (Verdú and Galante 2001).

Females of the oniticelline, *Attavicinus monstrosus*, which breed in debris in ant nests, but in well-formed balls, lays eggs in poorly-defined chambers in the balls. In many of the groups that oviposit in dung masses other than in well formed balls or pears, such as many Onthophagini, the egg is nevertheless in a distinct chamber where it is attached in an erect position. In some other groups such as in *Copris* (Coprini), the egg lies in a chamber within the dung provision itself, but the chamber is lined with a black secretion produced by the female which hardens to form a smooth finish. The secretion is thought to have antibiotic properties. In *Phanaeus* (Phanaeini) the brood balls are covered with a

Fig. 4.1. Dissected abdomen of female *Pachysoma glentoni* (South Africa) illustrating the size of the single developed egg (white mass). (Photo Lena Stenseng).

thick soil layer and the egg chamber is placed inside this. Some *Heliocopris* and *Ontherus* (Dichotomiini) construct a round cell from soil and faeces at the top pole of the ball, with a plug of dung fibres linking it to the brood ball. The latter eventually serves as a ventilation tunnel for the larva.

Various groups (e.g. *Pachysoma, Dicranocara, Byrrhidium*) living in desert regions of south-western Africa, which feed on and breed in dry dung and detritus are known to breed in burrows packed with loose fragments, something akin to members of the Geotrupidae (Scholtz *et al.* 2004; Deschodt *et al.* 2007). In the scarabaeine genus *Pachysoma*, eggs are laid in the loose accumulation of debris that makes up the brood provision in the nest (Scholtz *et al.* 2004). This is undoubtedly a reversal from a typical ball-rolling ancestor and was probably necessitated by the environmental conditions in which they live that do not permit rolling dry fragments into a ball.

In the basal genera *Dicranocara* and *Byrrhidium*, it is not clear whether this is the ancestral condition, or a reversal from the typical ball-forming pattern that was also merely necessitated by the environmental conditions. It is quite likely that many other unstudied species breeding in detritus also breed in an accumulation of fragments rather than a constructed ball.

Although the behaviour in the dichotomiines (and by implication, basal groups) *Pedaridium* and *Trichillum*, is similar in many respects to that of the Aphodiinae sister-group in which eggs are deposited directly into a dung mass, and the larvae live freely inside it (Verdú and Galante 2001), larval morphology is typical of those species living inside a pre-constructed brood. It is, thus, very likely that this behaviour is a reversal to an ancestral feeding type, rather than the primitive type itself.

4.3 LARVAL DEVELOPMENT

Eggs of most species are deposited in specially prepared chambers and the emergent larvae merely tunnel into the dung to feed.

Unlike adults, dung beetle larvae have hard, biting mouthparts, and are capable of grinding the coarser and drier dung on which they feed into smaller digestible fragments. Goidanich and Malan, (quoted by Cambefort (1991a)) demonstrated that the microflora in the larval food are very similar to those in the larval intestine. These include aerobic and anaerobic bacilli and various fungi. The authors reported that the bacterial content of fresh brood ball dung is high, but drops to about half that after a few days. However, the bacterial content increases from 2 – 17 times the basic level in the fermentation chamber of the larval gut, where there is a dense culture of these cellulose-digesting bacteria that they depend on for nutrition. After excretion, the bacterial content of the faeces drops again to that of fresh dung, after which it is re-ingested. This is repeated several times with the dung quality improving every time it is ingested and leading ultimately to increased efficiency in resource utilization.

All dung beetle larvae live and feed inside the food provided by the adults, (an undoubted autapomorphy for the Scarabaeinae), and clearly the provision of food in a secure environment has contributed to dung beetles' high success rate and has resulted in the lower fecundity needed to maintain viable population levels.

In spite of the generally favourable conditions that adults create for immature development, much of breeding behaviour is dedicated to ensuring maximum brood production. Not only is food provided in a secure environment for larval development but numerous parental behavioural activities have evolved to ensure this. These are the essence of breeding behaviour:

- the amount of larval food sequestered;
- the measures taken to protect the brood from fungi and desiccation, and;
- whether the developing larvae are sufficiently distant from each other to avoid conflict and the spread of disease between them.

There are also several obvious advantages to larvae developing in a food mass and in a secure subterranean environment:

- the larvae are surrounded by food so no energy is expended in acquiring it;
- micro-climatic conditions are moderate, with small fluctuations in temperature and moisture over the generally short development period of most species and;
- the immatures are generally well protected against parasites and predators.

Each of these factors contributes to the generally high breeding success rate of most species, and sets them well apart from their relatives without any form of brood care.

4.3.1 Amount of food sequestered

Competition at the dung source will usually determine the amount of dung available to the adults for brood preparation, and in the case of tunnellers, the space available beneath the dung for nesting may be severely limited. In the case of rollers, where the amount of dung they are physically capable of manipulating during ball-formation and -rolling is limiting under optimal conditions, competition may further limit the time an adult is allowed to spend forming a ball, thus producing a sub-optimal food supply for the larva which, in turn, may eventually result in a smaller or callow adult with decreased chances of survival. A small adult is even more constrained physically in the amount of dung sequestered, which results in still smaller adults. An extreme case of this has been recorded for *Circellium bacchus* in which adult length varies between 22.0-47.0 mm (X = 36.3 mm), and is apparently a direct consequence of the amount of food available for the developing larva (Kryger *et al*. 2006a). This developmental flexibility is necessary for this flightless species, which lives in dense bush away from potential aggressive competitors against which it is markedly inferior (Nicolson 1987), and uses virtually any type of dung that is available in approximately adequate quantities. Females form brood balls alone often very slowly, taking up to 24 hours to form a brood ball, and then they may roll it distances of up to 100 m away from the dung source. It compensates, however, for the sometimes sub-optimal supply of larval food by having some of the most intense brood care known in the Scarabaeinae.

4.3.2 Protection of brood

Whether to coat or not to coat, to abandon or not to abandon, these are the questions? Some groups coat their brood balls with clay, others do not, and usually those that coat the brood with clay abandon it, while those that don't coat the brood, usually stay with it and care for it. However, some that coat also care for the brood, and some that do not coat abandon it. So, again, as with so much of dung beetle breeding biology, the hunt for "patterns" is complicated by lack of consistency amongst the different groups, as well as within a group under different sets of environmental conditions, and hints that the latter are more likely to have set a particular pattern than phylogeny has. Clearly coating balls with clay is time and energy consuming, but abandoning the brood affords more reproductive episodes, thus higher lifetime fecundity. Not coating the balls, on the other hand, but then investing a huge amount of time and energy in caring for the brood, possibly reduces risk to the brood but undoubtedly lowers lifetime brood production. Coating may also provide protection against pathogenic and competitive fungi, and against competitors for the dung such as termites.

As a general rule the tunnellers that bury dung masses without later remodelling them into balls (Type 1 nesters) do not coat the dung masses and usually abandon them, and those groups that form distinct brood balls or pears, may or may not coat them, and may or may not abandon them. The latter include those tunnellers that form the balls in the nests, or the rollers that form and roll them above ground. However, there are numerous exceptions to the rule.

A less common pattern is one in which a sequestered dung mass is coated with soil after burying, and then used a few days later for brood construction. Both rolling (*Scarabaeus aegyptiorum* – Sato and Imamori 1986) and tunnelling

(*Copris armatus, C. boucardi* – Halffter and Edmonds 1982) species are known to coat the buried dung mass with clay and to leave it for a few days before it is used for brood ball construction. This is thought to aid in anaerobic "fermentation" of the dung, and also to delay desiccation (Halffter and Edmonds 1982), or to kill insect competitors in the dung such as fly larvae. However, it may equally also be a tactic used to postpone egg-laying when females are not physiologically quite ready to lay eggs.

So, what are the trade-offs between the energetic expenditure of coating and abandoning the brood against not coating, but caring for it? And what about species which do not coat the balls but still abandon them and ones that coat the balls yet still care for them? Few empirical data exist, but species feeding on high protein diets such as carrion and fungi usually make smaller balls (about half as large) than similar-sized dung feeders, coat them with clay, and care for them. However, because of the high quality food, larval development is about twice as fast (about three to four weeks) on these substances (millipede carrion, *Sceliages* – Forgie *et al.* 2002; vertebrate carrion, *Canthon cyanellus cyanellus* – Favila 1993; mushrooms, *Coptorhina* – Frolov *et al.* 2008) as equal-sized species feeding on herbivore dung, and parents can repeat the breeding episodes more often, thus compensating for the time spent brooding. Favila (1993) and Halffter *et al.* (1996) demonstrated that in the absence of parental care in *Canthon cyanellus cyanellus* and *Copris incertus*, respectively, brood survival is greatly reduced, or all are destroyed by fungus. Halffter *et al.* (1996) also quoted survival rates from other studies where the female or both parents had been experimentally excluded and compared them to survival with parents in attendance, and reported offspring survival rates of 59% against 93% in *Copris fricator*, 32% versus 76% in *C. diversus*, 68% against 98% in *Canthon cyanellus*, and no surviving offspring if the female was excluded from developing *Scarabaeus (Kheper) nigroaeneus* brood.

Halffter *et al.* (1996) experimentally excluded females of the sub-social species, *Copris incertus*, from brood, to determine the effect of survival on the different immature stages in the laboratory in comparison to brood attended by the female. The surface of all of the unattended brood balls became brittle and the balls and brood were invaded by *Metarrhizium* and *Cephalosporium* fungi in the pupal stage of development. Halffter *et al.* (1996) used key-factor analysis (based on Begon and Mortimer 1986 – see details in Halffter *et al.* 1996) to determine the effect of parental care on mortality between subsequent stages, and to compare *k*-values of the transition stages based on 95% confidence limits, as well as between the two treatments. In the analysis, mortality factors between stages ($k = \log_{10}$ of numbers of individuals at stage t - $\log_{10}$ of numbers of individuals at stage $t + 1$) are related to the total mortality factor ($k_{\text{total}} = \log_{10}$ of numbers of individuals at the egg stage – $\log_{10}$ of individuals at the adult stage) by means of linear regressions. Those with significant correlation coefficients indicated that a mortality factor at that stage was important in determining population change. Halffter *et al.* (1996) implemented this analysis by calculating the k – value at each stage and k_{total} for each of the treatment repetitions. They then calculated the regression coefficients of each individual k – value on the total generation value, and thus determined the stage at which mortality was significantly correlated with total mortality.

Figure 4.2 illustrates k – values for the different age intervals in the treatment and control, and from egg to adult. Although there was mortality in all stages in the treatment nests, the greatest mortality factor (k_i) was recorded in the transition from pupa to adult. There was also some mortality in all but one of the control nests, but k – values were not significantly different within and

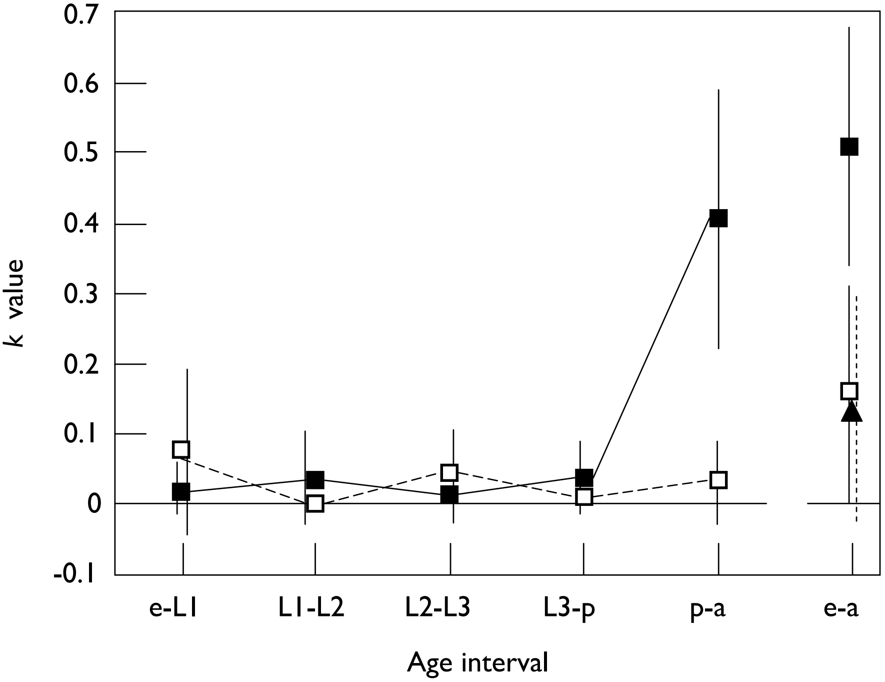


Fig. 4.2. Changes in the mortality factor (k) and 95% confidence intervals (vertical lines) in the transition between stages during larval development in *Copris incertus*.
Filled squares = without parents; empty squares = with parents (terraria handled); Triangle = with parents (control, terraria not handled), discontinuous vertical line indicates confidence interval for the control; e: egg; L1: first stage larva, L2: second stage larva, L3: third stage larva, p: pupa; a: adult. (Adapted from Halffter *et al.* 1996).

between control and treatment nests if the transition from pupa to adult is excluded, as shown by the 95% confidence intervals.

Key-factor analysis for the treatment and control (Fig. 4.2, e-a) showed a clear difference between balls with parents in attendance and those without. A Kruskal-Wallis test comparing k_{total} between treatment and control indicated significant differences between them ($T = 10.27$, $P = 0.006$). Non-parametric comparison indicated that k_{total} was significantly higher in the treatment when compared to the control. Halffter *et al.* 1996 also tested for the effect of handling on the treatment nests and found no effect.

Favila (1993) recorded that broods of *Canthon cyanellus cyanellus* with parental care were significantly more successful than broods without parental care (Larval stage 2, vs L1: $\chi^2 = 15.5$, $P < 0.001$ and L3 vs L1: $\chi^2 = 42.77$, $P < 0.001$) and were not contaminated with fungi. Survival of larvae up to adult emergence was high in nests with parental care up to L2 and L3 stages, but there were significant differences between the two treatments in the number of adults emerged (L2 vs L3: $\chi^2 = 9.09$, $P < 0.05$). Broods without parental care were quickly contaminated with fungus, and larvae apparently died of starvation because of the fungal attack of the food. Edwards (1988) and Kryger *et al.* (2006a) demonstrated similar rates of attrition for *Scarabaeus* (*Kheper*) *nigroaeneus* and *Circellium bacchus* immatures, respectively, unattended by the female.

From these results it is clear that parental care is critical for brood survival in these species, and Halffter *et al.* (1996) interpreted the high mortality in the pupal stage as a result of the fact that larvae were able to maintain the integrity of the brood ball's inner wall by plastering cracks that resulted from the absence of female care and so exclude fungi. The sessile pupae, on the other hand, were incapable of doing so and were, consequently, attacked by the pathogens. Halffter *et al.* (1996) also discussed the importance of the parents, (although this was not tested in the laboratory), of protecting the brood from kleptoparasitic dung beetle species, predators such as Histeridae beetles, and other detritus feeders such as earthworms.

So, what of species without this level of sub-social brood care? Most species in which brood is abandoned after oviposition have deeper nests, and the brood balls are coated with clay in what Halffter and Edmonds (1982) called the "ecological equivalent" of sub-social brood care. There appear not to be any published studies of immature survival rates in species that coat and abandon their brood, so discussion of a "comparable" situation is not possible, and even if such studies existed, too many different factors are involved in each of the processes to make comparison meaningful. The fact that numerous species have one or the other of these two alternative breeding behaviours, or one of a host of intermediate ones, is evidence that both are obviously equally successful.

4.3.3 Larval spacing

Brood is usually in the form of a constructed mass, either of brood balls or pears, but in some groups, such as in many Onthophagini and some Onitini, cylindrical "sausages" are constructed with larvae evenly spaced throughout. Nests may consist of single or multiple balls or pears, each with one developing larva, or brood sausages with poorly-defined margins, and larvae feeding more or less communally.

The close proximity of broods to one another has the potential to cause the spread of disease and allow easy access from one to another by pathogens. This has been overcome to some extent in most species by eggs being laid at intervals in a brood mass, where larvae develop a short distance from siblings which are separated only by a variable amount of the dung and distance. This is the pattern in most Onthophagini but also some others such as some Onitini, and although it is an intuitively "primitive" behavioural pattern, the Onthophagini are a highly derived group, and amongst the most fecund. The development of a breeding pattern in which brood balls are separated from each other, either by an air space, or a soil plug, further enhances brood separation. The most derived examples of this pattern are found in the Coprini

4.4 PUPATION

The larvae of all major scarabaeoid groups pupate in a cocoon produced from food material cemented together with faeces which forms a sometimes very flimsy structure as in some Scarabaeinae (e.g. the dichotomiine *Paraphytus* – Cambefort and Walter 1985; and the scarabaeine *Pachysoma* – Scholtz *et al*. 2004), to a very hard case in some related Cetoniinae and Dynastinae (Ritcher 1966).

All dung beetle pupae are protected inside the original food mass or in the burrow dug by the parents, although tunneller larvae usually construct a pupal chamber around themselves (recorded exceptions are *Pedaridium* and *Trichillum* larvae – Verdú and Galante 2001). This consists of a smooth inner wall produced by faeces manipulated with the mouthparts, and plastered with the external anal lobes or "Fabre's trowel" in the characteristic behaviour first described by the renowned French entomologist of that name, and an exterior of soil and food remains adhering to it (Halffter and Edmonds 1982). This is considered to be an extension of the repair response that dung beetle larvae exhibit when their feeding cavity is breached, and is thought to seal the feeding chamber from potential pathogens. Unlike tunneller larvae, those of roller species do not construct a defined chamber around themselves but pupate inside the cavity formed by the feeding larva, the exterior of the ball effectively forming the cocoon.

Dung beetle pupae are characterised by well defined structures that project from the body wall, and which are hypothesised to minimise contact between the pupa and the surrounding fecal shell, and so lower the risk of contact with pathogens. (These are exceptionally long in *Trichillum* pupae which merely lie in a larval feeding cavity and not in a constructed pupal chamber – López-Alarcón *et al*. 2009). Halffter *et al*. (1996) recorded very high pupal mortality in *Copris incertus*, a species with well developed maternal care, when the female was experimentally removed from her brood. The authors attributed the high mortality at this stage to the fact that pupae, unlike larvae, were unable to maintain the integrity of the brood ball's inner wall by plastering cracks that resulted from the absence of female care and the invasion of the pupal chamber by pathogenic fungi (see detail in Chapter 5.9).

An exception to the typical pupal morphology and behaviour has been recorded in *Pachysoma* (Scholtz *et al*. 2004). The pupa lies loose in the larval food remains (detritus and dry dung fragments) inside the larval feeding burrow and lacks the projections from the body wall that are universal in the pupae of all other known species. Presumably the dry, sandy substrate and coarse food remains that surround the pupae do no attract potentially pathogenic fungi to the same extent that the more typical dung remains of most other dung beetles do so there was little pressure to retain them from their ancestor.

CHAPTER 5

SPECIAL MORPHOLOGICAL FEATURES OF DUNG BEETLES

Dung beetles share various morphological features with other members of the Scarabaeoidea, since many of these are adaptations to the mainly fossorial way of life of most members of the group. These include a somewhat convex body shape, large fore body which houses the leg and wing muscles, and toothed and flattened fore tibiae. There is an expansion and slight "folding" of the anterior margin of the head, and the head appendages are in a ventral position, where they are protected during digging. The eyes are protected by an extrusion of the genae to form a protective canthus, which lessens soil abrasion during digging. There is also a tight seal between the abdomen and covering elytra, and spiracles opening under the elytra, both of which serve to reduce soil, and possibly parasites such as mites, entering the sub-elytral cavity in which the essential organs (which are covered by only thin sclerites), and the spiracular openings to the trachea lie, and perhaps also to reduce water loss. However, various morphological attributes specific to dung beetles are immediately obvious in many species.

In rollers the most obvious is the presence of long legs, reaching in the sisyphines, absurd extremes (see Plate 12.18); and in tunnellers the presence of horns in many species is striking (see Fig. 5.5). Most species are dull and appropriately cryptically coloured against the dark background of dung and soil that they frequent but some species are, somewhat unexpectedly, given their habitat, brilliantly metallic coloured.

Tunnellers have retained the more typical characteristics of the ancestral fossorial beetle, particularly those of the legs which are relatively short and thick and clearly adapted for digging. Rollers, on the other hand, have much more elongated legs, particularly the last pair, an apparent adaptation for rolling a ball. Tunnellers, thus, have morphological attributes more specialised for burrowing, and rollers those for rolling.

The rollers, however, have traded burrowing ability off against competitive ability at the dung source – the faster a roller is at making and rolling balls, the worse it is at digging burrows (e.g. the South African species *Neosisyphus spinipes* pays the ultimate cost of extremely long legs which preclude them from digging efficiently and they often abandon their balls on the soil surface or attach them to a piece of vegetation). Although rollers can quickly form a ball and remove it from the focus of competition, and then bury it somewhere suitable, being less well adapted for burrowing they can only dig shallow burrows, albeit at a slow pace, if necessary (e.g. *Circellium bacchus* may roll balls up to 100 m from the source and take 24 hours to bury them – Kryger *et al*. 2006a). The rollers are further constrained in the amount of dung they can sequester, since it is restricted to the amount they can collect and roll under competitive pressure, which ultimately affects the amount of dung available for breeding (e.g. the East African roller *Scarabaeus (Kheper) platynotus* rolls large balls of 7-9 cm diameter and may form as many as four broods from them – Sato and Immamori 1987).

Although tunnellers can relocate more dung and produce more offspring per breeding episode than similar sized rollers, they have the fierce competition for burrow space beneath the pad to contend with. They can, however, sequester up to ten times more dung for breeding than do rollers of roughly equal size and bury it 2-3 times deeper, but probably at greater energetic cost. Large tunnellers such as *Heliocopris* species bury enough dung to form 5-10 tennis ball sized brood balls at depths of up to one metre (Klemperer and Boulton 1976), while large rollers such as various *Scarabaeus (Kheper)* species feeding from the same source may roll one similar-sized ball, which may eventually be used to form two broods buried at a depth of 20-30 cm.

5.1. MOUTHPARTS

The mouthparts of most Scarabaeoidea are fairly "typical" for insects which usually have sclerotized mandibles performing the primary function of cutting and grinding the food. Dung beetles have deviated considerably from the basic structure and the possible functions of the different mouthparts have been controversial for decades.

In all dung beetles the mouthparts consist of membranous and hairy labrum-epipharynx and mandibular incisor lobes, and finely and robustly ridged molar areas of the mandibles, the convex one fitting tightly into the opposing concave one. The membranous and hairy parts remove large dung fragments from the food and scoop liquid components into the oral cavity (Halffter and Matthews 1966). Until recently (Cambefort 1991a), it was presumed that the molar lobes then crushed large particles into much finer ones which were then imbibed, but Holter (2000), Holter *et al*. (2002) and Holter and Scholtz

(2005, 2007) conclusively demonstrated that no trituration of dung particles takes place. Food is collected by the maxillary palps, the large particles are brushed out by filtration setae on the mouthparts, and the remaining paste is then squeezed by the molar lobes, while superfluous liquid is led away from the pharynx through the filtration channels. The remaining small particles are thus concentrated, and are then ingested.

In the series of papers on dung beetle feeding Holter and his co-workers, (Holter 2000; Holter, Scholtz and Wardhaugh 2002; Holter and Scholtz 2005, 2007) determined that adults of all the species, representing all of the African tribes, that they studied feed on tiny particles in the liquid fraction of dung. These varied from < 5 µm – 130 µm in diameter but most species feed on particles of less than 50 µm in diameter. Holter and Scholtz (2007) also determined what percentage of the dung of several herbivores was made up of particles of less than 20 µm, in other words suitable for most dung beetles. They also analysed the nitrogen value of the fraction made up of particles of less the 20 µm. This was done for Danish horse, sheep and cattle dung in different seasons, and for African elephant (*Loxodonta africana*), white rhino (*Ceratotherium simum*) and Cape buffalo (*Syncerus caffer*) dung in summer in South Africa. Their results showed that 20 – 50% of the dung of all the species analysed consisted of particles of < 20 µm, and that this fraction made up 40 – 90% of available nitrogen in the dung. See Chapter 6.3.3.

5.2. EYES

A large proportion of the world's dung beetle species fly strongly and many are nocturnal or active under dim light conditions in forest or dense vegetation. This requires two dependent biological characteristics of the beetles, good flight capabilities and sound vision since eye structure and function are primarily associated with flight navigation. Most dung beetles have both. The size, superficial appearance and internal structure of dung beetle eyes are characteristic of their patterns of flight activity and have been well-studied by Meyer-Rochow (e.g. 1978), Gokan (e.g. 1990) and Caveney and McIntyre and colleagues (Caveney and McIntyre 1981; Warrant and McIntyre 1990a,b; Caveney, Scholtz and McIntyre 1995; McIntyre and Caveney 1998).

Dung beetle eyes are situated to the front and side of the head and in most species they are partially or completely divided by an intrusion of the gena or cheek, called the canthus (Fig. 5.3). The main function of the canthus is to protect the surface of the eye from abrasion while the beetles are digging in the soil. It also divides the eye into two functionally different organs, with the ventral "eye" used mainly for vision and the dorsal "eye" for navigation. The former is usually larger than the latter and both eyes are larger in nocturnal than in diurnal species. They are usually greatly reduced in size in flightless species (Scholtz 2000; Dacke *et al.* 2002).

The compound eyes of insects can be classified on the basis of function into apposition eyes which are characteristic of insect orders with mainly diurnal activity, and superposition eyes which are generally found in insect orders whose members are usually crepuscular or nocturnal (Caveney and McIntyre 1981).

In a typical apposition eye, the photoreceptor cells abut the crystalline cone and effectively receive light only from the lens system of the ommatidium in which they reside because of the optical isolation of the ommatidia by screening pigment (Warrant and McIntyre 1990b). The design strategy is to achieve a reasonable compromise between resolution and sensitivity in the compound eye.

The superposition eye (Fig. 5.1), on the other hand, is characterized by a clear zone which allows parallel light entering the eye through many facets to cross between ommatidia and to focus on the photoreceptor cells of the ommatidium whose optic axis is in line with the direction from which the light originated (Caveney and McIntyre 1981). The aperture of the superposition eye is set by the number of ommatidia contributing to a single image, whereas in the apposition eye the maximum aperture is limited by the diameter of a facet.

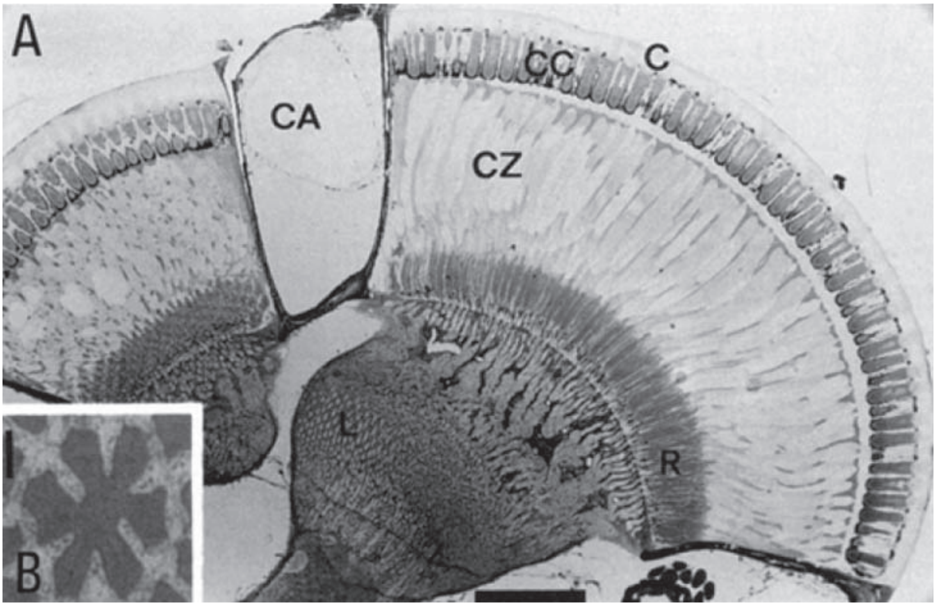


Fig. 5.1. (A) Longitudinal light microscope section through a dorsal (left of section) and ventral eye (right), with canthus (CA) between, of *Onitis*. C – cornea; CC – crystalline cone; CZ – clear zone; R – retina; L – lamina. (From Warrant and McIntyre 1990a).

All dung beetles have permanent superposition compound eyes, whether day- or night-active and in all of these the eye is of "eucone" construction in which the refractile crystalline cone is separate and well developed. The corneal lens is attached to the crystalline cone beneath which is a clear zone and a species-specific variable-sized light-sensitive rhabdom formed by the microvilli of retinula cells (Caveney and McIntyre 1981; McIntyre and Caveney 1998). This is different to the compound eyes of less specialised diurnal scarabaeid beetles such as some Melolonthinae which adapt by pigment migration to a functionally apposition state in bright light (Warrant and McIntyre 1990b; McIntyre and Caveney 1998).

In general, nocturnal species have large hemispherical eyes with a smooth or weakly-facetted outer corneal surface. No screening pigment lines the borders of the corneal facets and behind each facet lies a large crystalline cone and a wide clear zone. Crepuscular species also have large eyes but faceting of the cornea is more marked; and the crystalline cone may have a slight waist. The eyes of diurnal species, on the other hand, are considerably smaller than similar-sized nocturnal and crepuscular species, the corneal facets are strongly bi-convex and they are lined with screening pigment. The crystalline cones have a distinct waist or they taper markedly, and the clear zone is narrow relative to eye size (McIntyre and Caveney 1998).

In polarisation-sensitive dung beetles, the arrangement of the microvilli in the rhabdom follows a common pattern; the ones in each rhabdomere are organised in only one of two orthogonal directions (Meyer-Rochow 1978; Dacke *et al.* 2003a). With maximum sensitivity to light polarised parallel to the direction of the microvilli (references in Dacke *et al.* 2003a), this arrangement tunes the two groups of receptors to orthogonal planes of polarisation. Opponency between the two sets of receptors enhances the polarisation contrast and makes the system independent of the intensity of the light stimulus. This rhabdom design is generally confined to a narrow strip at the dorsal rim of the eye, termed the dorsal rim area (DRA). (Figs 5.2, 5.3).

In two species studied so far (both of which are South African rollers, *Pachysoma striatum* and *Scarabaeus zambezianus*), roughly the top half of the dorsal eye consists of a DRA which is used for polarised light detection for navigation (Dacke *et al.* 2002; Dacke *et al.* 2003a). In the ventral eye and the ventral half of the dorsal eye of *S. zambezianus*, microvilli from seven of eight retinula cells, which run in different directions in different rhabdomeres, form the rhabdom and appear flower-shaped in cross-section. In the DRA, the microvilli of the seven cells run in only two directions, forming an almost heart-shaped structure in cross-section (Dacke *et al.* 2003a; Fig. 5.4). The two sets of receptors with parallel microvilli which are orientated at 90° to each other can be found only in the rhabdoms in the DRA and these satisfy the requirements

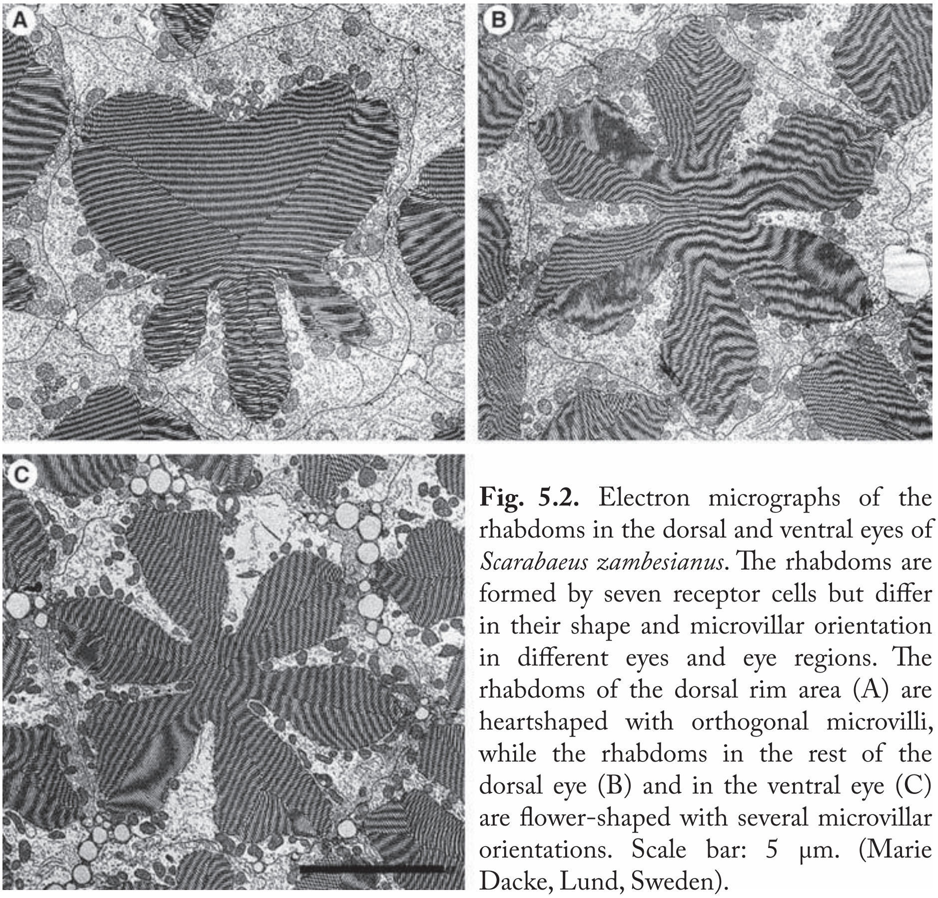


Fig. 5.2. Electron micrographs of the rhabdoms in the dorsal and ventral eyes of *Scarabaeus zambesianus*. The rhabdoms are formed by seven receptor cells but differ in their shape and microvillar orientation in different eyes and eye regions. The rhabdoms of the dorsal rim area (A) are heartshaped with orthogonal microvilli, while the rhabdoms in the rest of the dorsal eye (B) and in the ventral eye (C) are flower-shaped with several microvillar orientations. Scale bar: 5 µm. (Marie Dacke, Lund, Sweden).

for a polarization opponent analyzer. A second important characteristic for high polarization sensitivity is that the microvilli are aligned along the length of the rhabdom (Dacke *et al*. 2003a).

Light levels after sunset fall rapidly and continuously and the sensitivity of the detector becomes more critical for polarised light orientation. This is the situation faced by *S. zambezianus*. *Pachysoma striatum*, on the other hand, is active during the day in one of the brightest habitats on earth, a coastal sand desert. Dacke *et al*. (2003a) compared the eye structure of these two species, with emphasis on the rhabdoms of the DRA (Fig. 5.4, Table 5.1). The rhabdoms in *S. zambezianus* are much longer and almost three times as wide as in *P. striatum* (Table 5.1). This allows the former's receptors to collect more light and, consequently, be more sensitive. Furthermore, the tracheal tapetum of *S. zambezianus*

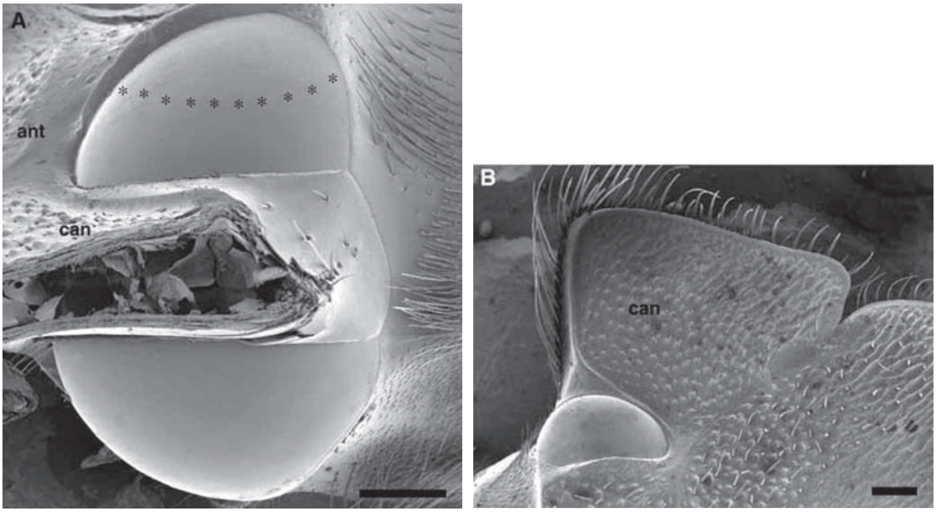


Fig. 5.3. (A) Scanning micrograph of the dorsal and ventral eye of *Scarabaeus zambesianus*. For correct orientation, the anterior (ant) direction of the animal is indicated. A lateral view of the head of the beetle shows the canthus (can) that totally separates the eye into a dorsal and a ventral part. The asterisks mark the border of the dorsal rim area that covers approximately half the dorsal eye, narrowing towards the ends. (B) Scanning micrograph of the dorsal eye and canthus. Scale bars: 500 µm. (Marie Dacke, Lund, Sweden).

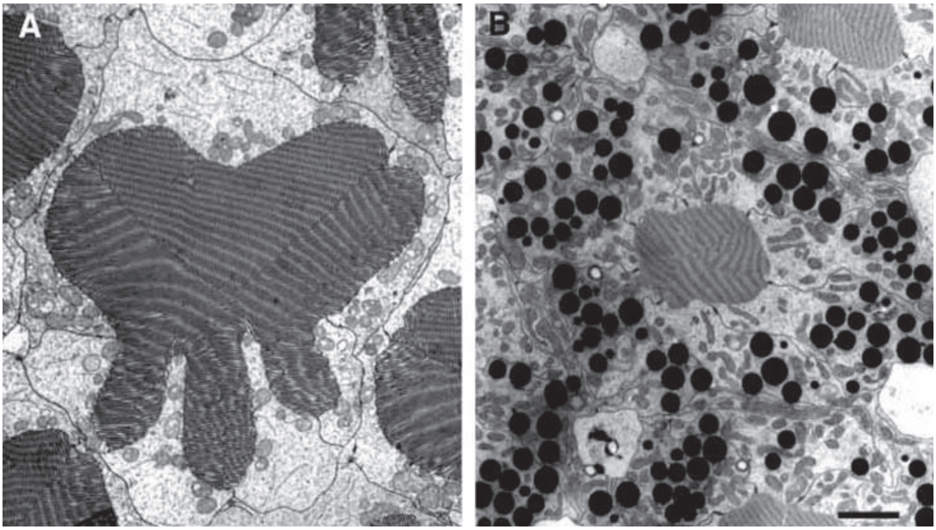


Fig. 5.4. Cross-sections of dorsal rim area (DRA) -rhabdoms in the crepuscular beetle *Scarabaeus zambesianus* (A) and the diurnal beetle *Pachysoma striatum* (B). Note the difference in the size of the rhabdom and amount of pigmentation, both morphological adaptations to the time of activity. Scale bar: 2 µm. (Marie Dacke, Lund, Sweden).

Table 5.1. Dimensions of rhabdoms and focal lengths in the dorsal rim area of two dung beetle species.
d, rhabdom diameter; *l*, rhabdom length; *f*, focal length. Measurements were taken from electron microscope sections (*d*) and light microscope sections (*l*,*f*). *d* is calculated from the area of the non-circular rhabdoms. (After Dacke *et al.* 2003a).

Species	***d* (μm)**	***l* (μm)**	**f (μm)**
Scarabaeus zambesianus	11	120	555
Pachysoma striatum	4	78	328

reflects light back through the rhabdom for a second time, effectively making the rhabdom twice as long. Dacke *et al.* (2003a) also compared the optical sensitivity (see references in Dacke *et al.* 2003a) of the two species using:

$$S = \left(\frac{\pi}{4}\right)^2 A^2 \left(\frac{d}{f}\right)\left(\frac{kl}{2.3 + kl}\right) \tag{1}$$

Where A is the diameter of the superposition aperture, f is the posterior nodal distance of the eye, d and l are the rhabdom diameter and length, respectively, and k is the extinction coefficient of the rhabdom (taken as 0.00067 μm^{-1} from the literature). Since A was unknown for both species the authors were unable to obtain an absolute value for S but using the values of d, l and f for the two species they obtained values of $S = 9.6 \times 10^{-5} A_{sz}^{2}\ \mu m^2$ sr for *S. zambezianus* and $S = 1.7 \times 10^{-5} A_{ps}^{2}\ \mu m^2$ sr for *P. striatum*. A_{sz} and A_{ps} are the unknown diameters of the superposition eyes of *S. zambezianus* and *P. striatum*, respectively, but even if they are considered equal, the former species' DRA is still 5.6 times more sensitive to a light source than the latter's. However, because *S. zambezianus* is a crepuscular / nocturnally active beetle it can be expected to have a much wider superposition aperture than the diurnal *P. striatum* (McIntyre and Caveney 1998). Moreover, the rhabdoms in the DRA of *S. zambezianus* are isolated from each other by a tracheal sheath, while those of *P. striatum* are isolated from each other by light-absorbing pigments which would make the sensitivity difference even greater (Warrant and McIntyre 1991).

5.3 HORNS

The presence of horns and other exaggerated structures in males of various animals, amongst them many groups of Scarabaeoidea, has long attracted attention amongst naturalists, and as early as 1871 Charles Darwin wrote extensively about their importance as weapons used in conflict between males for the attention of females. Although many divergent beetle groups have independently acquired horns (Arrow 1911) and other cuticular outgrowths (see Emlen *et al.* (2005b)), it is in the Scarabaeoidea that they have diversified extravagantly. Many species of male stag beetles (Lucanidae) have huge mandibles, whereas in the Scarabaeidae subfamilies Dynastinae (rhinoceros beetles), Cetoniinae (fruit chafers) and the Scarabaeinae dung beetles, the structures are mostly on the head or thorax. Amongst the latter groups, the structures in Scarabaeinae have been studied best, mainly by Emlen and collaborators, in the context of sexual selection (see Emlen *et al.* 2005b for an eloquent treatment of the subject; also see Chapter 11.

Horns and mandibular extensions are found in males, and occasionally in females, of some genera, at least, of all groups of tunnelling dung beetles, but are widespread in Coprini, Phanaeini, Oniticellini and Onthophagini. However, they have only been studied in Phanaeini (Otronen 1988; Rasmussen 1994), Onthophagini (see Emlen *et al.* 2005b) and Oniticellini (Lailvaux *et al.* 2005; Pomfret and Knell 2006). Horn structure and the evolution of different types in the Onthophagini, most species of which bear horns in males, have been systematically studied by Emlen *et al.* (2005b), and their findings are probably widely applicable to most tunnelling dung beetles.

A large proportion of *Onthophagus* species bear horns, and most of these are sexually dimorphic with males horned and females hornless, and furthermore, males are usually dimorphic for horn size – they either bear large or small horns. The diversity of the horn types in the males of the Onthophagini is wildly extravagant, with numerous different shapes and sizes present on a wide variety of positions on the head and thorax (Emlen *et al.* 2005b; see Fig. 5.5). These Emlen *et al.* (2005b) grouped into five classes based on their location: those on the back of the head; as outgrowths from the vertex; those on the middle of the head; from the frons, and; those in front as clypeal extensions. The horns that developed as thoracic outgrowths arose either from the centre or from the sides of the pronotum. Horned females are found only in the same tribes as are horned males.

Large- and small-horned species are present in different proportions in most populations where they employ different tactics to access females – large-horned males guard burrow entrances against intruders, and small-horned males sneak past guards or tunnel directly into the burrow where the female is present.

The production of horns is energetically costly, with compensatory trade-offs in resource allocation during development of those species with enlarged horns. Species with large horns often have smaller than normal structures that develop adjacent to them, principally antennae and eyes but also testes and

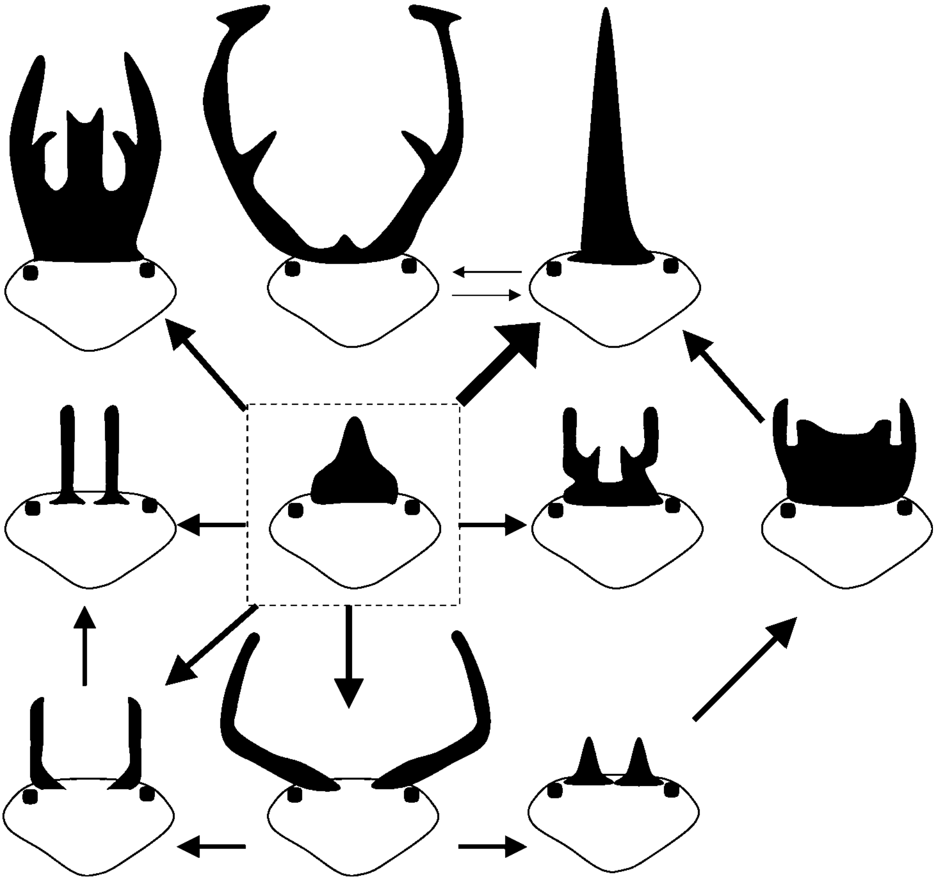


Fig. 5.5. Different horn shapes and their evolutional origin in various Onthophagine groups. Redrawn from Emlen *et al.* 2005b.

wings (Kowano 1997; Nijhout and Emlen 1998; Emlen 2000, 2001; Knell *et al.* 2004; Emlen *et al.* 2005b; Tomkins *et al.* 2005). Horns developing on the thorax reduce development in wings, and consequently, flight capability; those developing on the middle or front of the head probably impact on antennal development and olfactory capabilities; and those developing on the back of the head reduce the size of eyes and likely impair vision. However, males must still be able to see, smell and fly in order to functional normally.

Emlen *et al.* (2005b) mapped ecological characters onto their phylogeny and produced three tests of the mechanisms of divergence involving each of the proposed trade-offs: horns versus wings; horns versus antennae; and horns versus eyes. Dung beetles need to fly between sequential breeding locations, so wing size is likely to affect dispersal distance – those that fly short distances between food sources usually occur in high density populations, so gains in thoracic horns are more likely to evolve in lineages with crowded populations. Their data supported this assumption with seven of the 11 gains of thoracic horns occurring in lineages with high population densities (concentrated changes test: $P = 0.003$). In contrast, gains of head horns, which were not predicted to trade off against wings, were not associated with crowding (one of five gains, $P = 0.767$).

Because beetles use their antennae to detect odour plumes, it would be expected that these would be least traded off against in habitats where odour plumes are difficult to detect, such as open areas. On the other hand, odours are less likely to be dissipated in closed situations such as forests. So, if antennal reduction is traded off against horns, then those on the head of forest species would be selected for. Emlen *et al.*'s (2005b) data, once again, supported this hypothesis: four of the five gains in head horns were in forest species (concentrated changes test: $P = 0.059$); and gain of thoracic horns, in contrast, was not associated with forest habitats (three of 11 gains, $P = 0.921$).

It is well known that nocturnal insects have large eyes compared to their diurnal relatives, and that this is apparently for seeing better under low-light conditions. Many dung beetles are strictly diurnal or crepuscular (see Caveney *et al.* 1995), and this is reflected in eye size. Growth of head horns in *Onthophagus* reduces eye size by an impressive 30% (Nijhout and Emlen 1998; Emlen 2000, 2001). Consequently, Emlen *et al.* (2005b) tested whether horns at the base of the head might be costly to nocturnal species, but because head horns were common in many of the taxa they studied, they focused on losses of the horn, rather than gains. They found that of nine observed losses of head horns, seven occurred in lineages with nocturnal species (concentrated changes test: $P = 0.000$).

Studies of three different *Onthophagus* species (*O. nigriventris, O. taurus, O. binodis*) provide evidence that there is a phenotypic trade-off between investment in horns and testes growth (Simmons and Emlen 2006), yet in comparison of 25 others they failed to find the expected negative correlation between horn and testes size. One of their explanations for this was that resource allocation trade-offs associated with horn and testes development has not affected long-term patterns of beetle evolution, and that the time scales involved in the evolutionary diversification of these species were sufficient to permit horns and testes to develop relatively independently of each other.

Parzer and Moczek (2008) recorded that relative investment into horns in *Onthophagus taurus* exhibited a strong negative correlation with relative investment into male genitalia size (SS = 0.0001, $F = 107.84$, $r^2 = 0.092$, $P = 0.009$; non-standardised regression: SS = 0.0046, $F = 4.662$, $r^2 = 0.55$, $P =$

0.1635), thus revealing a strong signature consistent with a resource allocation trade-off between both structures. The authors found a similar pattern across 10 *Onthophagus* species (SS = 0.0597, F = 38.48, r^2 = 0.81, P = 0.0003; non-standardised regression: SS = 0.0046, F = 4.662, r^2 = 0.55, P = 0.1635). Thus an increase in the investment into horns coincided with a significant decrease in investment into genitalia.

5.4 LEGS

In adult beetles, all parts of the normal insect leg are usually distinct although in a few cases the tarsi may be lost, as in the front legs of some Scarabaeinae (Crowson 1981).

Legs of adult dung beetles are typical of general burrowing beetles which manifest mainly in the broad, dentate fore tibiae. With change from adaptations to typical soil-burrowing behaviour and coincident morphology, the middle and hind legs, particularly in rollers become progressively more elongated reaching the outrageous extremes found in some Sisyphini. Many groups of rollers have also lost the front tarsus completely, presumably because of the pressure on these somewhat flimsy structures during ball-rolling when the front legs press down on the ground to roll the ball backwards. The fore tarsi have been lost in all Scarabaeini and many Canthonini. At the apex of the fore tarsi there is often a more or less straight terminal spur, which may be sexually dimorphic in some groups, tending to being curved or spatulate in males in these groups. Tarsi on all legs usually end in a pair of claws, although in some ultra-psammophilous species such as the Namib Desert canthonine, *Hammondantus*, the claws are obsolete (Scholtz and Howden 1987a).

Femora of hind legs may be slightly inflated in some dung beetle species, with, in some male *Onitis*, a strong ventral spine, the function of which is unclear.

The long legs in rollers have come at the cost of two trade-offs (Hanski and Cambefort 1991c): a morphology well suited for making and rolling balls, against a morphology suited for burrowing; and between the ease with which a ball of dung is rolled and the size of the ball, which represents the total resource for potential offspring. Hanski and Cambefort proposed that the faster a roller is at making and rolling balls, the less adept it would be at digging burrows. The African *Neosisyphus spinipes*, which has extremely long hind legs, has possibly paid the ultimate price, virtually forfeiting burying balls at the cost of extremely long legs. It often abandons brood balls at the soil surface or attaches them to a plant after rolling them some distance, without even attempting to bury them.

5.5 WINGS

Most dung beetles fly strongly and often over long distances, an apparently obvious necessity for an animal dependent on widely dispersed and ephemeral food sources. Winged species have well developed thoracic flight muscles and strongly sclerotized wing veins to stiffen the wings during flight. Most species lift and open the elytra slightly prior to take-off to enable the wings to fold out and expand but the Gymnopleurini have dispensed with this mechanism, having a distinct notched lateral pleural area through which the wings can be expanded without lifting the elytra. Yet, in spite of flight being an important requirement for successfully locating food and mates, many species have dispensed with flight altogether. This apparent paradox is discussed below and in Chapter 9 on loss of flight in dung beetles.

5.5.1 Relationship between wing reduction and reduction in other organs in dung beetles

Reduction of the wings is the most obvious feature in flightless dung beetles but thoracic and other sclerites as well as apparently unrelated structures such as eyes may undergo parallel modification to a greater or lesser degree.

The metatergum forms the roof of the metathorax, the segment that bears the membranous flying wings. It exhibits a wider range of variation in flightless forms than does any other region of the body (Smith 1964). It is clear that the tergum may undergo more or less extensive and parallel modification after the ability to fly is lost, and there is also an approximate correspondence between the degree of reduction displayed respectively by wings and tergum. The first step in the modification of the tergum of an incipiently flightless beetle appears to occur before the wings become reduced, and involves a general decrease in sclerotization, together with a reduction in size of the phragmata and of the width of the lateral arms of the postnotum (Smith 1964).

The metapleuron forms the side of the metathorax but undergoes little modification in most flightless species except that the pleural wing processes become ill-defined as the wing becomes greatly reduced (Smith 1964).

The metasternum constitutes the floor of the wing-bearing segment and affords the ventral insertion areas of the tergosternal and pleural flight muscles. Anteriorly it is indented to receive the mesocoxae, and it articulates posteriorly with the metacoxae. The metasternal plate decreases in length relative to the rest of the thorax in wingless species where it is approximately twice as long as wide; in winged species it is approximately as long as wide.

Flightlessness in beetles may be associated with more or less secure joining of the elytra along the midline and it has been suggested that this modification may help reduce respiratory water loss (see Chapter 10.1), or that this feature may provide additional support for the elytra which is no longer afforded by the weakened metatergum. Chown *et al*. (1998) compared the body shape of winged and flightless species of South African Scarabaeini and Canthonini. They selected closely related winged and flightless species to avoid introducing phylogenetic constraints. They concluded that the flightless species studied (three Scarabaeini and five Canthonini) have a more rounded body shape than equivalent-sized and related winged species (four Scarabaeini and three Canthonini), and that flightless Canthonini have a more rounded body shape than flightless Scarabaeini. Furthermore, they found that desert-living flightless species have the most rounded body shape which they attributed to its improved capacity for water retention.

The shoulder (humeral angle) of the elytron of a winged beetle is usually sharply angled to accommodate the edge of the metatergum and wing articulations and this region may become rounded in flightless species (Fig. 5.6). This is particularly noticeable in species with the metatergum greatly reduced and with full wing reduction which become markedly globose as result of the overall shortening of the thorax and increased dorsal convexity.

The eye of winged dung beetles has a raised margin with bristles, whereas in flightless species the eye is reduced in size and surrounded by a smooth margin (Fig. 5.7). When a species loses its flight capabilities the ommatidium numbers decrease and they simplify concurrently with loss of flight but the basic structure remains the same. (See Chapter 9).

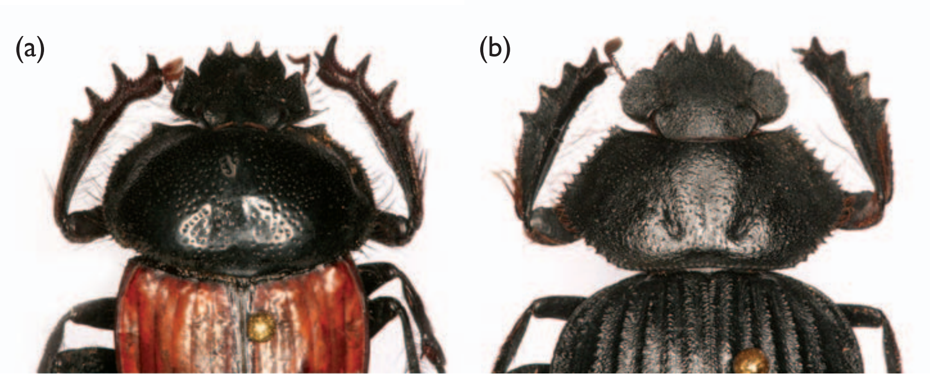


Fig. 5.6. Dorsal views of (a) fully-winged dung beetle (*Scarabaeus rubripennis*) and (b) flightless *Pachysoma striatum* (south-western Africa) of similar size (18 mm) illustrating humeral angle (shoulder).

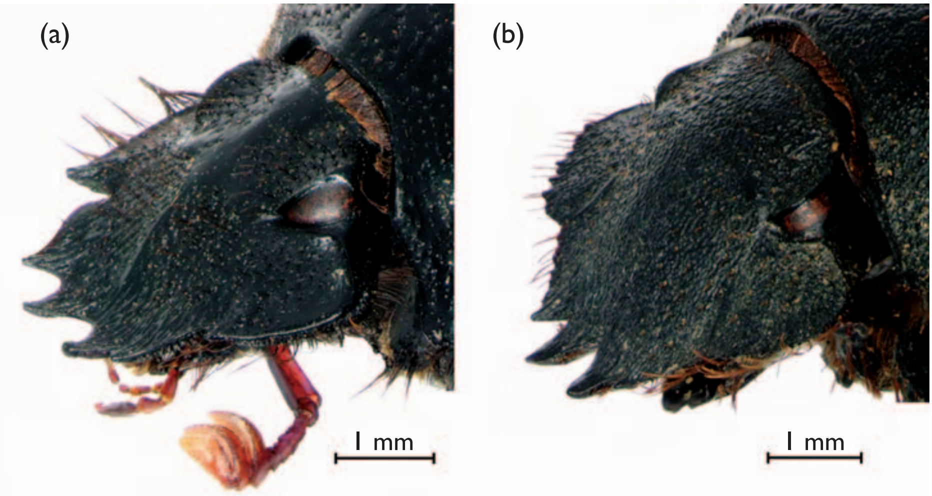


Fig. 5.7. Dorsal eye of diurnal dung beetles: (a) well developed in winged *Scarabaeus rubripennis* and; (b) smaller in flightless *Pachysoma striatum* (both south-western Africa) of similar size (18 mm). Scale bar = 1 mm.

5.6 SPIRACLES AND THE SUB-ELYTRAL CAVITY

Adult dung beetles have eight pairs of functional spiracles, two thoracic and six abdominal (Crowson 1981). The first pair is large, and lies more or less ventrally, in the membrane between the hypomera of the prothorax and the mesepisterna, and is treated as the "mesothoracic" pair. The second pair of thoracic ("metathoracic") spiracles is situated immediately below the wing articulations, close in front of the metapleural ridge and above the mesepimera. They are always concealed by the closed elytra. The first and subsequent abdominal spiracles (in segments 1-6) also lie under the elytra, and open into the sub-elytral cavity (SEC), an apparently primitive situation in beetles (Crowson 1981) and one closely associated with, particularly, burrowing groups, where the spiracles are well protected from abrasion and from soil particles and parasitic mites entering the tracheal system. In volant beetles the elytra have special locking mechanisms which increase the rigidity of the structure and afford protection to the soft abdomen beneath. In flightless species, the elytra may be more or less permanently fused along the midline, and be tightly sealed by a dense layer of microtrichia along the lateral margins, thus forming a well-sealed chamber. All dung beetles when not flying have the elytra closed and the SEC more or less functional, while flightless dung beetles have the cavity permanently and tightly sealed. See Chapter 10.1, 10.4.

5.7 ABDOMINAL GLANDS

Glands of mostly ectodermal origin, and with various functions, are quite common in beetles, and may occur on any part of the body (Crowson 1981). These may secrete protective wax and open on various parts of the body surface, especially of beetles in arid areas where they are thought to reduce surface transpiration; they may be pygidial in origin and produce defensive secretions; or produce pheromones that have sexual functions; or label the food they are eating. Some of these types of glands are known from dung beetles although the field is still wide open for detailed study.

Pluot-Sigwalt described the morphology of the abdominal tegumentary glands in Scarabaeinae in a series of papers (see Pluot-Sigwalt 1991 for a full list of references). Among these are glands in the sterna and pygidium, which she recorded in most of the typical rollers she studied, but were absent in the tunnellers, and rollers whose rolling behaviour has not been observed, and who are considered doubtfully capable of rolling (several Australasian and Madagascan taxa, as well as the Neotropical *Cryptocanthon* and *Canthochilum*, which have been considered "close" to dichotomiine tunnellers (see Halffter and Halffter 1989). An exception amongst the "true" rollers was *Sisyphus*, which also lacked the glands.

The sternal glands cover a large area of the abdomen and are sexually dimorphic, characteristics that make them unique to the Scarabaeinae. The glands are inactive during the maturation feeding period and only become active when reproductive behaviour commences. The secretion of female-attractant pheromone by male *Scarabaeus (Kheper)* species (Tribe 1975; Edwards and Aschenborn 1988) involves the extrusion of thin columns of toothpaste-like pheromone-impregnated wax from a depression on either side of the first abdominal sternite (Tribe 1975). The males stand in a head-down position, and brush the filaments off by repeated combing of the abdomen with the setose hind tibia. The secretions then volatilize in puffs of white vapour.

The pheromone-producing depressions consist of several hundred minute openings resembling a sieve, which are supplied by a large gland complex underlying the depression. Both sexes have long hairs along the tibial margin, but in the male these are concentrated to form brushes. Immediately posterior to the depressions of the anterior portion of the second, third and fourth abdominal sternites lies a single row of rigid bristles which are curved towards the depression.

Pheromone dispersal functions by the hind legs being retracted simultaneously inwards toward the sides of the body, and then extended simultaneously. The movement causes the tibial brushes to brush against the pheromone filaments emerging from the pores in the depression against the rows of curved bristles. This causes puffs of pheromone vapour to rise from both sides of the beetle (Tribe 1975). This is repeated every 20-30 seconds until a female arrives or the male starts to roll a ball.

The males of *Canthon cyanellus*, a common Central American carrion-feeding roller, secrete a chemical substance from their seventh abdominal sternite onto the surface of the balls being rolled. The primary aim of this is thought to be to attract females over a short distance, but the secretion is also apparently repellent to *Calliphora* blow flies (Bellés and Favila 1984; Favila 1988; (Ortiz-Domínguez *et al*. 2006).

5.8 THE FEMALE REPRODUCTIVE SYSTEM

Most beetles have two ovaries with varying numbers of ovarioles yet dung beetles are unique in having only one complete ovary [the left] and one ovariole. This is an apparent synapomorphic state for dung beetles since all other Scarabaeoidea, including the Aphodiinae, the purported sister group to the Scarabaeinae, have two ovaries and six ovarioles, on average (Ritcher and Baker 1974). This is considered to be the basal condition in scarabaeoids.

Nesting behaviour in dung beetles is closely tied to the physiological and developmental state of the female reproductive system. Nesting will not take place until the female has mated and until the ovary has matured (Halffter and Edmonds 1982).

Martinez and Huerta (1997) studied ovarian development and morphological variation in the *corpus allatum* and in the type A neurosecretory cells of the *pars intercerebralis* in relation to maturation and nesting in *Copris incertus*. This is a Mexican species with well developed nesting and brood care behaviour. They found that there is a relationship between basal oocyte size, *corpus allatum* volume and the amount of neurosecretions in the A cells of the *pars intercerebralis*, and that for each behavioural stage there is a corresponding physiological state of these organs.

When females emerged from the soil these organs were found to be inactive. The pre-nesting phase started after the females emerged, and lasted on average about 68 days. Mating took place between 10 and 30 days after emergence. Females were reproductively active for about 340 days during which time they bred from one to four times, each reproductive period lasting about 112 days. The resting-feeding period between breeding episodes lasted about 50 days.

At the onset of the pre-nesting period the ovaries were immature, with no oocytes, the *corpus allatum* had low volume and the *pars intercerebralis* showed abundant neurosecretory granules which indicated that secretion had not yet started. After about 10 days post-emergence the basal oocyte started to develop, *corpus allatum* volume increased slightly and granules in the *pars intercerebralis* decreased visibly.

At the end of the pre-nesting period, females started to feed on the dung cake provisioned by the nesting pair (see Chapter 4.1.2). At this time, the basal oocyte had increased 3-4-fold in size since about the middle of the pre-nesting period, the *corpus allatum* had tripled in volume and the *pars intercerebralis* cells contained low amounts of neurosecretory granules.

At ovulation, which coincided with brood ball formation from the dung cake, the oocyte reached maximum size (about 5 mm), *corpus allatum* volume dropped to about that of the pre-nesting stage and the *pars intercerebralis* contained low amounts of neurosecretory material. The female then, over the course of a few days, made 3-6 brood balls in which she laid eggs.

During the brood care phase of the reproductive cycle the basal oocyte was gradually reabsorbed and *corpus allatum* volume remained low while neurosecretory material in the *pars intercerebralis* started to increase again. This state continued more or less without change until the brood matured and the female left the nest whereafter she began the resting-feeding phase and the reproductive cycle was again repeated.

In studies of the effects of mating and male secretions on ovarian development, Cruz and Martinez (1998) and Martinez and Cruz (1999) recorded that male mesadene secretions (from the accessory reproductive glands) induced *corpus allatum* and *pars intercerebralis* activity which triggered ovarian maturation, egg-laying and nest building in the ball-roller *Canthon cyanellus cyanellus*. In this species, as well as several other dung beetle species quoted by these authors, mating is indispensable for ovarian maturation, egg laying and nesting to occur, and it is the affect of the male mesadenes that precipitate it. During mating male dung beetles produce a spermatophore containing abundant seminal fluids which consist mainly of the accessory gland secretions. Most of this seminal fluid has high concentrations of proteins, glycogen and acid muco-polysaccharides (= a nuptial gift) (Cruz and Martinez 1992, quoted by Cruz and Martinez 1998) as has been found for diverse insect groups such as [other groups of] Coleoptera but also in Diptera, Lepidoptera and Orthoptera (references in Cruz and Martinez 1998; Vahed 1998). These have been found to pass into the female's spermatheca and into the haemolymph after lysis of the spermatophore after which it reaches target sites directly or via hormones that control reproductive output (references in Cruz and Martinez 1998).

The morphology of the dung beetle spermatheca has been implied to restrict the order of fertilization to the most recent male that mates with the female. The spermatheca is almost c-shaped with a strong muscle between the two "arms" in all tribes except the Sisyphini (López-Guerrero and Halffter 2000). It is a long coiled tube in the latter.

What reproductive and behavioural advantages does a c-shaped spermatheca offer the female? López-Guerrero and Halffter (2000) support the findings by Cruz and Martinez, discussed above, that the first copulation is essential for the completion of vitellogenesis. However, the first male to mate with the female is not necessarily the male that will co-operate in nesting. The spermatozoa of subsequent matings push those of earlier matings to the back "arm" of the spermatheca, thus rendering them less accessible for fertilization. This mechanism of sperm precedence permits the female to benefit from the first copulation to initiate reproductive behaviour, but to fertilize her eggs with sperm from the last male who will serve as her nesting partner (also see Favila *et al.* 2005; and Chapter 11 on "sexual selection"). The c-shaped spermatheca, with strong muscles and a long, thin duct permits the ejection of very few spermatozoa simultaneously, but ones of the female's "choosing" and at exactly the moment necessary (López-Guerrero and Halffter 2000).

Another advantage of the shape of the spermatheca and being able to store sperm is that the female can successfully nest alone when she locates food and when males are not present, and although females co-operating with males during nesting are able to produce more brood than those nesting alone, successful single nesting is known for most species studied (López-Guerrero and Halffter 2000; also see Chapter 4.1.5.1).

What, then, is the benefit of the energetically expensive mesadenes included in the spermatophore of the first male to mate with a female? His investment benefits the female but does not contribute to his own fitness since, in all likelihood, the female's eggs will be fertilized by successive matings with other males. So, males are unlikely to have been selected to provide parental investment before fertilization because of the uncertainty of parentage (Vahed 1998). It has therefore been argued that donations made by males to their mates such as nuptial food gifts are more likely to represent a form of mating effort than parental investment (Vahed 1998).

5.9 LARVAL MORPHOLOGY

All groups of Scarabaeoidea have generally superficially similar larvae. Most are c-shaped, white fleshy "grubs" with a well sclerotised head capsule and well-developed legs. Most are free-living in soil or decomposing plant matter. Their virtually universal soil-frequenting habits are the putative ancestral ones for the group (Scholtz and Chown 1995) and their morphology reflects these habits. Dung beetle larvae, however, are enclosed in their food in a burrow, well protected from environmental extremes and predators, and as a result of these changes from the ancestral habitat, have lost some of the basic morphological attributes still held by their relatives, and they have acquired other characteristics adaptive to their specific environmental demands.

Since dung beetle larvae are virtually always found in a cavity in a brood mass, this immediately distinguishes them from all relatives that might be found under similar conditions but life in a spherical cavity has selected for two of the main structures that characterise them, and are probably autapomorphous for the Scarabaeinae (Edmonds and Halffter 1978; Grebennikov and Scholtz 2004). These are the "coprine hump" and the flattened, fleshy-lobed anal segment (Fabre's trowel). Both of these characteristics are functionally related to movement within a confined spherical space. The larva wedges itself in the space, with the flattened anal area applied to one surface and the dorsum of the hump to the opposite surface (Halffter and Matthews 1966). This leaves the fore body free to move up and down for feeding. To change position, the larva applies the head and hump against the surface, and contracts and swings the hind body forward to a new position, and then reverts to the feeding position.

Both of these typical characteristics of dung beetle larvae have additional functions to the ones just mentioned. The dorsal hump is the external manifestation of the enlarged hind gut, which in most species is considered to function as a fermentation chamber in which microbial decomposition of the cellulose that makes up the major component of the larval diet, takes place. The fleshy anal lobes also function as a plastering trowel. The function was first noted by the famous French entomologist Fabre, and he described it as a plastering trowel used by the larva to smear the inside of the feeding cavity with its own faeces, which is inoculated with bacteria, then re-ingested to aid in digestion, and also to patch breaches in the ball.

5.9.1 The case for *Pachysoma* larvae

The south-west African scarabaeine genus *Pachysoma* is unusual in many respects (Scholtz *et al*. 2004). This extends to the larvae as well, which, in a complete reversal from the unique specialization of living and feeding inside an enclosed dung mass which is universal in dung beetles, have reverted to the ancestral free-living mode, albeit in a food mass provided by the adults in a secure burrow. The behavioural changes have also resulted in morphological reversals similar to that found in distantly-related free living relatives.

Edmonds and Halffter (1978) provided a list of characters that, in combination, are unique to *Scarabaeus* larvae [*Pachysoma* is *Scarabaeus*' sister-taxon see 12.2.2] but *Pachysoma* larvae differ in several other exclusive characters, all of which can be attributed to their evolutionary change from living inside the confines of a ball to a free-living life style reminiscent of that of their distant relatives (Scholtz *et al*. 2004).

The following characters are clearly different to those of *Pachysoma*'s relatives (Scholtz *et al.* 2004). (1) The number of antennal segments has been reduced from three to two – a reduced number of antennal segments is presumably still adequate for tactile movements in the soil. (2) Maxillary stridulatory teeth are reduced – these are thought to be used in communication with the adult female outside the ball and may become reduced in the absence of the need to communicate. (3) The stiff abdominal setae, common in ball-living larvae, and which are presumably used to aid locomotion in the ball, are lost in the free-living larvae. (4) Spiracles are much smaller than those of their relatives – large spiracles, which are apparently necessary to enable respiration in the oxygen-poor environment of the brood-ball, are superfluous in the free-living situation. Smaller spiracles may also be more efficient at excluding fine soil particles that are largely absent in a ball, and may restrict the loss of moisture from the trachea, something that is more likely to occur in loose sand rather than in the confines of a ball. (5) The coprine hump, which is so characteristic of larvae living in brood-balls, and is thought to aid locomotion inside the ball, is lost in free-living larvae, as is (6) the highly modified lobular anal segment that is used for plastering faeces on the cavity wall in the ball, and in ball-repair. (See Fig. 5.8)

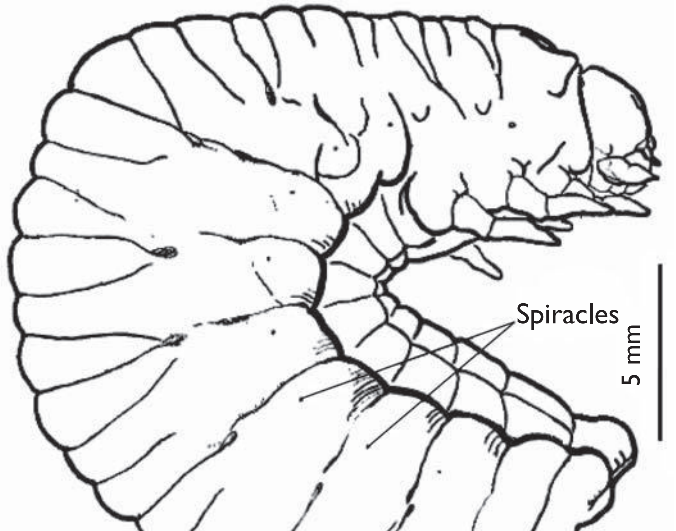


Fig. 5.8. *Pachysoma* larva illustrating atypical dung beetle larval shape. Characteristic is the absence of the "coprine hump" which is diagnostic of larvae maturing inside a ball, and very small spiracles.

5.10 DUNG BEETLE COLOUR

Most dung beetle species across the taxonomic and behavioural spectrum are black or otherwise dark-coloured. This extends to representatives of all of the tribes and members of each of the major behavioural groups, i.e. tunnellers, dwellers and rollers, and includes diurnal and nocturnal species. The high incidence of darkly-coloured species in most dung beetle assemblages is generally explained by assuming that it renders them cryptic against a dark background of dung and soil, and affords them some protection against predators. Furthermore, most species are assumed to be ectothermic and dependent on heat absorbed from the environment, and, if this were true, dark colours would be physiologically more advantageous than pale colours. (Many rollers, however, have been recorded to raise their body temperatures endothermically, and all are dark-coloured – See 8.1.1)

What then of species with other than dark colours, and especially those with brilliant iridescent colours? Four tribes have high proportions of pale or brightly-coloured species: the Phanaeini, in which most species are brightly coloured (see Plates 12.3, 12.4) the Onthophagini with species showing a wide range of colours from mottled yellow / brown (see Plates 12.9 – 12.11) to bicoloured in combinations of bright and dark colours, to those with brilliant colours (especially in *Proagoderus*); Oniticellini, in which many species are mottled yellow / brown (*Euoniticellus, Oniticellus, Tiniocellus*) or have contrasting bands of black and white (*Tragiscus* – Plate 12.8) and Gymnopleurini, with some species showing bright iridescent colours (*Garetta, Gymnopleurus*). The first three tribes are represented by exclusively tunnelling species, the latter by rollers. Most brightly coloured species are diurnal. In the other tribes species coloured other than black or dark brown are much rarer.

Black, brown and yellow colours are assumed to be pigment colours in insect cuticle. Iridescent colours, however, (or more correctly, the perceived colours), are not produced by chemical composition of the exoskeleton, but by specific cuticular ultra-structure that generates colour through the selective reflection of particular visible wavelengths. The ultra-structure and optical processes vary between insect taxa, and include: light-diffraction grating arrangements on the exoskeleton surface; spectral effects from light-scattering structures or photonic crystals within the cuticle and; cuticular ultra-structure that induces thin-film or multilayer interference (Kinoshita and Yoshioka 2005). Colour generated by multilayer interference is characteristic of many beetle families (Kinoshita and Yoshioka 2005) including the Scarabaeidae (Neville and Caveney 1969; Hegedüs *et al*. 2006), and more specifically in dung beetles of the subfamily Scarabaeinae (Neville and Caveney 1969; Brink *et al*. 2007; Davis *et al*. 2008a).

Such multiple cuticular layers, with their different refractive indices, cause greater transmission or absorption of certain wavelengths across the visible light spectrum, and greater reflection of others, thus generating both the perceived exoskeleton colour and its intensity (Kinoshita and Yoshioka 2005).

In scarabaeid beetles the ultra-structure responsible for reflectance shares properties with cholesteric liquid crystals (Neville and Caveney 1969). These optically active structures occur in the exocuticle and comprise identical microfibrillae arranged in parallel. They give the impression of having been laid down in sheets, as the microfibrillae of each successive level are offset to the left at a slight angle until they describe a complete 360° rotation and form multiple helicoidal structures (Neville and Caveney1969). This left aligned spiral structure of the exocuticle causes left circular polarization of light, which was first recorded by Michelson (1911 in Hegedüs *et al.*, 2006), but it is rare in nature (Hegedüs *et al.*, 2006). However, it is the rule in all dung beetles studied to date, including *Phanaeus* and *Onitis* (Neville and Caveney 1969), and *Gymnopleurus* species (Brink *et al.* 2007).

The pitch or perpendicular thickness of each complete 360° helix in the optically active layers dictates which wavelengths of light are absorbed, and which are reflected (Neville and Caveney 1969; Brink *et al.* 2007). Thus, differences in pitch lead to differences in wavelengths of reflected light, and the perceived colour of the beetle. In scarabaeid beetles, pitch has been manipulated experimentally by boiling a portion of green-reflecting cuticle (Neville and Caveney 1969). This caused it to expand and reflect longer, red wavelengths, whereas applying finger pressure caused it to contract and reflect shorter, blue wavelengths. However, natural differences in pitch and the perceived reflected colour would presumably arise primarily from variation in the development of ultra-structure within the nascent adult exoskeleton during the pupal stage.

Dung beetles show a good deal of variation in exoskeleton colour. In some species, different sclerites reflect different dominant colours, particularly prothoracic discs and elytra (Vulinec 1997). However, individuals of many iridescent species are essentially monochromatic. Although some monochromatic species show the same dominant colour in all individuals, many are polymorphic, comprising two or three colour varieties. Thus, the same species may be represented by individuals that are entirely cupreous, entirely green, or entirely blue. However, it should be emphasized that, although these colour varieties are essentially monochromatic, if the dominant reflected wavelengths are close to the spectral transition between different perceived colours then there is a bi-chromatic reflectance effect, particularly if viewing the exoskeleton at different angles.

Section B

PHYSIOLOGICAL AND BEHAVIOURAL ECOLOGY

Clarke H. Scholtz

CHAPTER 6
FOOD AND FEEDING IN DUNG BEETLES

6.1 FEEDING IN ADULTS

It is generally accepted (Cambefort 1991a; Scholtz and Chown 1995) that dung beetle food evolved from a diet of decomposing detritus with a probable dependence on microbes, especially fungi, involved in the decomposition process. Cambefort (1991a) eloquently explained the possible mechanism involved which was essentially that at the beginning of the decomposition process humus consists of large fragments of vegetable matter and an inoculum of microbial decomposition agents. As decomposition proceeds, the particles become smaller and the microbes increase. When this takes place in a moist environment the humus becomes saturated and takes on a pasty consistency of very small particles and increasing levels of carbohydrate- and protein-rich microbes. This broth of nutrient-rich liquid then makes up the bulk of the food retrieved from the humus. Concurrent with the evolution of this specialised diet would have been the modification of the mouthparts from typical strong, biting mandibles, such as those found in almost all of the major dung beetle relatives, to the soft, flexible mandibles with a filtering apparatus, found in virtually all dung beetles. The step from feeding on the liquid components of well decomposed detritus to dung, especially of herbivores, was an easy one in view of the similarity of the substrates; dung being little more than small plant fragments, water, sloughed epithelial cells of the animal that voided it, and microbes. The explosive radiation of mammalian herbivores during the Tertiary would have created niche space for the dung beetles to radiate in concert.

We have discussed elsewhere (Chapter 1.3) whether those species that feed on non-dung food evolved directly from a humus-feeding lineage, or whether they switched from a dung-feeding ancestor to the current diet. However, in almost all cases, liquid or partially liquid food has remained the common factor (the only known exception, the south-west African scarabaeine *Pachysoma glentoni,* feeds on hard detritus – see below). Whether the basal groups such as the Neotropical *Bdelyrus* and *Bdelyropsis* and the African

Paraphytus evolved directly from detritus-feeding ancestors, or have reverted to saprophagy because of the availability of well-rotted, moist humus in the forests where they occur, is moot. Feeding on mushrooms in the African *Coptorhina* is, likewise, difficult to explain – the genus lies near the base of the phylogeny of the Scarabaeinae (Philips *et al*. 2004b; Monaghan *et al*. 2007; Sole and Scholtz 2009) and feeds on fungi in the form of large basidiomycetes (Frolov *et al*. 2008). Once again, whether this is a direct derivation from primitive fungal dependence in its ancestor, or a much later reversal from a dung diet is impossible to tell.

The most basal groups yet identified belong to a clade of dung beetles restricted to extremely arid areas of south-western Africa where they subsist on dry dung accumulations of rock hyraxes (*Procavia capensis*, Hyracoidea: Procaviidae). They feed on the dung fragments in underground burrows after very irregular rainfall (Deschodt *et al*. 2007). If, as several phylogenies hypothesise (Monaghan *et al*. 2007; Sole and Scholtz 2009) these beetles actually represent a lineage of the most basal living beetles known, then we may hypothesise that they evolved from a dung-feeding lineage, and have been forced by environmental changes into their highly restricted habitat to subsist on obviously very poor quality food, albeit "dung". This has also undoubtedly happened in the derived Scarabaeini group *Pachysoma*, which live under broadly similar conditions in roughly the same geographical area, and which have without doubt switched from wet-dung feeding to dry detritus (Holter *et al*. 2009).

If one can, consequently, assume that dung-feeding is an apomorphic trait for dung beetles, all other modern feeding patterns must then be secondarily derived from dung-feeding.

6.2 WHAT DUNG BEETLES EAT

Although it has long been known (Madle 1934; Halffter and Matthews 1966; Halffter and Edmonds 1982) that dung beetles feed on tiny particles in the mostly liquid fraction of dung, the actual size of the particles consumed and their origin remained unclear until recently because it was widely believed (Miller 1961; Halffter and Matthews 1966; Halffter and Edmonds 1982; Cambefort 1991a) that dung beetles triturate large dung fragments into small particles before imbibing them. Holter and colleagues, in a series of recent studies (Holter 2000; Holter Scholtz and Wardhaugh 2002; Holter and Scholtz 2005; Holter and Scholtz 2007) have accurately measured the sizes of the imbibed particles, explained the filtration mechanism, and convincingly dispelled the notion that dung beetles triturate their food.

Until recently the feeding biology of adult dung beetles was poorly understood. Traditionally two hypotheses (reviewed by Holter 2000) have been advanced to explain the fact that the pasty gut contents of dung beetles are made up of very small particles. The first of these is that the beetles feed by licking up dung with the hairy, pad-like maxillary galea and squeezing liquid from it by action of the mandibular molar lobes. The liquid and its suspension of tiny particles run through narrow furrows known as filtration channels ("*Filterrinnen*" of Madle 1934) in the molar surface into the pharynx and then into the gut. The larger components of the dung are then rejected. The second hypothesis proposes that large dung particles are collected by the maxillae, but are then ground by the ridges ("tritors") of the tightly-fitting molar lobes, and the small particles are imbibed (Miller 1961; Hata and Edmonds 1983).

Holter (2000), working with European dung-feeding *Aphodius* (Aphodiinae), which have structurally and functionally similar mouthparts to those of the Scarabaeinae, was able to show experimentally that neither of these hypotheses is probable. Using a technique which will be discussed below, Holter was able to demonstrate that even though the particles eaten were small, many were still much too large to pass through the filtration channels. So the first hypothesis was rejected. His experiments also showed that the second hypothesis was untenable because there was no evidence that the small particles imbibed were the results of comminution of larger fragments. He also argued that there was little to be gained by the beetles grinding large pieces and feeding on the resultant fragments because in all probability they consist mainly of indigestible cellulose and lignin. Holter (2000) then proposed a third hypothesis – that the food is collected by the maxillary palps, (as suggested by Madle 1934), the large particles are brushed out by filtration setae on the mouthparts and the remaining paste is then squeezed by the molar lobes while superfluous liquid is led away from the pharynx through the filtration channels. This concentrates the remaining small particles, which are then ingested.

Holter *et al.* (2002), Holter and Scholtz (2005) and Holter and Scholtz (2007) studied the food of tunnellers and endocoprids, that of rollers, and of the quality of available dung beetle food ingested by adult dung beetles that feed on fresh herbivore dung, respectively.

In the first of these studies Holter *et al.* (2002) determined the maximum size of food particles ingested by 15 species of tunnelling and endocoprid dung beetles. Twelve of the species were tunnellers (8 African, 2 Palaearctic and 2 Australian) which represented all of the Old World paracoprid tribes (Coprini, Dichotomiini, Onitini, Oniticellini and Onthophagini); the other three species were African endocoprid members of the Oniticellini. The species also represented groups with a feeding preference for fine (ruminant) or coarse (elephant and rhinoceros) dung, or with no apparent preference. The beetles ranged from very small to large (fresh body weights of 0.05 g – 7.4 g), and all ingested minute food particles (maximum diameter 8.0 µm – 50 µm). There was a statistically significant but small increase in particle size with body weight.

Holter *et al.* (2002) used the techniques developed by Holter (2000) for determining the size of food particles ingested by *Aphodius*. This was as follows. Small latex or glass balls of any two known diameters (2, 5, 10, 14, 18, 25, 40, 63 and 83 µm diameter-balls were available) were mixed evenly into dung (Cape buffalo, *Syncerus caffer*; wildebeest, *Connochaetes taurinus*; or cattle) and the relative numbers of different-sized balls in the dung to be fed to beetles were determined from subsamples. These were taken by squeezing the dung through a mesh with an aperture size that was at least three times the diameter of the largest balls, and hence no obstacle to their passing through. The sample was placed on a microscope slide, mixed with a drop of glycerol and water, and covered with a cover slip. Balls of both sizes were then counted under a microscope at 200 – 1000x magnification until at least 50 of the rarest size category had been recorded. Mixing was considered satisfactory when three samples were statistically homogeneous. This seeded dung was then offered to beetles that had been kept in moist soil at ambient temperature and starved for 2-3 days.

The starved beetles were offered a small quantity of ball-seeded dung and allowed to feed for about 45 minutes in the dark at room temperature, after which they were killed instantaneously in boiling water and a sample of the midgut contents removed by dissection. Samples were mixed with glycerol as described above and the balls counted using a microscope. Depending on availability of the test species, between three and eight individuals were dissected. Because ball numbers in the gut samples were highly variable, comparisons of the counts had to be standardised. This was done according to the method described by Holter (2000) which basically requires the calculation of the probability, β (%), that a large ball in the dung collected by the mouthparts would pass through the filter and be ingested, assuming that the small balls in the same material would have a 100% probability of ingestion. A value of β = 100% means that the large and small balls occur in the same proportion in the gut contents and in the original dung mixture, which suggests uninhibited ingestion of both particle sizes. β values of less than 100% indicate that the mouthpart filter restricted the passage of larger balls relative to the smaller ones.

To assess whether dung beetles grind large dung particles and imbibe the resultant small fractions, Holter *et al.* (2002), following the methods developed by Holter (2000), compared the size of dung fractions of dung fed to two African dung beetle species, *Copris amyntor* (Coprini) and *Heteronitis castelnaui* (Onitini), with that in the gut after feeding.

This was done by isolating particles of 100 – 180 µm in size from fresh buffalo dung by wet sieving. These were stained with Periodic Acid Schiff which stains carbohydrate a bright magenta colour. Two grams (w/w) of stained fibres were then mixed thoroughly into 12 g of buffalo dung, together with an appropriate quantity of 5 µm balls as inert markers. The previous experiments had indicated that 5 µm balls passed unhindered through the filter apparatus of the above species. However, because the mixing led to comminution of some of the larger particles, some small stained fragments (2 – 5 µm, as determined by comparison with the latex balls) were present in the sample that was fed to the beetles as above. Gut samples were then taken after feeding, and the ratio of small fragments relative to latex balls compared with the ratio in the sample fed to the beetles. A relative increase in small fragments would indicate comminution of large fragments.

In the tunnellers and endocoprids sampled, the maximum diameter of ingested particles varied from 8.0 – 50.0 µm, and although the increasing diameter was statistically significant with increasing body weight, the increases were numerically small (Fig. 6.1). Particle size of dung eaten was unaffected by dung type and tribe to which the beetles belong.

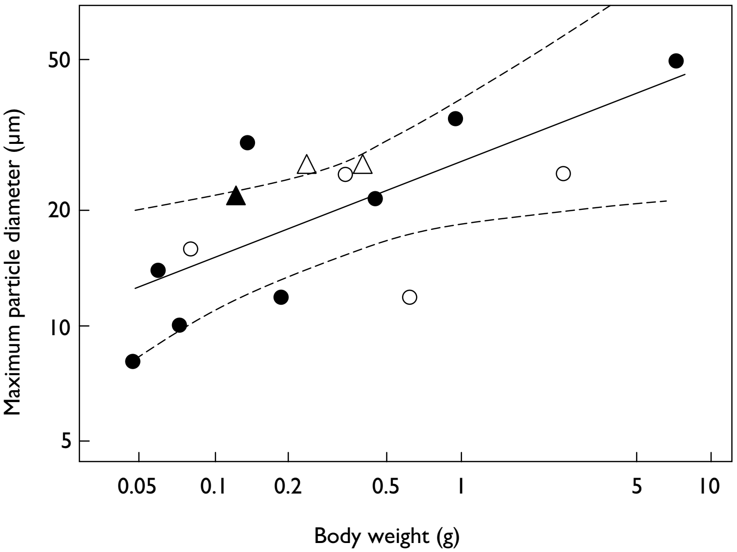


Fig. 6.1. Maximum diameter of ingested particles in relation to mean fresh body weight for 15 species of Scarabaeinae. Logarithmic scales on both axes. Empty symbols: species preferring rhino/elephant dung. Filled symbols: species preferring other types of dung or generalists. Circles: tunnellers (paracoprids). Triangles: endocoprids. The regression line log $Y = 1.431 + 0.252 \times \log W$ ($r^2 = 0.502$ $P<0.01$) with 99% confidence limits (dashed) is also shown. (After Holter *et al.* 2002).

Holter and Scholtz (2005), using the same techniques discussed above, determined the maximum size of ingested particles in 11 species of ball-rolling, adult dung beetle of the tribes Scarabaeini, Gymnopleurini, and Sisyphini (four, four, and three species respectively). Holter and Scholtz (2007) added the data from a twelfth species, the large canthonine *Circellium bacchus* to this set. Mean body sizes of the beetles ranged from 0.33 to 7.2 g fresh weight. They only ingested particles with maximum diameters of 4.0 – 130.0 µm. Hence rollers, like the tunnellers and endocoprids feeding on fresh dung discussed above, filter out larger, indigestible plant fragments and confine ingestion to small particles of higher nutritional value. Unlike in the tunnellers and endocoprids, however, maximum diameter of ingested particles increased significantly with body weight, whereas taxon (tribe) had no additional effect. Because big rollers accept larger particles than do tunnellers of similar weight, the slope of the diameter-against-weight regression for rollers was significantly higher than that found for tunnellers (Fig. 6.2). An explanation for this could be that a typical food ball made by a roller is consider-

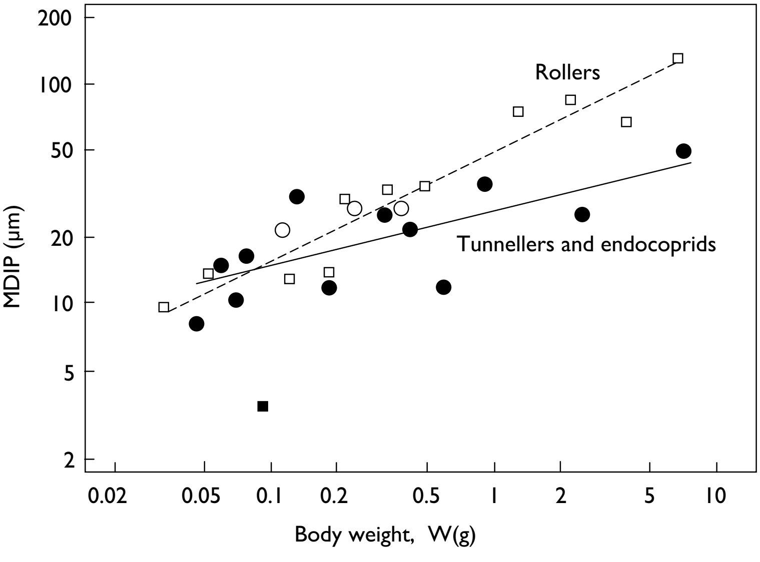


Fig. 6.2. Maximum diameter of ingested particles (MDIP) in relation to mean fresh body weight for tunnellers + three endocoprids (filled circles, solid regression line) and rollers (open squares, dashed regression line). Log 10 scales on both axes. The regression for rollers [log MDIP = 1.69 + 0.48log W($r^2 = 0.92$; $P < 0.0001$)] includes one, two, four, and four species in the tribes Canthonini, Sisyphini, Gymnopleurini, and Scarabaeini respectively. The regression for tunnellers and endocoprids [log MDIP = 1.43 + 0.25log W($r^2 = 0.50$; $P < 0.01$)] includes three, three, four, and five species in the tribes Coprini, Onitini, Oniticellini, and Onthophagini respectively. (After Holter and Scholtz 2007).

ably smaller than the amount of dung available to a feeding tunneller of the same size. If the roller were as choosy about particle size as the tunneller, it might not get enough food. This applies to large rollers in particular because their food balls contain a higher proportion of coarse fibres than those made by small species.

6.3 FOOD QUALITY

Since the extreme selectivity of a particular fraction of the available dung by dung beetles implies a trade-off between a probable improvement in food quality over an inevitable decrease in quantity, Holter and Scholtz (2007) posed the following questions on the dung quality of various types of herbivore dung selected by, and quantity available to, dung beetles. The first question was which quantitative improvement of ingested food resulted from extreme choosiness of particle size compared with the total available in a dung pat? The second was how much of the dry matter, carbon and nitrogen in a dung pat is actually available to dung beetles? Finally, what is the effect of maximum particle size and the kind of dung on that proportion?

Holter and Scholtz (2007) analysed fresh dung of large wild African herbivores during peak dung beetle activity, that of both ungulate and monogastric species (buffalo – *Syncerus caffer*, white rhino – *Ceratotherium simum*, and elephant – *Loxodonta africana*) as well as that of Danish cattle, sheep and horses grazing on pasture in summer.

Because most of the beetles whose food particle size preference had been determined were found to feed on particles of an average diameter of about 20 μm, Holter and Scholtz (2007) determined the fraction of dung comprised of particles of this diameter in the fresh dung of the animals listed above. They used two different techniques for obtaining this fraction, "sieving" and "filtering". For the first technique a small quantity of dung was sieved through a series of sieves with successively smaller mesh sizes from 1 mm to 20 μm. For the second technique a small quantity of dung was pressed through mesh of 20 μm. The 0 – 20 μm fraction produced by both techniques was analysed for nitrogen and ash content.

The two techniques yielded slightly different data sets (Fig. 6.3; Table 6.1).

6.3.1 Water content of dung

Water content of the dung sampled by Holter and Scholtz (2007) ranged between 76-89% of total wet weight. For sheep and horse dung from animals feeding on lush spring graze it was at the higher end of the range, while that of the African mega-herbivores was at the lower end. These were broadly similar

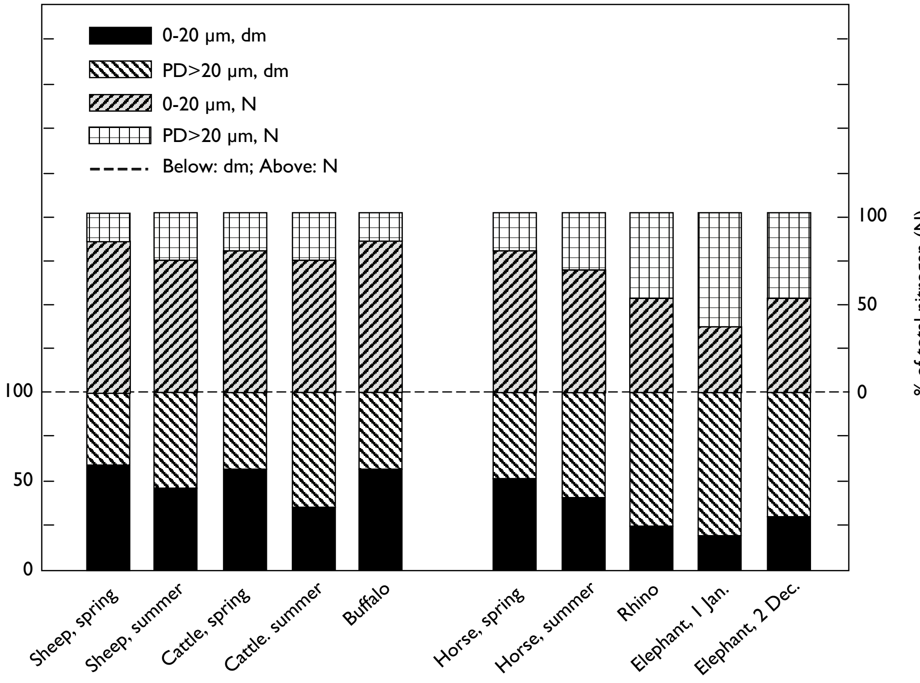


Fig. 6.3. Percentages of total dry matter and nitrogen in bulk dung present in dung particle size fraction 0 – 20 μm and in the remaining dung with particle diameters (PD) larger than 20 μm. (After Holter and Scholtz 2007).

to results by Rougon *et al.* (1990) from cattle dung in the dry season in the arid African Sahel (71%), and Edwards (1991) from subtropical South Africa in the wet season who recorded water content of zebra (*Equus quagga*) dung at 75-80%, and for wildebeest (*Connochates taurinus*) dung at 74-78%. The latter species, although nominally a dung-pellet producer, produces pats of clumped pellets when feeding on lush graze. Dung pellets from a mixed feeder (browser / grazer), impala (*Apyceros melampus*), had a fairly high moisture content in a very wet year (67-71% – Edwards 1991), and drier dung in a less wet year (52% – Paetel 2002). Paetel (2002) recorded the dung pellets of giraffe (*Giraffa camelopardalis*), an exclusive browser, to contain 54% water. Holter and Scholtz (2007) recorded that most of the dung beetles observed in the field in the Kruger National Park, South Africa, preferred wet elephant dung over drier antelope pellets, which concurred with Paetel's (2002) study at the same place. The preference was in spite of higher nitrogen content of impala and giraffe pellets. Various species of rollers, however, sometimes (e.g. *Scarabaeus (Kheper) nigroae-*

Table 6.1. Properties (mean values) of different particle size fractions in four types of fresh dung. Non-bracketed data for the small-particle fractions are based on *sieving*, bracketed values on *filtering*. Column V gives the amount of the size fraction that must be ingested to obtain 1 mg of nitrogen. VII is the carbon:nitrogen (C/N) ratio, assuming 50% carbon in the organic matter. Weights, percentages and C/N ratios are based on dry weight. (After Holter and Scholtz 2007).

Dung	**Dung fraction**	**% nitrogen**	**% of bulk dung dry matter in fraction**	**% of bulk dung N in fraction**	**mg ingested fraction per mg ingested N**	**mg bulk dung with the amount of the fraction given in V**	**C/N ratio**
	I	**II**	**III**	**IV**	**V**	**VI**	**VII**
Sheep, May 2005	0-20µm	5.17 (5.95)	56	87	19 (17)	34	9.9 (7.3)
	0-106µm	4.64	65	91	22	33	11
	Bulk	3.33	100	100	30	30	12.8
Buffalo, January 2003	0-20µm	3.37 (4.48)	56	87	30 (22)	53	11.2 (8.6)
	0-106µm	3.00	66	91	33	51	12.3
	Bulk	2.18	100	100	46	46	18.1
Rhino, January 2001	0-20µm	2.51 (2.77)	25	52	40 (36)	159	12.7 (12.0)
	0-106µm	2.28	31	58	44	143	14.0
	Bulk	1.20	100	100	83	83	34.2
Elephant, January 2001	0-20µm	2.33 (2.80)	20	40	43 (36)	222	15.2 (12.6)
	0-106µm	2.20	24	46	46	192	16.3
	Bulk	1.14	100	100	87	87	38.9

neus – impala and giraffe, Edwards and Aschenborn 1988) or preferentially feed on dung pellets (*Scarabaeus galenus* – impala, Ybarrondo and Heinrich 1996). Edwards (1991) recorded that no breeding took place in *Euoniticellus intermedius* in dung with water content of less than 65% and it is very likely that little feeding would take place at lower water content either, since the small particles consumed by adult beetles are mainly suspended in liquid.

6.3.2 Ash content of dung

Holter and Scholtz (2007) recorded ash contents of the dung they sampled and found it to vary unpredictably (irrespective of the origin of the dung), between 11-27% of the dry weight of the dung, and they concluded that a large percentage of the ash weight was made up of silica from soil swallowed while the animals were grazing. Although some grains were small enough to be ingested by the dung beetles they were unlikely to affect the food quality of the dung.

6.3.3 Nitrogen content of dung

The nitrogen content, which is a reasonable approximation of the "quality" of herbivore dung, varies seasonally (Edwards 1991; Holter and Scholtz 2007), being higher in summer (wet season) than in winter (dry season), and among herbivores, although there is no apparent consistent pattern between browsers and grazers. The lower nitrogen content of dry season dung is unlikely to have a major effect on dung beetles because of their generally low activity during this period, although Rougon and Rougon (1982) recorded considerable activity by a few species in the Sahel in the dry season.

Rougon *et al.* (1990) recorded the nitrogen content of cattle dung in the dry season in the Sahel to be about 1% by weight of dry matter, while Edwards (1991) recorded the nitrogen content of zebra and wildebeest dung during the wet season in South Africa to be 1.2-1.6% and 1.5-2.2% respectively. Paetel (2002), also during the wet season in South Africa, recorded the average nitrogen content of zebra, buffalo and wildebeest to be 1.2%, 1.3% and 1.5% respectively. Holter and Scholtz (2007) analysed the nitrogen content of dung of Danish sheep (3.33%), and African buffalo (2.18%), white rhino (1.2%) and elephant (1.14%). All of these percentages are for bulk dung, which as pointed out above, includes a large fraction that is inaccessible to dung beetles because of the large size of most of the particles. When the nitrogen content of the fraction that the beetles actually feed on is analysed, a different picture emerges – that of a substantially higher percentage than that found in the bulk dung, and consequently, much higher quality food.

Holter and Scholtz (2007) analysed the nitrogen content of the 20 µm fraction of sheep, buffalo, rhino and elephant dung obtained by the two techniques, "sieving" and "filtering" discussed above and found it to be roughly double that found in the bulk dung. These were as follows, results from sieving first, followed by those from filtering: sheep (5.17 / 5.95%), buffalo (3.37 / 4.48%), rhino (2.51 / 2.77%) and elephant (2.33 / 2.8 %). A break-down of the percentages of the total dry matter and nitrogen in bulk dung present in the particle size fraction of 0-20 µm of several African and Danish herbivores analysed by Holter and Scholtz (2007) is presented in Fig. 6.4.

Because nitrogen content is affected by ash content in the analysed sample, a more reliable and widely used index of food quality from organic matter is the carbon : nitrogen (C/N) ratio (see references in Holter and Scholtz 2007), and the lower the ratio the better the quality. Paetel's (2002) study yielded ratios of 22, 25, 32 and 37 for impala, buffalo, elephant and zebra respectively. Holter and Scholtz (2007) recorded ratios of between 12-14 for dung of domestic livestock

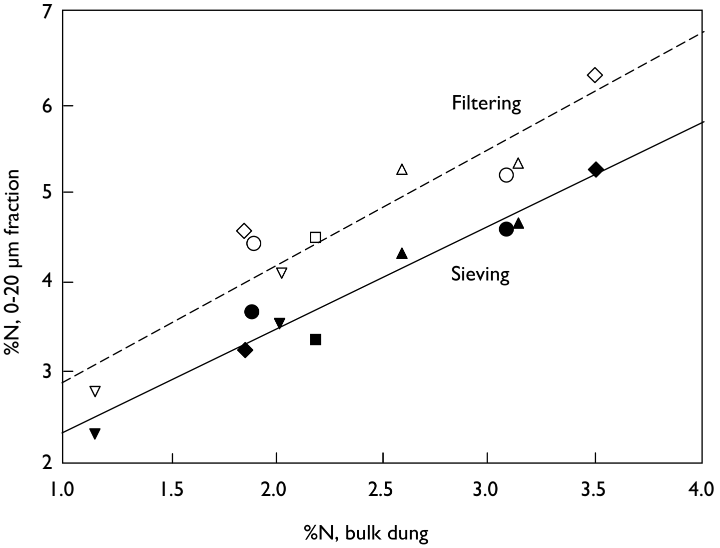


Fig. 6.4. Nitrogen concentrations (% of dry weight) in the 0 – 20 µm particle fraction based on two different techniques, *sieving* (filled symbols, solid regression line) and *filtering* (empty symbols, dashed regression line) against concentrations in bulk dung. Symbols represent: triangle = sheep; square = African buffalo; diamond = horse; circle = white rhino; inverted triangle = African elephant. Regression for sieving: $Y = 1.12 + 1.16\,X$ ($r^2 = 0.96$; $P = 0.0004$). Filtering: $Y = 1.55 + 1.32\,X$ ($r^2 = 0.90$; $P = 0.003$). (After Holter and Scholtz 2007).

feeding on lush pastures in spring in Denmark to those of 34 and 39 in rhino and elephant dung respectively. These figures are generally low compared to those of the food of many decomposers, with ratios of above 40 the norm for most types of litter recorded (see Holter and Scholtz 2007). Even the C/N ratios of foliage are not much lower than the "worst" recorded in dung, with an average ratio of 31 recorded by Elser *et al*. (2000, according to Holter and Scholtz 2007) for 406 plant species. However, the figures given above are for the C/N ratios of bulk dung – when the ratios are calculated for the appropriate particle size fraction that the beetles actually feed on the figure improves dramatically, more so in the dung of mega-herbivores with figures of between 12.0-12.7 for the 0-20 µm fraction of rhino dung, and 12.6-15.2 for elephant dung.

6.3.4 Carbon content of dung

The optimum C/N ratio in the assimilated food of a heterotrophic organism is supposed to be roughly twice the ratio of the organism itself because extra carbon, in addition to that used for tissue production, is needed to cover energy expenses (Holter and Scholtz 2007). Since the C/N ratio of a "typical" insect is roughly 5-7 (references in Holter and Scholtz 2007), the optimum ratio of the assimilated food of dung beetles should be about 10-20 (Holter and Scholtz 2007). The ratio of ingested food of the dung beetle species Holter and Scholtz (2007) sampled was about 7-13, which is at the low end of the optimality range, and that of the assimilated food would be expected to be even lower. The reason for this is that most of the nitrogen in the dung is derived from microbes and sloughed epithelial cells of the animals that voided it, whereas the carbon probably consists of tiny particles of indigestible plant fragments composed mainly of lignocellulose. So, what is the origin of the digestible carbon? If it is not directly from the plant fragments, then in all likelihood it is from the same source as the nitrogen, i.e. from microbial biomass. The C/N ratio of microbial biomass, which is probably dominated by bacteria, is 5-7 (references in Holter and Scholtz 2007), and since this is equivalent to only half of the optimum assimilable food, there is a surplus of nitrogen relative to carbon. Therefore, the dung beetles need to ingest double the amount of nitrogen required in order to provide adequate quantities of nutritional carbon.

6.4 FEEDING IN *PACHYSOMA GLENTONI* – A SPECIAL CASE

The extraordinary evolutionary success of dung beetles (as discussed elsewhere in this book) is readily explained by a variety of behavioural, morphological and physiological adaptations. Some of the more obvious ones are: the ability to fly and quickly locate fresh dung; feeding on tiny particles suspended in liquid in the dung; breeding in a dung mass; and larvae specialized for living, moving and feeding inside the confines of a solid dung mass. The south-west African Scarabaeini genus *Pachysoma*, in some of the most remarkable reversals yet described for dung beetles (Scholtz *et al*. 2004), has dispensed with all of those major attributes that contributed so significantly to dung beetle success, and which undoubtedly evolved over eons under extreme environmental pressure. Some of these will be discussed in the sections that follow.

The 13 species of genus *Pachysoma* are restricted to a narrow strip of the extremely arid west coast of southern Africa from roughly Cape Town (34°S), South Africa, in the south, to Walvis Bay (23°S), in Namibia, in the north. Rainfall in the area varies between about 50-400 mm per year, but regular dense coastal fogs provide surface water for plants and animals. All of the species are flightless and feed on dry dung pellets of various, mostly small herbivores, such as rodents and hares, but also on sheep dung, and, in the Namib Desert, that of oryx (*Oryx gazella*) and / or on detritus. Some of the species feed mainly on dung, others on dung and detritus, while *P. hippocrates* and *P. glentoni* feed only on detritus.

All species forage during daytime by dragging the items forwards, held in the hind legs, to a pre-constructed burrow. The beetles forage repeatedly, often over a large area, which requires accurate navigation, something that is achieved using polarised light as an orientation cue (Dacke *et al*. 2002). When sufficient food for feeding or breeding has been accumulated the entrance is blocked and the beetles feed or breed. The dry food is masticated, in a yet undescribed way, and apparently large fragments ingested. If the outcome of the burrow provision is for breeding, an egg is laid in the loose accumulation of dry dung and detritus fragments, and the nest abandoned (Scholtz *et al*. 2004).

Although the crude food preferences for all of the *Pachysoma* species are known, food quality and feeding have only been studied in detail in *P. glentoni* (Holter *et al*. 2009), and they are quite unlike anything yet described for dung beetles, since the species behaves as a typical detritivore in all respects. This is the more remarkable because microbial decomposition of the detritus is apparently limited by lack of water in the desert area in which the species occurs, so a dependence on microbes to provide or supplement nutrition is unlikely.

Scholtz (1989) studied the dung-pellet-feeding *P. striatum* and postulated that the beetles bury the dry pellets in moist sand, that these absorb moisture from the soil, and that these are then fed on after mandibular trituration by the beetles. Holter *et al*. (2009) set out to test three hypotheses that flowed from the earlier study by Scholtz (1989), but in view of the generally accepted hypothesis that dung beetles depend on micro-organisms, largely fungi, for a significant part of their nutritional requirements, they considered the possibility that fungi would be especially important when feeding on detritus. They, consequently, tested the following hypotheses: (1) the detritus fed on by *P. glentoni* absorbs water underground; (2) fungi grow on the moist detritus; (3) the beetles feed mainly on the fungi.

Holter *et al.* (2009) studied *P. glentoni* at a site on the west coast of South Africa, about 200 km south of the coastal site where Scholtz (1989) studied *P. striatum*. Rainfall at the site averages about 165 mm per year and relative air humidity remains above about 60% throughout the day. The beetles were active on firm sand about 10 km inland from the coast.

Holter *et al.* (2009) marked a number of open burrows into which the beetles were dragging food. When these were back-filled and closed by the beetles they were noted as day 0. Thereafter 3-7 burrows were excavated for each age-class: 1, 2, 3, 5, 6 and 7 days after burrow closure. The detritus in the burrows and the beetles in the nests were collected as was a sand sample for moisture analysis. The detritus samples were later separated into two weighed roughly equal portions, the one portion dried to stop microbial decomposition and placed in air-tight containers for eventual analyses of water, carbon, nitrogen and organic matter content. The other portion was placed in vials of pure methanol and refrigerated for later ergosterol determinations. Ergosterol is a recognized biomarker for fungal biomass (see references in Holter *et al.* 2009). The water content of the soil samples was also determined.

Determination of the water content of the sand expressed as a percentage of the dry weight of the sand yielded a result of 0.52 ± 0.182%, and except for higher moisture levels from detritus collected by beetles active immediately after a light shower of rain, there was no significant effect of increasing moisture levels of stored detritus with age. The ergosterol concentrations were highly variable, ranging from 24 to 530 $\mu g\ g^{-1}$ with a mean value (± SE) of 229 ± 28 $\mu g\ g^{-1}$ ergosterol g^{-1} organic matter, which corresponds to about 75 mg fungal biomass g^{-1}. The best model of ergosterol concentration (ERG) as a function of any other measured factor, although weakly significant, was a simple linear regression: $ERG = -327 + 277 x \log_{10}(\%H_20)$ ($r^2 = 0.15$; $P = 0.045$). Although ERG increased slightly with increasing water content, the regression still left 85% unexplained variation. The authors found no significant relationship between ERG and age of food stores.

Because carbon : nitrogen (C/N) ratios are independent of inorganic matter (mainly sand in this study), Holter *et al.* (2009) used them to quantify N in the food stores. The ratios varied between 26.4 – 43.3, with a mean value (± SE) of 34.7 ± 0.86 (n = 27). The best model ($r^2 = 0.55$) for C/N included several independent variables, although only the effect of water was weakly significant with a tendency towards lower C/N ratios with higher water content.

Most of the beetles had abandoned their feeding burrows by the 7th day after closure.

The authors were able to reject each of the hypotheses they had proposed. The first was that they found no evidence to support the assumption that buried detritus absorbs water from the surrounding soil. The other two hypotheses predicted that fungus would grow on the detritus, and that this would be the primary food of the beetles. Since there was no evidence (based on the ergosterol concentrations on the detritus) that fungi grew vigorously, the first of these was rejected. The last could be rejected because the C/N ratio in the lost C and N was the same for both, 60%, indicating that no microbial assimilation had taken place. If not so, the proportions of C/N would have changed since C would have been lost from the system and N would have been traceable in the samples. This indicates that all C and N assimilated were by beetle feeding.

Holter *et al.* (2009) found that, although about 85% of the fungal biomass present at the start of the experiment disappeared (Table 6.2), and, assuming 50% C and a C/N ratio of 15 in fungi (see references in their paper), and 85% assimilation of both N and C by the beetles, they obtained roughly 17% and 5% respectively of their assimilated N and C from fungi that presumably grew on the detritus before burial. If this assumption is correct, then 83% of the nitrogen and 95% of the carbon assimilated came from the detritus, which corresponds to assimilation of about 57% and 58% of the N and C originally present in the detritus. There was some (mostly very coarse) detritus left in all abandoned 7-day-post-closure burrows, which indicates that about 60% of the ingested detritus was actually assimilated by the beetles. This is considerably better than assimilation efficiencies of below 20% for several other terrestrial detritivores feeding on "better" moist temperate woodland litter (references in Holter *et al.* 2009), and indicates either that *P. glentoni* feeds on higher quality food or / and

Table 6.2. Mean (±SE) initial and final properties of detritus stores collected for feeding by single *Pachysoma glentoni*. (OM = organic matter; C = carbon; N = nitrogen). (After Holter *et al.* 2009).

Attribute	**Store age (days)**		**% Change from 1 – 2 to 7 days**
	1 – 2 (*n* = 5)	**7 (*n* = 5)**	
OM	1.1 g ± 0.033	0.45 g	-60
Water	0.95 g ± 0.146	0.47 g	-51
C	0.626 g ± 0.032	0.250 g	-60
N	0.0212 g ± 0.00194	0.00835g	-61
Fungal biomass	0.075 g ± 0.0251	0.011 g	-85
C:N	34.5 ± 2.26	34.9	1

it has a more efficient digestive system than other invertebrates studied. Also, surprisingly, the detritus that the beetles were feeding on had a much lower C/N ratio than expected, about 35. That of Danish beech litter is about 45, and that of the straw of several grain crops in Denmark varied between 40 and 184 (Holter and Scholtz 2007). Elser *et al.* (2000, quoted by Holter and Scholtz 2007) recorded the C/N values of the foliage of 406 terrestrial plant species and calculated a mean for these of 36, so consequently, the approximate value of the food of the average herbivore, and very close to that of the detritus on which *P. glentoni* subsists.

In conclusion, *P. glentoni* feeds on detritus, albeit of high quality, unlike any of its distant and immediate relatives, which, without exception, feed on tiny particles of high nutritional quality in a suspension of liquids. It does this by chewing the large fragments over a period of days in an underground chamber using a presently-unknown mechanism, although from the structure of the mandibles (Harrison and Philips 2003), this was suspected. This development was, undoubtedly, the major evolutionary change in the group's ecology that was apparently caused by the progressive aridification of the region since the Miocene, and the advent of advective fog over the past 2-3 million years (Sole *et al.* 2005) which provides some free water.

6.4 FEEDING IN LARVAE

In all studied species larval food is provided by the adults, an undisputed autapomorphy for the Scarabaeinae since no other members of the family provide for their larvae. Even in the species thought to be amongst the most basal living taxa, nest provisioning is obligatory. This varies from very simple provisioning of a burrow with dung fragments and nest abandonment after oviposition by the adults (e.g. African *Dicranocara*), to the very elaborate nest construction and sophisticated brood care found in many species.

It appears as if the parents collect dung from the source without any real selection of a particular fraction, and the mass sequestered usually contains a representative sample of the original dung supply. Although it is well known that the sequestered dung is then reworked in the burrow where large items such as sticks and leaves (that were either in the dung that was collected or that attached to the mass while being transported to the burrow are removed), there is little evidence for any meaningful refining of the brood mass before ovipostion. However, in a recent study, Marcus Byrne and collaborators (University of the Witwatersrand; unpublished) demonstrated that in the small African species *Euoniticellus intermedius*, the female constructs brood balls from significantly smaller particles than those found in the bulk dung from which the balls were constructed. The authors do not suggest a mechanism for this process, but conclude that the smaller particles probably increase the nutritional value of the larval food.

In most species there is some isolation of the egg from the supply of food provided for the larva. In some species the egg lies in a poorly-defined space (e.g. *Attavicinus monstrosus*); in many others the egg lies in a distinct chamber where it is cemented in an erect position (e.g. *Onthophagus*); and in some other groups such as *Copris*, the female lines the egg chamber with a dark secretion which hardens into a smooth capsule (Halffter and Edmonds 1982). Very little has been written about the nature of the egg chamber lining or the pillar on which the egg is cemented, but it has been speculated that: the pillar minimises the surface area of the egg that is in contact with the moist dung in order to protect it from excessive moisture, or to limit microbial contact; the lining contains anti-microbial properties, or that it provides certain nutrients to the newly-hatched larva (Halffter and Edmonds 1982); the lining contains an inoculum of symbiotic microbial agents that will aid the larva in digestion of the dung (Halffter 1997).

Byrne and colleagues tested whether the pillar or lining produced by *Euoniticellus intermedius* contained some sort of "maternal gift" to the larvae, of either digestion-aiding symbionts, or a special nutritional package to facilitate feeding in the early stages of larval development. In a series of experiments they tested whether the females possibly smeared the eggs with microbial symbionts at laying, or whether the maternal gift contained microbes. They also determined the nutritional quality of the gift.

They surface-sterilized batches of eggs and then placed them into sterilized and non-sterilized dung balls, and into brood balls with a deposit placed by the female, as well as into artificial ones in which a deposit was manually placed. They also exposed sterilized larvae to sterilized gift, and placed others in artificial balls without gift. They then compared development of larvae bred from sterilized eggs, with that of larvae emerged from non-sterilized eggs; development of larvae reared in sterilized dung, with that of ones reared in non-sterilized dung; and mortality between larvae reared from balls with and without gift.

Sterilizing eggs had no effect on larval development, but larval mortality was strongly influenced by the presence of a maternal deposit, since larvae reared in balls without it showed significantly higher mortality than those reared in brood balls with one (Chi square $\mathrm{df}_{(3,58)} = 7.85$, $P = 0.492$). The majority of deaths occurred during the first-instar. There was no statistical difference between mortality of larvae reared in sterile dung compared to non-sterile dung. Beetles reared in synthetic brood balls without maternal gift, showed significantly higher larval mortality than those reared in balls with the maternal gift, regardless of the origin of the brood ball (Chi square $df_{(2,59)} = 12.6889$, $P = 0.0018$). Larvae reared from sterilized, maternally-constructed brood balls with a maternal deposit were significantly larger and took significantly less time to develop than larvae reared in artificial balls with a manually placed maternal deposit. The ratio of carbon:nitrogen of new brood balls was significantly lower than that of bulk dung ($P = 0.0003$). The maternal gift had a C/N ratio of 10.49 ± 0.07, which was significantly lower than that of raw dung and the new brood ball ($P = 0.0001$ and $P = 0.0001$ respectively).

Consequently, Byrne and colleagues were able to demonstrate convincingly that microbes play no part in larval feeding, either in digestion or as nutrients, and that all of the larval food is thus originally plant derived. They also indicated that the combination of maternal manipulation of the brood ball and the provision of a nutritionally-enhanced maternal gift, although not essential, substantially benefit the larvae.

6.5.1 Effect of quantity and quality of food on larval morphology

Plasticity in adult dung beetle size is a well-known phenomenon, and although the reasons for its expression have not been well documented, it is generally assumed to be as a result of variation in the quantity of food available to the developing larva. The variation is often of an order of about 50% but in the African *Circellium bacchus* it is much greater; body length varies from 22.0 – 47.0 mm (Kryger *et al.* 2006) and live weight between 3.7 – 11.0 g (Nicolson 1987).

Studies by Emlen and Moczek and collaborators (Emlen 1994, 1997; Moczek 1998; Moczek *et al.* 2002) on two "horned" *Onthophagus* species (*O. acuminatus*, a Neotropical forest species, and *O. taurus*, a circum-Mediterranean and Asian native) have demonstrated that both food quantity and quality express different sized individuals, and result in males of two different morphs – big-horned and small-horned males – and that these have different mating strategies (see Chapter 11 for discussion of these strategies).

Onthophagus acuminatus is a small paracoprid lowland forest species that feeds mainly on howler monkey (*Alouatta palliatta*) dung. Males are dimorphic in horn length (Emlen 1994). Large males (prothorax width greater than 3.35 mm) possess a pair of horns on the head (≥ 0.4 mm), which vary in length as a function of body size ($y = 1.13x - 3.13$, $r^2 = 0.75$, $n = 258$). Horn lengths of small males (< 0.4 mm) are described by a different allometric relation ($y = 0.35x - 0.90$, $r^2 = 0.69$, $n = 303$; comparison of slopes, Student's t test, $t = 20.379$, d.f. $= 557$, $p < 0.001$) (Emlen 1994).

Emlen (1994) was able to demonstrate that changing larval food conditions predictably in *O. acuminatus* altered progeny morphology, and he clearly showed an effect of rearing environment upon horn length variation. He recorded that sibling males bred from balls formed by the female, and others also formed by a female but artificially increased in size with extra dung, produced significantly different horn morphs. Horn lengths of males reared from large brood balls were over seven times larger than those of their brothers reared from small brood balls (X ± s.d. for large brood balls = 0.765 ± 0.26 mm, n = 48; X ± s.d. for small brood balls = 0.1 ± 0.045 mm, n = 43; paired t – test on family means, t_{22} = 16.055, two-tailed p = 0.0001). In the same paper, based on a series of breeding experiments with males of different horn morphs, Emlen was able to confirm that in *O. acuminatus* male horn length showed no detectable heritable variation. Consequently, he was able to convincingly demonstrate that horned and hornless male morphs are facultative developmental alternatives correlated with individual differences in body size.

In a subsequent paper, Emlen (1997b) demonstrated that variation in diet in *O. acuminatus* not only influences the absolute length of a male's horns (i.e. the conditional expression discussed in his 1994 paper; Fig. 6.5), but also the length of the horns in relation to body size (Fig. 6.6). He found that the scaling relationship between male horn length and body size shifted in response to experimental manipulation of larval diet; males fed a low-quality diet had longer horns at any given body size than sibling males reared on a higher-quality diet.

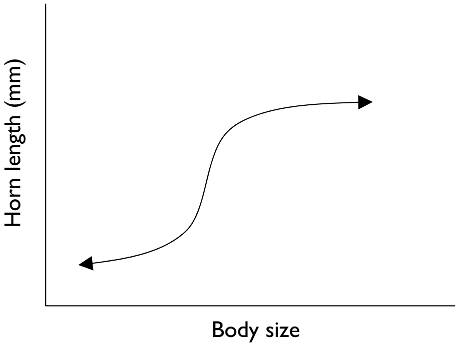


Fig. 6.5. Illustration of conditional expression of beetle horns. Traditional conditional expression: male horn length depends on body size attained during development. Environmental conditions affect male horn expression through their effects on body size, not through changes in the scaling relationship. (After Emlen 1997b).

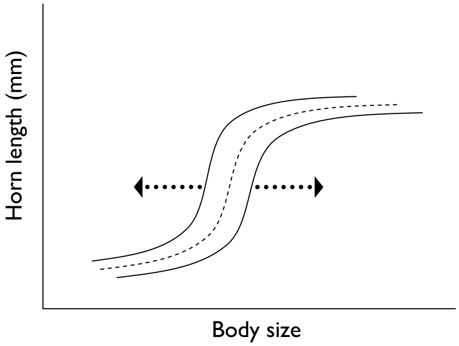


Fig. 6.6. Illustration of conditional expression of beetle horns. Allometry plasticity: the scaling relationship between horn length and body size is sensitive to changes in the environment, so that males produce relatively longer horns under some conditions than they do under others. (After Emlen 1997b).

Emlen (1997b) found that the scaling relationship between horn length and body size shifted during the season in the field in Panama where the research was undertaken, and he proposed that they might be a plastic response to variation in the environment. The seasonal shifts occurred within a single beetle generation, so Emlen was able to discount an evolutionary change and look to environmental effects for the observed plasticity. The beetles were significantly larger during the transition periods from wet to dry and from dry to wet, than either during the wet or dry seasons. Furthermore, from the experimental manipulation of food quality, Emlen found that the allometric relationship between horn length and body size shifted, so that over a similar range of body sizes males fed on high-quality food (howler monkey dung) had relatively shorter horns than sibling males reared on poorer quality food (a 50 : 50 mixture of howler monkey and cow dung).

In order to understand the functional significance of these observations, Emlen (1997b) looked at how quantity and quality of food for *O. acuminatus* varied in the field, and speculated on whether this variation is likely to affect how selection acts on horns.

The amount of dung available to a developing dung beetle larva is directly dependent on the amount provisioned by the female parent, so in the presence of a plentiful dung supply and little competition, females can provision nests with large quantities of dung. Conversely, when dung is limited or competition fierce, brood balls are smaller. Under different environmental conditions over the same time span, both dung availability and competition vary tremendously, hence some nests will be provisioned with large quantities of dung, and others with smaller amounts so the frequency of occurrence of horned and hornless males can be expected to be roughly the same. However, seasonal shifts in monkey diet (from a mixture of fruits and leaves to primarily leaves, depending on seasonal availability) result in gradual changes in dung quality. Dung from the former diet has higher energy content than that of the latter (references in Emlen 1997b). Thus the dung available simultaneously to all dung beetles in the area is of similar quality and may predict changes in the size distribution of the beetle population.

The significance of male size in the population is because of the two distinct mating tactics employed by males during access to females, those of "guarding" and "sneaking" in which different horn lengths are appropriate. Horns assist in guarding female tunnels but hinder movement in them, hence sneaks are hornless, so disruptive selection generated by this mating system should favour males able to facultatively express horns only when they are likely to guard tunnels (Emlen 1997b) (Fig. 6.7). In the *O. acuminatus* population studied, whether a male guards or sneaks, depends on his relative body size; those larger than

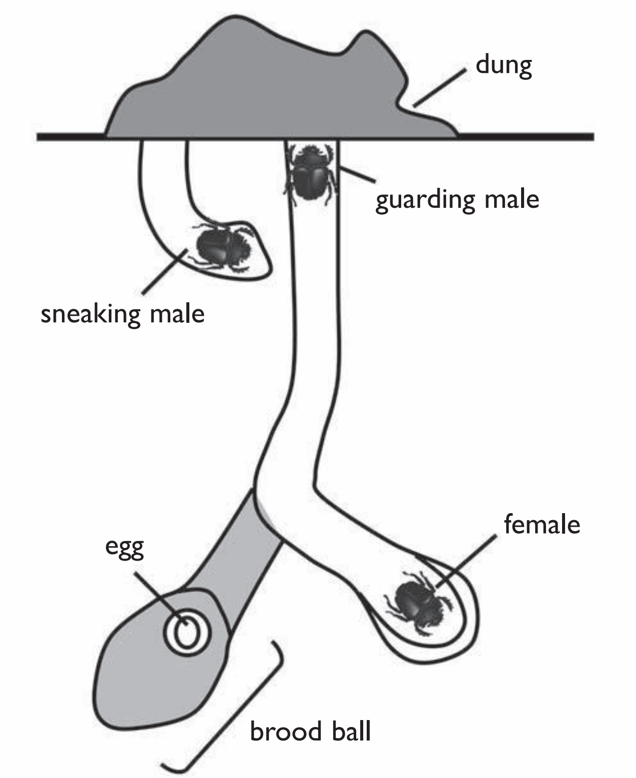


Fig. 6.7. Model for sexual selection on male horns and horn allometry in *Onthophagus acuminatus*. Illustration of the two reproductive behavioural tactics employed by males. Females dig tunnels beneath dung, and pull dung to the ends of the tunnels to provision larvae. Males encounter females either by `guarding' (large horns) the entrances to these tunnels, or by `sneaking' (small horns) into tunnels through side-tunnels that intercept guarded tunnels below ground. (After Emlen 1997b).

most of their competitors guard and those smaller than their competitors sneak. Consequently, horn morphology and mating tactic will coincide optimally when males begin horn production at the same body size that they switch between sneaking and guarding tactics (Fig. 6.8).

Emlen's (1997b) study thus revealed that when dung quality is high and most individuals grow large, males would begin horn production at a larger body mass than when the dung quality is low and most individuals are small. During the transitional seasonal changes between wet and dry periods and vice versa, the allometry shifted to the right, whereas during the dry and wet seasons when the average body sizes were smallest, the allometry shifted to the left (Fig. 6.8).

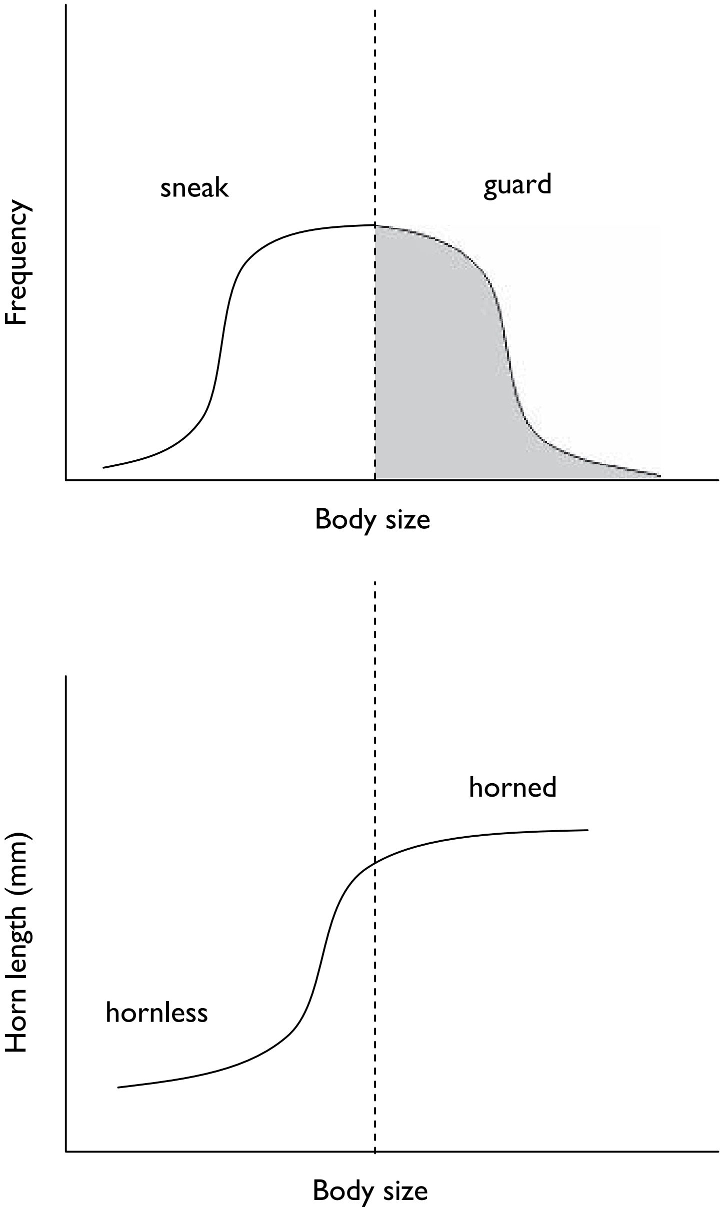


Fig. 6.8. Male behaviour depends on relative body size. Larger males guard (shaded area under top curve) and smaller males sneak (open area). Horn morphology and behaviour correlate perfectly whenever the horn length±body size allometry (bottom) is positioned along the body size axis such that the body size separating horned from hornless morphologies (i.e. the inflection of the sigmoid curve) coincides with the body size where males switch from guarding to sneaking behaviours (dashed line). (After Emlen 1997b).

6.5.2 Parental determination of quality and quantity of larval food

A study by Moczek (1998) suggested that adult dung beetles are able to measure resource quality when they provision food for their offspring and then to adjust food amounts accordingly. He studied beetles from a population of the circum-Mediterranean and Asian species, *O. taurus*, which was accidently introduced into the USA and has subsequently become the dominant onthaphagine in open pastureland in North Carolina, where Moczek studied them. It is a generalist dung feeder but feeds most commonly on horse and cow dung in natural pastures.

Moczek (1998) reared *O. taurus* larvae in the laboratory in brood balls of known mass that were constructed by the adult beetles from field-collected homogenised horse and cow dung. Emergent adults were killed and size (using prothorax width as an estimate of body size) and horn length measured. He used ANCOVA's to quantify the effects of diet quality on adult body size with resource type as a class variable, and brood ball size representing resource quantity as a covariate. He used nonparametric Mann-Whitney *U* tests to test for resource-dependent differences in the extent of male horn development. In a separate experiment Moczek also set up 12 pairs of wild-caught beetles and allowed six pairs to breed first on horse dung for four days, then on cow dung for a further four. The order of treatment was reversed with the other six pairs. Furthermore, because of the possibility that differences in brood ball weight could be due to natural differences in water content, he also reweighed balls after they had been dried. Data were analysed using a matched-pairs signed-rank test (references in Moczek 1998).

Moczek's (1998) results concurred with those of Emlen discussed above, that food availability during larval development predictably determines adult morphology. An increase in weight of brood balls of either dung type resulted in the development of larger adult body sizes (horse dung, $p < 0.01$; cow dung, $p < 0.05$; Table 6.3, Fig. 6.9). However, the quantity of the resource required to achieve similar developmental results differed significantly between dung types ($p < 0.0001$ for y intercepts, $p > 0.1$ for slope; Table 6.3, Fig. 6.9a). Based on these results it appeared that horse dung was a higher quality food and that only half as much was required to yield a particular beetle size, compared to that of beetles reared on cattle dung. These results also confirmed the existence of a critical food quantity threshold separating horned and hornless males reared on both dung types, although the threshold differed considerably between the males reared on the different dung types (Mann-Whitney U – test on horn length / brood ball weight ratios: $z = 3.38$, $p < 0.0001$, Table 6.3, Fig. 6.9b). This, again, suggested that in order to compensate for the lower quality of cattle

Table 6.3. ANCOVA for the effects of larval *Onthophagus taurus* food quantity (brood ball mass) and quality of resource (horse dung versus cow manure) on adult body size for both sexes combined. Sums of squares (SS) are type III. ** $p < .0001$. (After Moczek 1998).

Source of variation	df	SS	F
Brood ball mass (BB)	1	4.74	29.27**
Resource (R)	1	2.75	16.98*
BB X R	1	0.36	2.20
Total	85	22.49	
Error	82	13.27	

dung, an adult must sequester about 50% more dung per brood ball to produce the same sized individuals as those bred on horse dung.

Although Moczek (1998) provided the parent beetles with an unlimited dung supply during the rearing experiments, they seldom used more than 2 g of horse dung to yield large (> 5.0 mm) adults, while the same quantity of cattle dung, albeit such a quantity was seldom collected by the adults, yielded individuals smaller than 3.5 mm (Fig. 6.9b). More typically, when adults sequestered cattle dung for brood balls, they used more than 3 g per ball, an amount never used for the construction of brood balls from horse dung (mean fresh weight, horse dung = 2.09 g, SD = 0.32 g; cow dung = 3.08 g, SD 0.37 g; Wilcoxon matched-pairs signed-rank test: $p < 0.001$; $n = 12$). Moczek found that the dry weights of brood balls showed similar statistically significant differences, suggesting that differences in water content alone do not explain brood ball weight variation between the dung types (dry weight, horse dung = 0.85 g, SD = 0.12 g; cow dung = 1.29 g, SD = 0.21 g; Wilcoxon matched-pairs signed-rank test: $p < 0.001$; $n = 12$). Although both dung types supported the development of a horned male morph, the threshold quantity required to initiate horn growth differed substantially between resources (2.78 g of cow dung; 1.28 g horse dung). Consequently, these results support Moczek's hypothesis that adult *O. taurus* are able to measure the quality of the resource and to correspondingly adjust the quantity of the food provided for their offspring.

So, here we have an example of two readily available natural dung resources, which adult dung beetles can easily distinguish and which they correspondingly vary in amount when constructing brood balls. In nature these beetles not only encounter dung sources of varying quality but the dung sources are patchy and ephemeral. For adults that provision food for their offspring this may entail a trade-off between the total number of offspring for which food can potentially be provided, and the average amount of food available to individual offspring.

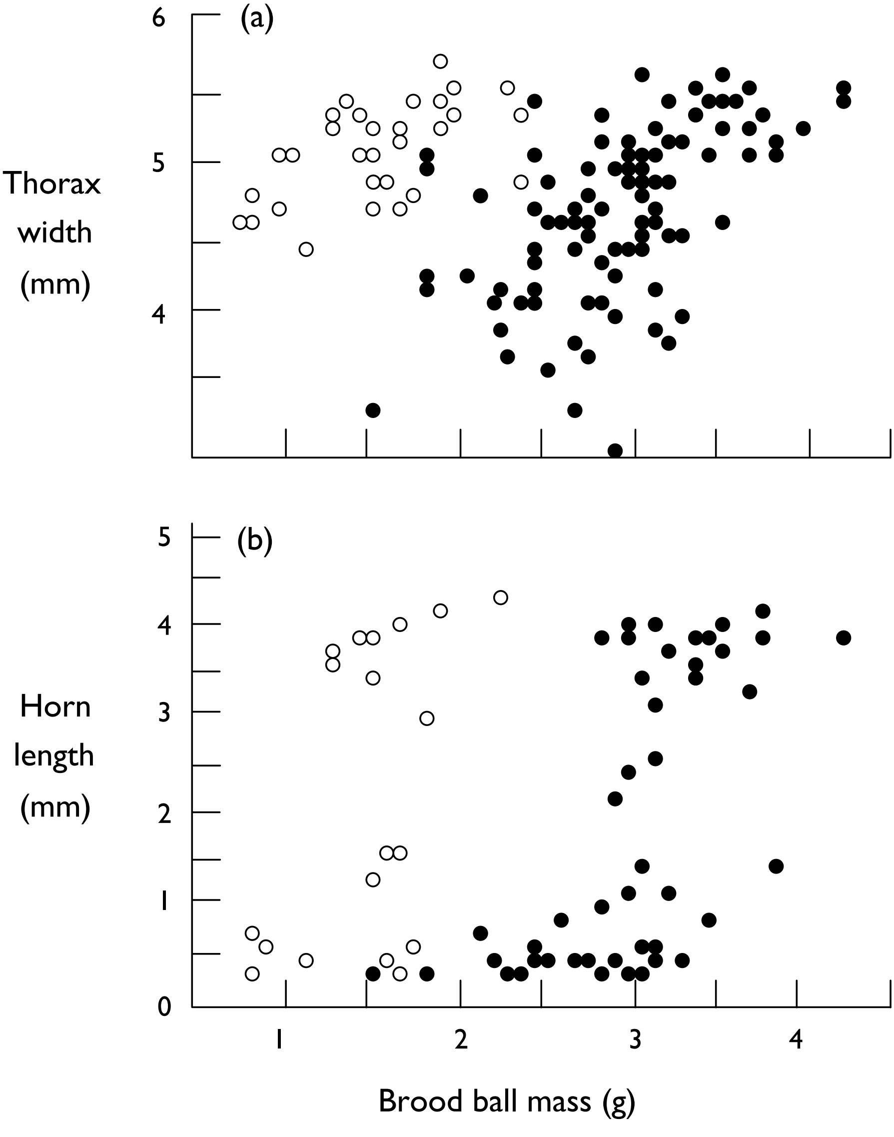


Fig. 6.9. Effects of quantity and quality of larval *Onthophagus taurus* diet on adult development. (a) Adult body size increases linearly with diet quantity on both horse (open circles) and cow dung (filled circles). In comparing relationships between body size and brood ball mass in cow versus horse dung, highly significant differences were found in y intercepts ANCOVA, $p < .0001$; Table 6.3), but not in slope ($p = 0.14$; Table 6.3). (b) Horn development in males increases discontinuously with increasing food amounts of either quality with a substantially higher threshold for the amount of cow dung (filled circles) required to initiate horn expression. (After Moczek 1998).

Therefore, adjusting the amount of food provisioned according to food quality may maximise parental fitness by optimizing the allocation of parental investment into offspring. The mechanism by which *O. taurus* measures resource quality, however, is unknown (Moczek 1998).

CHAPTER 7

ENVIRONMENTAL INFLUENCE ON THE DEVELOPMENT OF COLOUR

In dung beetles limited attention has been paid to the biological attributes or environmental responses that might drive developmental differences in ultrastructure and the resulting variation in exoskeleton colour. As regards biological attributes, breeding ratios in *Phanaeus difformis* (Blume and Aga 1976) and experimental cross-breeding ratios in *Canthon cyanellus cyanellus* (Favila *et al*., 2000) indicate that colour polymorphism may be under simple Mendelian genetic control. However, observations in Africa suggest that colour polymorphism might also be a response to environmental influences, particularly in those species in which a single colour variety dominates populations, e.g. *Gymnopleurus humeralis* (Davis and Génier 2007; Davis *et al*. 2008a), and geographical change from one colour to another appears to parallel altitude, rainfall and temperature regimes. However, patterns are variable. In species, such as *Gymnopleurus humanus*, some populations are dominated by a single colour variety, whereas others comprise more than one colour morph (Davis and Génier 2007; Davis *et al*. 2008a), perhaps representing points of transitional environmental conditions. In still other species, two or more colour varieties frequently co-occur and the patterns are less obviously attributable to environmental variation at a macro-scale.

7.1 COLOUR POLYMORPHISM

Davis *et al*. (2008a) conducted a quantitative study to support or disprove some of the observations mentioned above. They studied the monochromatic species, *Gymnopleurus humanus*, which is a dominant member of dung beetle assemblages in the arid southwest of Africa where it appears to show a latitudinal gradient in colour polymorphism, from the warm temperate southern Nama Karoo in South Africa (32-33° S), to the subtropical southwest of Angola (14-15° S). Furthermore, the low physiognomy of the scattered plants of this arid, late summer rainfall region was thought not to unduly influence results, as it offers little shade and would, therefore, be a limited modifier of local microclimate, and, exclude any possible, linked, exoskeleton colour response. Across the distributional range of *G. humanus*, altitude varies from approximately 600 m to 1700 m, and rainfall from 75 m to 425 mm per annum. However, the greatest abundance is centred in annual rainfall regimes below 300 mm on a mosaic of deep and stony soils, and this is where their study sites were selected. They sampled from populations across the latitudinal gradient to ask two questions. Firstly, as extreme dominance of cupreous individuals had been observed in northern populations (central Namibia), and other colour morphs had only been recorded in the south (southern South Africa), would blue individuals dominate southern populations? Secondly, although geographical variation in exoskeleton colour of *G. humanus* was supported by observations, would this variation be correlated with or independent of physical variables?

Earlier observations showed that populations in the southern half of the species' range, from southern South Africa (32° S) showed various color forms while those, as far north as central Namibia (23° S) were dominated by individuals with cupreous exoskeletons so Davis *et al.* (2008a) collected study material from this region for their study. This latitudinal range comprised the Nama Karoo uplands in the south, and the central Namibian uplands in the north, with intervening latitudes occupied by the lower-lying valleys of the Fish, Orange and Hartbees rivers, and their tributaries. Study sites were selected using GIS maps to ensure that material was sampled from across the entire range of climatic conditions present in the study region. These varied with topography, latitude, and rainfall, all of which may have an influence on temperature. Owing to the irregular distribution of topography, study sites were selected by treating the altitude / rainfall regimes in uplands separately from temperature regimes.

Davis *et al.* (2008a) created maps of average annual rainfall by reclassifying measured or interpolated data of 5 x 5 km polygons on GIS maps of the study region. They also created a map for interpolated, mid-winter average minimum temperature for June which was reclassified to create eight temperature regimes for the study area. These were graduated at 1.5°C intervals across a range from -2.0°C to 8.5°C, and study sites were selected for each temperature regime.

The beetle exoskeletons were measured for reflected photo-wavelengths across the entire visible spectrum using digital reflectance spectrophotometry as described by Brink *et al.* (2007). As these measurements took several hours for each beetle, logistics demanded that they were made of only a selected sub-sample of the trapped material (70 specimens from 18 sites, 12 in the south and six in the north).

Davis *et al.* (2008a) standardized the measurements for all 70 of the selected specimens by taking readings from the same body sclerite, i.e. a relatively horizontal point just anterior to the centre of the posterior margin of the prothoracic disc, which overlies the flight and walking muscles. These beetles were then ranked according to peak values in measured magnitude of reflected wavelengths. They were used as a colour template against which the peak reflected colour wavelengths of all other material were estimated by comparison by eye in natural sunlight. Figure 7.1 shows that the wavelengths at the peak magnitude of reflectance in the sampled beetles were tightly distributed across the measured range and were, therefore, a valid sample on which to base these estimates.

Their results confirmed that exoskeleton colour in *G. humanus* is iridescent although it is muted, possibly by the light-scattering effect of dense surface micro-granulation. Measured specimens mostly reflected across a narrow range of wavelengths, with peaks in magnitude that varied from the blue to the red ends of the visible light spectrum in different individuals (Figs 7.1, 7.2).

Populations of *G. humanus* showed different patterns of colour distribution between individuals at different study sites across a south-north geographical gradient. These different patterns were divisible into three or four clusters by ordination. Blue or a combination of blue and green individuals (Fig. 7.1, cat-

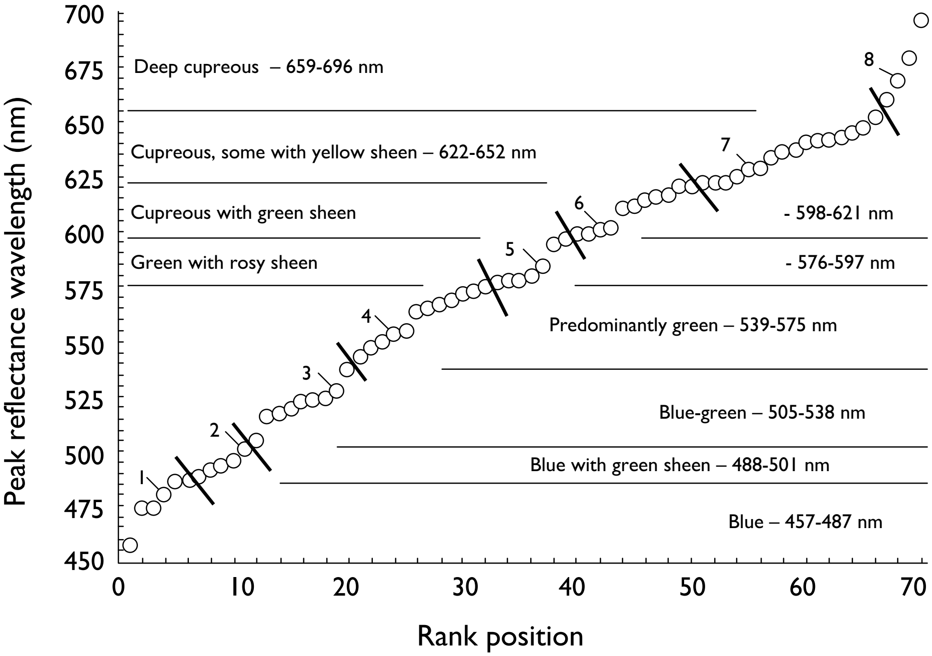


Fig. 7.1. Rank measured values (nm) for peak intensity of reflectance from 70 individuals of *Gymnopleurus humanus*. These beetles are divided into eight waveband categories on the basis of perceived colour of the exoskeleton. (After Davis *et al.* 2008a).

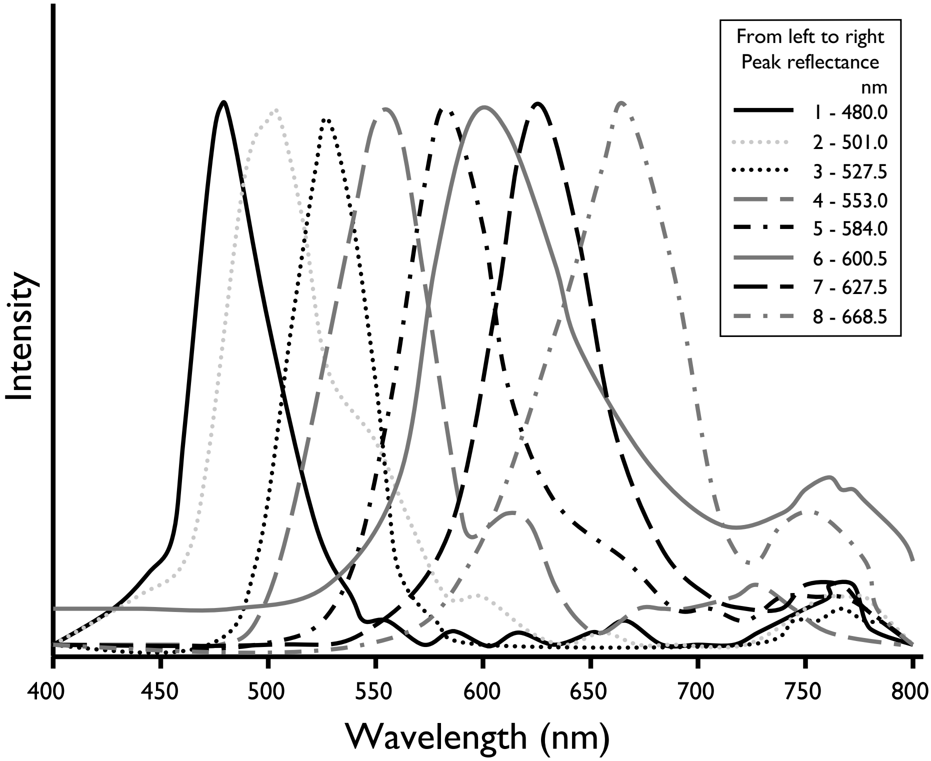


Fig. 7.2. Patterns of intensity of reflectance from eight *Gymnopleurus humanus* beetles across the visible wavelengths, each representing one of eight bandwidth categories defined according to perceived exoskeleton colour (see Fig. 7.1). (After Davis *et al.* 2008a).

egories 1-4) dominated populations at sites centred on southern uplands with low minimum June temperatures. Beetles with cupreous exoskeletons were absent or extremely rare at these sites. The next cluster of sites was centred just to the north of the first one, but at lower altitude with warmer minimum June temperatures. For the most part, all eight colour categories co-occurred at these sites, although most populations were dominated by individuals with rosy-green or cupreous-green exoskeletons (Fig. 7.1, categories 5 and 6,). At the slightly more northerly cluster of sites, populations were dominated by cupreous-green, and cupreous individuals (Fig. 7.1, categories 6 and 7), with blue individuals extremely rare or absent. The last cluster of six sites was centred on a more northerly region with variable altitude, but warmer minimum June temperatures than the southern area occupied by the first 12 sites. Populations at these sites were dominated by individuals with cupreous exoskeletons (Fig.

7.1, category 7), although several more southerly sites showed sizeable proportions of cupreous-green individuals. Blue and green individuals were rare or absent from these sites.

Multiple regression indicated that mean exoskeleton colour bias at the 24 sites was strongly and significantly correlated with mean monthly minimum temperature, but not with altitude or average monthly rainfall (Table 7.1). Separate linear regressions of colour bias on these physical variables were largely supportive (rainfall not significant: $t_{22} = -1.66$, $P = 0.11$, $r^2 = 0.11$; minimum temperature highly significant: $t_{22} = 12.53$, $P<0.001$, $r^2 = 0.88$), although altitude also had a limited significant influence ($t22 = -2.12$, $P<0.05$, $r^2 = 0.17$). A further linear regression of colour bias on latitude also showed a strong correlation ($t_{22} = -6.34$, $P<0.001$, $r^2 = 0.65$), however, lower minimum temperatures are strongly interdependent with progression towards higher latitude ($t_{22} = -5.56$, $P<0.001$, $r^2 = 0.58$).

Contrary to Davis *et al.*'s (2008a) results, Favila *et al.* (2000) consider that colour polymorphism is under genetic control in the diurnal necrophagous American tropical rainforest canthonine, *Canthon cyanellus cyanellus*. *Canthon cyanellus* shows a wide variation of cuticular colour from orange / yellow to dark blue, and many of the subspecies are recognized, to a large extent, by colour differences. *Canthon cyanellus cyanellus* is a shiny green subspecies although some individuals found in tropical forests of southern Mexico have a coppery pronotum with some reddish reflections (Favila *et al.* 2000). Favila *et al.* (2000) were able, in the laboratory, to cross-breed individuals from opposite extremes of the reddish pronotum and green body spectrum, and produce individuals with green bodies and reddish pronotum, as in the parents; all-green and pure red individuals in Mendelian proportions. Using individuals of "normal", hybrid and red stocks, Favila *et al.* (2000) carried out nine different crosses, and evaluated reproductive success of green and red beetles by comparing (*t*-test) the number of brood balls

Table 7.1. Results for multiple regression of log 10 transformed physical factors on mean estimated wavelength of reflectance from the exoskeleton of populations of *Gymnopleurus humanus* at 24 study sites in southern Africa.
* Significant $P < 0.001$. Coefficient of determination (r^2) for regression model = 0.89. (After Davis *et al.* 2008a).

Physical factors	t_{20}	**Probability (*P*)**
Altitude	0.87	0.392
Average annual rainfall	0.80	0.432
Average annual minimum		
Monthly temperature	11.10	0.000*

produced by each, with offspring survival. They also tested (*G*-test) whether offspring survival was different between green and red beetles. Green x green and red x red crosses resulted in no difference between the mean number (± SE) of brood balls / female (11.72 ± 3.17 vs. 10.94 ± 3.03, respectively, t = 0.56, n.s.), nor between the survival rate of offspring produced by females (86.5% vs. 84.5%, respectively, G = 1.81, n.s.). Although red individuals such as those bred in the laboratory are never encountered in the field, Favila *et al.* (2000) concluded that such individuals probably did occasionally occur, and that the high variability in colour in different populations of *Canthon cyanellus* was probably controlled by similar genetic elements that determined the red laboratory population, and that these were probably all equally reproductively successful.

Given the limited data from these two studies, it is difficult to determine the relative roles of environmental versus genetic influences at present. Although Favila *et al*. (2000) obtained Mendelian ratios between colour morphs cross-bred in the laboratory, this evidence is countered by Davis *et al.*'s (2008a) results that show a strong correlation between environmental factors and colour variation in the field. However, as patterns in iridescent exoskeleton colour vary at both geographical and local scales, as well as between taxa, the relative importance of factors might also vary with scale and the apparent contradictions may be resolved by further research.

7.2 FUNCTIONS OF COLOUR

Various possible functions may be attributable to colour in dung beetles, and a special case may be made for iridescent colours (Vulinec, 1997). The functions fall into three categories. Anti-predation may be conferred through crypsis in muted colours; or by distraction; or aposematism, signifying distastefulness in brightly-coloured individuals. Both dark and bright colours may be involved in thermoregulation, and, in the case of bright colours, social signalling, for male advertisement and female mate choice.

Anti-predation in some species combines several of the above strategies. For example, exposure to danger as a result of life histories restricted to the soil surface, may be a reason both for the only recorded instances of parasitism on the Scarabaeinae by other insects, and for the number of protective devices developed by the African oniticelline, *Oniticellus egregius* (Davis 1989). Several distinctive protective devices are employed by *O. egregius* when disturbed or picked up. These comprise flipping into the air by releasing the front legs under tension; turning over and extending the legs, which renders the beetle more difficult to grip and exposes the mottled gold / yellow underside that is cryptic against a background of yellow dung fibres [the species is a coarse-dung-feeder]; or releasing a volatile fluid akin to oil of wintergreen that may be distasteful to predators (Davis *et al.* 2008b).

Brightly-coloured dung beetle species are often presumed to be aposematic, and there is abundant anecdotal evidence that many of these species produce noxious smells, and by implication, taste bad. However, with the exception of an early record in Africa by Arrow (1951 – quoted by Vulinec 1997), in which a captive baboon that was fed individuals of the brightly iridescent *Gymnopleurus virens* vomited as a result of eating the beetles, no empirical studies to test the effect of bright colours on potential predators appear to have been done.

It seems most likely that any advantage conferred by evolution of iridescence and colour polymorphism in *Gymnopleurus humanus* (discussed above), would relate to thermoregulation due to the different thermal properties of different colours. This is because absorbed light energy converts to heat, different colours absorb different wavelengths of light, and different colour wavelengths produce different amounts of heat. In particular, blue reflecting exoskeletons absorb red wavelengths that generate more heat energy than red reflecting exoskeletons that absorb blue wavelengths. Thus, the colour polymorphism from blue to red shown by the *G. humanus* example above, could be an advantage across the temperature gradient from cool to warmer regions. However, the thermal properties of the beetle exoskeletons need to be tested.

Vulinec (1997) studied the possible effects of bright colours on social signalling within and between the sexes in *Phanaeus* species, and those of some related groups, which as pointed out above, are often very brightly coloured. She set out from the assumption that if brilliant colours are to be used in signalling conspecifics, the beetles must be able to detect either the colours or some aspect of them. Something that Vulinec (1997) didn't mention or discuss at the time, but is immediately obvious, is the question of visibility in underground tunnels, where much of intra-sexual and heterosexual display, (if that is what it is), probably takes place. Subsequently, however, Kevina Vulinec, (April 2008, personal communication), commented that much of the sexual interaction in *Phanaeus* actually appears to take place at the above-ground burrow entrance, where visibility in these diurnal beetles is probably good. Halffter and Lopez (1977) reported that mating in *Phanaeus* usually takes place on the soil surface.

Vulinec (1997) photographed several species of *Phanaeus* and related genera at various angles, and under different lighting conditions. Males of all the species she studied have large horns, and, a characteristic that is possibly more exaggerated in phanaeines than any other dung beetle group, a very large flat pronotal shield (Edmonds 1972). Beetles were photographed from the front to simulate a beetle's eye view of another, interacting beetle, using daylight film and a ring flash. Iridescent reflectance changed dramatically with the angle and intensity of the light, as is typical of interference colouration, and the iridescence on the horn and clypeus disappeared completely when not illuminated directly. The same light reflected onto the subject changed the pattern on the prothorax. A front view of *Sulcophanaeus imperator* revealed large iridescent red spots resembling eyes on either side of the head, which in view of the angle and position, Vulinec considered it unlikely they would be visible to any potential predator. She also photographed iridescent beetles under UV lights, which demonstrated UV reflectance from various iridescent areas of the beetles, most notably from the expansive pronotal shield. The UV reflectance could only be seen at specific light angles, and small changes of light source direction extinguished it. Vulinec (1997) concluded that dramatic and abrupt changes in light reflectance due to angle, in both visible and UV spectra, could possibly be an efficient method of communication either between or within the sexes.

Although phanaeine males have large horns, they are apparently seldom used as weapons of combat since male-male aggression is rare and Vulinec (1997) suggested that combat is avoided by males assessing each other by the appearance of the horn which is enhanced by iridescence. Although the horn itself is not highly reflective, it is highlighted against the background of a bright pronotal shield.

Vulinec (1997) also claimed that the horns and reflective prothoracic shield could be used to attract females, and the larger and brighter the iridescent area, the more attractive the male. However, the pronotum of certain *Phaneus* species such as *P. vindex* can be partially obscured with phoretic kleptoparasitic flies, which are transported into the beetles' burrows where they lay eggs in the dung brood. The faster-developing fly larvae may then decrease the amount of food available to the beetle larvae, resulting in smaller or weaker individuals. Consequently, a heavy parasite load on a male might be visible to females, and may result in her choosing an alternative mate who is free of parasites that might affect her offspring.

CHAPTER 8

THE ROLE OF THERMOREGULATION AND ORIENTATION IN THE AVOIDANCE OF COMPETITION

Because of the patchy distribution and ephemeral nature of dung deposits, competition has driven various dung beetle attributes to enable them to find the resource quickly and to compete aggressively with conspecifics, as well as with other species for a share of it. Tunnellers avoid inter-specific competition by temporal partitioning of their activity periods. Rollers, on the other hand, may also avoid inter-specific competition by differentially responding to environmental temperature, and some compete intra-specifically by generating body heat endothermically to enable the hottest individuals to acquire dung faster, and to succeed better in combat with conspecifics. Furthermore, rollers use light in sophisticated orientation behaviour to enable them to move in a straight line directly away from the source of competition. However, there is also the conundrum presented by flightless species which have dispensed with flight capability, and consequently, the ability to generate heat endothermically, and probably, to lose their competitive edge over access to resources. These aspects are discussed in this section.

8.1 ENDOTHERMY PROVIDING FOR COMPETITIVE ADVANTAGE

Facultative endothermy is an option available only to adult insects with functional flight muscles (Chown and Nicolson 2004) and it functions mainly for pre-flight warm-up and flight, but in ball-rolling dung beetles body temperatures can be elevated during walking, ball-making and rolling (Bartholomew and Heinrich 1978; Heinrich and Bartholomew 1979). Both nocturnal and diurnal tunnelling and rolling dung beetles have been found to raise their body temperatures endothermically (Bartholomew and Heinrich 1978; Heinrich and Bartholomew 1979; Caveney *et al*. 1995; Chown *et al*. 1995; Ybarrondo and Heinrich 1996; Verdú *et al*. 2004). In all of these studies, temperatures were measured with thin thermocouples threaded into hypodermic needles with which the beetles were stabbed in the appropriate segment, and temperatures read with applicable thermometers.

The metathorax, which houses the wing muscles as well as those of the hind pair of legs, generates most of the heat and its temperature is always consistently higher than that of the prothorax whose temperature, in turn, is always higher than that of the abdomen (Bartholomew and Heinrich 1978). Metathoracic temperatures (T_{th}) during flight of around 40°C are common in the larger species studied, which is probably close to the upper lethal limit for most species. Muscles become adapted to operate optimally at these high temperatures because biochemical systems evolve to function best at a single, high temperature (Chown and Nicolson 2004). Smaller species, however, have lower take-off temperatures than larger ones.

Before flight dung beetles go through a series of predictable movements. Tunnellers partially emerge from the soil in response to an endogenous rhythm and wait with the fore-body exposed for conditions suitable for flight, which are usually cued by light intensity (Caveney *et al.* 1995; see below). They, and rollers already above ground, comb their eyes and antennae repeatedly with the front legs, elevate the elytra, and then lift off almost vertically into the air. Intact beetles show no external signs of movement during warm-up, but those with elytra and wings removed can be seen to pump the abdomen vigorously dorsoventrally. These respiratory movements presumably support the high levels of aerobic metabolism required for the high frequency isometric contractions of the muscles which produce the heat (Bartholomew and Heinrich 1978).

Bartholomew and Heinrich (1978), working in Kenya, recorded that the metathoracic temperature at take-off of nocturnal and diurnal dung beetles that they studied were not statistically different ($P = < 0.05$). The temperature of beetles weighing between 40 mg and 100 mg increased linearly with total body mass but did not rise to more than about 34°C, which was often only slightly above ambient. Caveney *et al.* (1995) reported from South Africa that crepuscular and nocturnal beetles an order of magnitude heavier than this were also able to raise their pre-flight metathoracic temperatures to 34°C, but this was often double the ambient soil temperature, and that *Onitis aygulus* (about 750 mg) could raise its thoracic temperature by as much as 19°C from an ambient temperature as low as 12°C. Both of these studies recorded that take-off temperatures of beetles with a mass of more than about 2.5 g invariably exceeded 40°C, but that the increase in temperature was mostly independent of mass. Bartholomew and Heinrich (1978) recorded that a nocturnal *Heliocopris dilloni* weighing 11.7 g warmed up at 3.7°C / min from an ambient temperature of 23°C and took off when its metathoracic temperature reached 42°C. A diurnal

Scarabaeus catenatus of 1.75 g warmed up 5.5°C / min at an ambient temperature of 29.0°C and took off when its metathoracic temperature reached 35°C.

At night, any excess of body temperature over that of the environment in insects is almost certainly due to endothermic heat production (Bartholomew and Heinrich 1978). Tunnellers warm up prior to crepuscular or nocturnal flight but then cool down again after flight, probably because of radiant heat loss, since the level of thoracic metabolism demanded for flight is not sustained during periods of terrestrial activity (Caveney *et al.* 1995). Rollers, on the other hand, maintain high temperatures after flight but are also able to endothermically maintain, or *de novo* generate, elevated temperatures during ball-making and rolling.

8.1.1 Endothermy in rollers

Rollers are unusual among insects that generate body heat endothermically since they are capable of generating and / or maintaining it during activity that is not directly related to flight. This is probably related to the fact that in insects one set of muscles may serve two or more quite different functions. In dung beetles the same muscle complexes are involved in both flight and walking, and although flight requires high temperatures (above 40°C in large beetles) and beetles can walk in a co-ordinated fashion at temperatures considerably lower than this (as low as 15°C), elevation of thoracic temperatures would increase not only the speed and power of wing movements but also those of leg movements (Bartholomew and Heinrich 1978).

8.1.1.1 Diurnal rollers

Diurnal rollers studied by Bartholomew and Heinrich (1978) in Kenya (*Scarabaeus (K.) platynotus, S. (K.) aegyptiorum* and *S. (S.) catenatus*) raised their metathoracic temperatures on average 3°C above the temperature of the dung source in the shade when forming balls. When they rolled balls in the shade, metathoracic temperatures were 6.0 – 8.5°C higher than ambient, and in sunshine the difference increased to between 8.5 – 11.5°C, which the authors attributed to the endogenously-produced heat being elevated by solar radiation. However, even when rolling in full sun their average body temperatures were 2.5 – 4.0°C lower than flight temperatures. Ball-rolling velocity increased linearly with thoracic temperature from 5 cm/sec to 20 cm/sec (Bartholomew and Heinrich 1978).

Ybarrondo and Heinrich (1996), working in South Africa, with the diurnal *S. (K.) nigroaeneus*, found broadly similar results to those of Bartholomew and Heinrich (1978) (Table 8.1). In the Kenyan study both inter- and intra-specific competition for dung amongst diurnal ball-rollers was low, and ball-forming and –rolling were slow, from 10-30 minutes per ball. Amongst individuals of *S. (K.) nigroaeneus* in the South African study, competition was often fierce and the metathoracic temperature (T_{th}) of winners of a contest over a dung ball (X = 39.2°C ± 3.5°C) was significantly higher than that of losers ((X = 36.9°C ± 3.7°C; paired *t*-test, $P < 0.01$, $N = 18$). Ball construction time varied from about 5 minutes under conditions of high competition to about 25 minutes when the beetles were unimpeded.

Verdú *et al.* (2004) studied thermoregulation in two closely-related crepuscular / diurnal *Scarabaeus* species, *S. sacer* and *S. cicatricosus* in Spain and, on the basis of their mechanisms of thermoregulation, explained how these sympatric species differentially respond to environmental temperature and so avoid competition with each other, which probably favours their co-existence. Both species have similar feeding and habitat preferences and both have bimodal activity peaks; *S. sacer* is most active at evening / dusk, and again at morning / dawn periods while *S. cicatricosus* is entirely diurnal with most activity during early to mid morning, and again from early to mid-afternoon. Ambient temperature during the *S. sacer* activity period averaged between 20-25°C, while that during *S. cicatricosus* activity was about 10°C higher. Although there was seldom temporal overlap between the species, occasional encounters led to fierce combat.

In this study, *S. sacer* maintained a near-constant high thoracic temperature (T_{th} = 39.5 ± 1.3°C; $n = 48$) through a wide ambient temperature range (T_a = 18.2-34.5°C), while a lower ambient-dependent abdominal temperature (T_{ab}) was observed (T_{ab} = 28.9 ± 3.4°C; $n = 48$). Increments of T_{th} in relation to T_a were recorded from 7.2-21.9°C (X = 16.3 ± 3.9°C). A similar pattern was observed during take-off (T_{th} = 36.4 ± 1.0°C; T_{ab} = 28.7 ± 4.0°C; $n = 12$).

Scarabaeus cicatricosus also maintained a near-constant thoracic temperature (T_{th} = 38.6 ± 1.4°C; $n = 48$) during flight through a wide range of ambient temperatures (T_a = 21.0-36.5°C). However, in this species T_{ab} was dependent on T_{th} (T_{ab} = 36.3 ± 1.7°C; $n = 48$). Increments of T_{th} with respect to T_a were recorded

Table 8.1. Thoracic temperature (T_{th}) and temperature regulation ($T_{th} – T_a$) by activity of *Scarabaeus* (*K.*) *nigroaeneus* in South Africa.

Activity	**N**	**T_{th} (ºC)**	**T_{th} - T_a (ºC)**
Flight	14	39.8 (1.3)	17.6 (1.7)
Warm-up	13	39.3 (1.3)	14.6 (1.7)
Walking	18	30.7 (4.8)	6.8 (5.3)
Burying	7	30.3 (4.8)	4.7 (4.9)

Note: Values are presented as mean (SD). (After Ybarrondo and Heinrich 1996).

from 2.8-15.5°C ($X = 7.3 \pm 2.8$°C; $n = 48$). A similar pattern was observed during take-off ($T_{th} = 38.2 \pm 1.1$°C; $T_{ab} = 37.2 \pm 1.0$°C; $n = 13$).

During flight, *S. sacer* showed an abdominal temperature excess ratio (R_{ab}) independent of T_a ($R^2 = 0.095$; d.f. = 47, $F = 2.362$, $P > 0.1$) which indicated that the abdomen is a passive thermal window and does not contribute to thermoregulation of the thorax. In contrast, *S. cicatricosus* had an R_{ab} that decreased significantly with T_a ($R^2 = 0.365$; d.f. = 47, $F = 12.909$, $P = 0.0001$). This indicates that the species regulates T_{ab} and T_{th} within narrow limits.

Because *S. sacer* flies at relatively cool temperatures and there is little chance of overheating, there is no need to shunt heat from the thorax to the abdomen, so the latter acts as a passive thermal window. However, *S. cicatricosus* is active during hot times of the day when overheating is possible, and it actively thermoregulates both thoracic and abdominal temperatures within narrow limits. Convective cooling is increased by shunting heat to the abdomen and then cooling it behaviourally as it has a less compact flight posture than *S. sacer*, and by extending the legs which generate turbulence around the flying beetle. Consequently, *S. sacer* generates high T_{th} to enable it to fly during the coolest times of the day, while *S. cicatricosus* has evolved strategies to avoid overheating when flying at the hottest time of the day. These differences enable the two species to co-exist in spite of very similar ecological requirements.

Amongst pairs of diurnal ball-roller species studied, the *Scarabaeus* species always have an active (male) partner who forms, rolls and buries the ball, and a passive (female) partner who clings to the ball being rolled and buried, whereas in the genus *Gymnopleurus* one partner pushes and the other pulls. Bartholomew and Heinrich (1978) recorded that in males of *S. (K.) platynotus* rolling a ball with female clinging to it in shade at an ambient temperature of 28°C, the male's metathoracic temperature averaged 37.6°C, whereas the female's averaged 31.4°C. In *Gymnopleurus laevicollis* the metathoracic temperature of the pusher and the puller did not differ significantly ($P < 0.05$). Ybarrondo and Heinrich's (1996) results for the metathoracic temperatures during ball-rolling of male and female pairs of *S. (K.) nigroaeneus* (Table 8.2) were very similar to those obtained

Table 8.2. Thoracic temperature (T_{th}) and temperature regulation ($T_{th} - T_a$) of *Scarabaeus* (*K.*) *nigroaeneus* in South Africa rolling balls of impala dung alone and as active or passive partner of a pair rolling together.

	N	T_{th} (°C)	T_{th} - T_a (°C)
Alone	58	33.0 (3.1)	6.5 (4.1)
Passive	13	32.5 (5.4)	5.7 (3.2)
Active	13	38.9* (3.5)	12.1* (3.9)

Note: Values are presented as mean (SD). * $p < 0.05$. (After Ybarrondo and Heinrich 1996).

for *S. (K.) platynotus*. Consequently, male energetic expenditure in the latter rollers is much higher than that of the female during the ball-making and -rolling part of the process, whereas in these species female brood care is highly developed and the female remains with the developing brood for up to months at a time. So, lower metabolic expenditure by the female during brood resource acquisition compensates for the energetic demands of the long period of brood care.

8.1.1.2 Nocturnal rollers

Night-time in Africa is when dung beetle activity at dung is at its most frenetic and competition at its fiercest. As soon as the sun sets thousands of individuals of many species may converge on a pile of suitable dung, turning it into a seething mass within minutes, and into a mat of dry fibres within an hour or two. Most of these species are small onthophagines, but larger onitines, coprines and dichotomiines contribute to the activity.

During a study of the effect of competition by tunnellers on the crepuscular / nocturnal roller *Scarabaeus (K.) laevistriatus*, Heinrich and Bartholomew (1979) placed out 500 ml samples of elephant dung at 2-hour intervals through the night during the peak dung beetle activity season in Kenya, and recorded the numbers of beetles arriving at the dung (Fig. 8.1). *Scarabaeus laevistriatus* activity peaked at about an hour after sunset, and although tunneller activity peaked about six hours later, there was considerable overlap in their activity shortly after sunset. At peak tunneller activity the authors recorded up to 3 800 beetles arriving at the dung source within 15 minutes of placing out the dung. The attractiveness of the dung then waned as colonisation increased, and virtually ceased after about 30 minutes by which time the dung had been reduced to a pile of fibres and rendered unsuitable for further feeding. This, then, is what *S. laevistriatus* has to contend with when trying to sequester sufficient dung for a ball. How does it overcome these obstacles?

Because of the fierce competition at dung, it is obvious that for *S. laevistriatus* to successfully sequester and roll dung unimpeded by the tunnellers, it must arrive at the dung source before the onset of activity by the latter, or it must quickly roll a ball soon after the dung is deposited. Heinrich and Bartholomew (1979) recorded two different methods of ball formation by *S. laevistriatus*. The faster and more common method was to simply cut off an external piece of the dung source, quickly form it into an approximately round shape, and then roll it away. These balls were poorly and loosely constructed. The other procedure was to burrow into the dung mass, and to slowly and deliberately construct a near-perfect sphere of densely compacted dung, which was then pushed out of

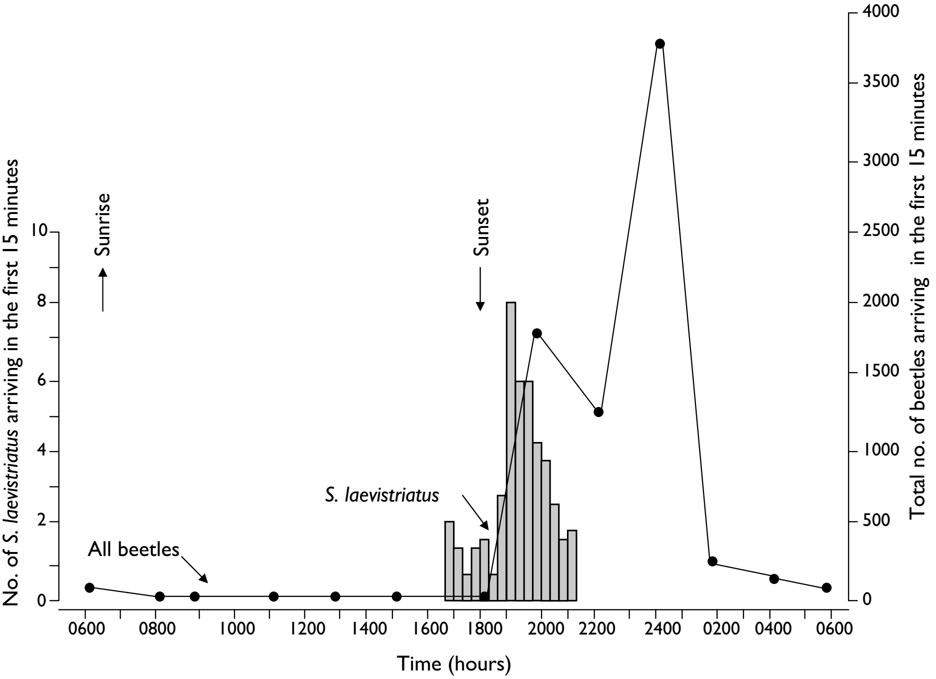


Fig. 8.1. Temporal pattern of activity of beetles at elephant dung in East Africa in summer. The histograms represent the number of *Scarabaeus laevistriatus* arriving within 15 min after the exposure of 4-10 litres of dung; the circles represent beetles of all other species (almost exclusively endocoprids) arriving within 15 min of exposure of 500 ml samples of fresh dung put out at 2-h intervals at different sites. (After Heinrich and Bartholomew 1979).

the dung mass and rolled away. The duration of ball construction varied from 1.1 to 53 minutes, with the "poor" balls needing an average of 7.6 minutes for construction, and the "good" balls more than double this time – on average 18.3 minutes (Table 8.3). Heinrich and Bartholomew (1979) did not comment on the eventual outcome of the two resultant ball types, but from our experience it seems apparent that the poorly-constructed balls were destined to be fed on by the roller (food balls), while the well-constructed ones were intended as brood balls. Clearly construction of the latter would be impossible under extreme competitive pressure from tunnellers.

Heinrich and Bartholomew (1979) measured body temperatures of *S. laevistriatus* at the onset of rolling and the time the beetles needed to roll balls. They also measured the effects of thoracic temperature on the outcome of contests over balls between conspecifics. This was done prior to tunneller activity at dung in the field or under screens from which tunnellers were excluded.

Table 8.3. Masses (g) of dung balls, durations of construction (min) and thoracic temperatures (ºC) and mass (g) of ball making *Scarabaeus laevistriatus*. (After Heinrich and Bartholomew 1979).

	Good Balls				**Poor Balls**			
	X	**Range**	**SE**	**N**	**X**	**Range**	**SE**	**N**
Ball mass	36	9-55	2.88	19	24.6	6-94	1.47	72
Duration	18.3	5.9-53	3.00	18	7.6	1.1-33	0.75	71
Thoracic temperature	34.9	28.5-42	1.02	19	32.9	25-40	0.53	72
Body mass	3.52	1.30-4.50	0.18	19	3.16	1.85-5.30	0.08	70

The thoracic temperatures of the beetles varied widely but remained above ambient, with those constructing good balls maintaining a thoracic temperature similar to that characteristic of flight (38.0 – 42.0°C). They maintained these elevated temperatures for up to 25 minutes while constructing brood balls, which was sufficient time for them to cool to within 1°C of ambient temperature (25°C) if they had been cooling passively. Beetles constructing poor balls, however, did not or could not maintain elevated thoracic temperatures. The time to construct balls generally decreased with increasing thoracic temperature, but Heinrich and Bartholomew (1979) were unable to explain whether this was because it took longer for cold beetles to construct balls, or because they cooled off because they took long to form the ball (Table 8.4).

Table 8.4. (A) Thoracic temperatures of *Scarabaeus laevistriatus* ball builders at the end of ball construction, and (B) duration of ball construction. (After Heinrich and Bartholomew 1979).

A. Thoracic temperatures of ball makers.

Thoracic temperature (ºC)	**Poor Balls**				**Good Balls**			
	X	**Range**	**SE**	**N**	**X**	**Range**	**SE**	**N**
< 30	11.1	2.0-33	1.79	21	40.9	29-53	12.1	2
30-34.9	7.27	1.5-21	1.22	21	14.9	5.9-31	3.65	7
> 35	5.28	1.1-19	0.71	29	16.0	6.3-25	2.33	9

B. Durations of ball construction.

Durations (Min.)	**Poor Balls**				**Good Balls**			
	X	**Range**	**SE**	**N**	**X**	**Range**	**SE**	**N**
< 5.0	34.5	27-40	0.68	31	…	…	…	…
5-14.9	32.5	25-40	0.82	31	35.2	31-42	1.32	9
> 15	28.7	25-39	1.40	9	35.1	29-41	1.70	9

When *S. laevistriatus* arrived at a dung pile they frequently attempted to steal balls from conspecifics that were present. This always led to vigorous fights of short duration (< 4.0 seconds) but not to any visible damage to either of the combatants. The builder of the ball successfully defended its ball as often as it lost it to an interloper, and this happened independently of the sex of the beetles ($x^2 = 2.067$; $0.5 > P > 1.0$). The outcome of the contests, however, was strongly affected by body size and thoracic temperature of the contestants, although the warm beetles usually won contests against cooler ones of any size. The mean mass of winners ($P < 0.02$) and their thoracic temperatures ($P < 10^{-6}$) were significantly greater than those of the losers, but the large difference in the levels of significance indicate that the effects of temperature are far greater than those of mass. The authors staged 116 contests between individuals of different sizes, and in 71 of those the larger beetle won (so the probability of the bigger beetles winning contests was about 0.6). However, of 112 contests where thoracic temperature of the contestants differed, 97 of the hottest won (a probability, thus of a hotter animal winning a contest over a colder one, of about 0.9). Out of a $\Sigma x^2 = 65.86$ ($P < 0.005$) for mass and thoracic temperature, the latter accounted for 91% of the x^2 value, indicating unequivocally that thoracic temperature is more important than mass in determining the outcome of contests.

Females (3.4 g) were significantly heavier than males (3.12 g) ($P < 0.001$) and they won a significantly greater number of contests over the smaller males (27 to 15; $P < 0.01$), an outcome predicted on the basis of size alone. Their thoracic temperatures did not differ significantly ($P < 0.1$).

Because the leg muscles are linked to those of the thorax, high thoracic temperatures contribute to high leg muscle temperatures, which enable dung beetles recently landed at a dung sources to quickly determine its suitability for ball construction, and if already heavily colonised by tunnellers, to leave again without having to undergo pre-flight warm-up. Consequently, because elevated thoracic temperatures speed up activity and so enable rollers to quickly roll balls before tunnellers invade them, or allow them to quickly leave an unsuitable dung source without expending excessive energy in repeated pre-flight warm-up exercise, elevated temperatures should be selected for to avoid this level of interspecific competition.

After dark, access to suitable dung for *S. laevistriatus* to roll diminishes rapidly because of the invasion by tunnellers, but one option available to the rollers is to steal a partially or completely formed ball from a conspecific. There is little risk of injury to the intruder, and the recently arrived beetle is invariable hotter than the one forming the ball, so theft of the ball is a safe, often successful, and energetically less costly option, than forming a new ball. Hence, high thoracic temperatures undoubtedly increase the success rate of forming or acquiring balls so would also be selected for.

From the research results discussed in this section there appears to be ample evidence to infer that competition between different species, as well as within some of those discussed, has been an important selective force for endothermy in dung beetles. So, how do flightless dung beetles without the mechanisms needed to warm up endothermically overcome some of the hurdles that apparently drove the process in flying beetles in the first place?

8.1.2 Facultative endothermy, and ectothermy in flightless dung beetles

An overwhelming majority of dung beetles fly strongly and actively and presumably use some of the mechanisms and processes discussed above to their advantage when competing for resources. However, a relatively small, but significant number of dung beetle species, is apparently or actually flightless. These are mainly restricted to regions or habitats considered to be “predictably stable” such as forests, mountains, islands and deserts (Scholtz 2000 – see Chapter 9). Loss of flight capability is probably driven by different selective pressures under each of the dominant sets of conditions that prevail in these areas, but in general energy conservation has been proposed as the reason why species living in cool areas don’t fly, and conservation of respiratory water for those in desert areas (Chapter 10).

Circellium bacchus is the largest ball-roller in Africa and it is flightless (Kryger *et al.* 2006). It is monotypic and currently considered to be a canthonine, but there is some doubt about this relationship (Philips *et al.* 2004b). It is day-active. The species is currently restricted to small fragments of dense thickets in the southern and eastern Cape of South Africa, and although it was originally thought to have been widespread in savanna regions of southern Africa (Chown *et al.* 1995), this has been largely discounted (Kryger *et al.* 2006). *Circellium bacchus* is well-known from the Addo Elephant National Park in South Africa because of the beetles’ size and abundance in the Park and their claimed association with elephant dung, but they are, in fact, generalist feeders and feed on virtually any available dung (Kryger *et al.* 2006). However, in view of their tennis-ball size, brood balls require large quantities of dung to provide for the needs of the developing larva. There is large variation in size (22-47 mm, X = 36.3, n = 80, Kryger *et al.* 2006) and weight (3.7-11.0 g; X = 7.3 ± 0.4 g, Nicolson 1987) of adults which is possibly greater than that found in any other dung beetle species, and may partially be explained by the fact that larvae reared on sub-optimal quantities of food emerge as small adults. This is a likely consequence of the scarcity of large quantities of dung in most areas of their distribution range, and the reason for their apparent success when huge quantities of elephant dung are readily available. Teneral *C. bacchus* always form and roll food balls (16-33 mm diameter, $X = 25.3 \pm 4.5$ mm, $n = 42$), whereas mature adults invariably feed at the dung source. Only females, without help from a male, roll brood balls (Kryger *et al.* 2006; Le Roux *et al.* 2008). Brood balls range in diameter between 43.5-64.2 mm ($X = 53$ mm ± 5.0 mm, $n = 50$; Kryger *et al.* 2006). Brood ball formation takes on average 65 minutes, but females have been observed (CHS, personal observation) to take as long as 24 hours to do so, and they may roll the balls long distances (7-80 m, $X = 27.6$ m, $n = 22$, Kryger *et al.* 2006 although they have been observed (CHS, personal observation) to roll as far as 100 m.

Circellium bacchus is strictly an ectotherm, and consequently, a poor competitor for dung with large winged ball-rolling species (Nicolson 1987; Chown *et al.* 1995), which, either because of the semi-arid conditions, or dense bush in which *C. bacchus* occurs, are scarce in the same areas.

Chown *et al.* (1995) compared the thermal biology of *C. bacchus* with that of a similar-sized, diurnally-active, winged roller, *Pachylomera femoralis*. The latter is widespread in savanna regions of southern Africa, from northern South Africa to Tanzania, so does not overlap in distribution with *C. bacchus*. Although the species is phylogenetically and nominally a roller, its behaviour is atypical, and in most instances of dung foraging individuals act mainly as tunnellers (see 4.1.5.2). This notwithstanding, they compete very aggressively for dung at a source.

Chown *et al.* (1995) used very similar methods for measuring thoracic, abdominal and ambient temperatures to those in the studies discussed above, and likewise measured beetles' temperatures during resting, rolling, pre-flight walking, post-flight walking, pre-flight warm-up, flight and walking speed. Obviously none of the parameters that are associated with flight could be measured for *C. bacchus*.

Summary statistics Chown *et al.* (1995) for T_{th}, T_{ab}, T_a and temperature excess ($T_{th} - T_a$) during resting/feeding, walking, ball rolling and/or flight are provided in Table 8.5, together with walking speeds. Temperature excesses ($T_{th} - T_a$) during feeding and rest were less than 0.5 °C in both *C. bacchus* and *P. femoralis* and there was no difference between the species (ANOVA $F = 2.88$, $P = 0.096$, $df = 52$, $n = 53$). The slope of the regression of T_{th} on T_a of beetles feeding, and/or at rest ($T_{th} = 1.043\ T_a - 0.848$, $r^2 = 0.794$, $P < 0.0001$, $df = 33$, $n = 34$), was not significantly different from one in the case of *C. bacchus* ($t = 0.462$, $P > 0.5$). However, in *P. femoralis*, the slope of the regression ($T_{th} = 0.605\ T_a + 11.640$, $r^2 = 0.696$, $P < 0.0001$, $df = 18$, $n = 19$) was less than one ($t = -4.08$, $P < 0.001$) but greater than zero ($t = 6.24$, $P < 0.001$).

Temperature excesses were slightly higher during walking than during feeding/rest in both *C. bacchus* and *P. femoralis* prior to flight, but very much higher after sustained flight in *P. femoralis* (Table 8.5). There was a significant difference in temperature excess between post-flight *P. femoralis*, and both pre-flight *C. bacchus* and *P. femoralis*, although there was no significant difference between the latter groups (ANOVA $F = 100.19$, $P = 0.0001$, $df = 67$, $n = 68$, pairwise comparisons using Tukey's HSD intervals). There was no significant relationship between T_{th} and T_a ($T_{th} = 0.567\ T_a + 12.95$, $r^2 = 0.615$, $P < 0.0001$, $df = 43$, $n = 44$) and between walking speed (ms^{-1}) and T_{th} (speed = $0.330\ T_{th} - 5.837$, $r^2 = 0.737$, $P < 0.0001$, $df = 19$, $n = 20$) in *C. bacchus*. In *P. femoralis* there was a significant relationship between T_{th} and T_a during walking prior to flight ($T_{th} = 0.657\ T_a + 10.484$, $r^2 = 0.597$, $P = 0.015$, $df = 8$, $n = 9$) but not in walking after flight (the slope was equal to zero, $t = 0.107$, $P > 0.9$). Walking speed did not covary with T_{th} prior to or after flight, although T_{th} accounted for 39% of the variation in walking speed when the two groups were pooled (walking speed $ms^{-1} = 0.0034\ T_a - 0.02$, $r^2 = 0.393$, $P = 0.001$, $n = 24$). An analysis of covariance, taking T_{th} into account, showed no difference between walking speed in *C. bacchus* and *P. femoralis* prior to flight (Table 8.5) but a significant increase in walking of *P. femoralis* after flight, compared with the former groups (ANCOVA main effects $F = 4.932$, $P = 0.012$, $df = 43$, $n = 44$, pairwise comparisons using Tukey's HSD intervals). Temperature excess during ball rolling in *C. bacchus* was similar to that found during other activities (Table 8.5) and the slope of the regression of T_{th} on T_{ab} ($T_{th} = 0.890\ T_a + 5.75$, $r^2 = 0.564$, $P = 0.0001$, $df = 33$, $n = 34$) was significantly greater than zero ($t = 6.21$, $P < 0.001$) but less than one ($t = -0.70$, $P < 0.001$).

In *P. femoralis* during flight, T_{th} ranged from 37.1 to 43.4 °C (Table 8.5) at T_a ranging from 24.3 to 29.3 °C and the slope of the regression of T_{th} on T_a ($T_{th} = 0.150\ T_a + 36.81$) was not significantly different from zero ($t = 1.01$, $P > 0.2$). The greatest temperature excess recorded was 17.4 °C and the lowest 10.0 °C, but Chown *et al.* (1995) explained that these are probably slight overestimations because beetles closed their elytra on capture, elevating T_{th} by 1 – 2 °C. Abdominal temperatures ranged between 32.8 and 40.8 °C (mean = 36.5 °C, SD = 1.74, n = 39) and the slope of the regression of T_{ab} on T_a ($T_{ab} = 0.305\ T_a + 28.37$) was significantly less than one ($t = -4.08$, $P < 0.001$). Immediately prior to flight, presumably on completion of pre-flight warm-up, T_{th}, T_{ab} and $T_{th} - T_a$, over a temperature range of 24.7 to 28.1 °C, were similar to the values found during flight (Table 8.5). Likewise, the slope of the regression of T_{th} on T_a ($T_{th} = -0.109\ T_a + 43.57$) was not significantly different from zero ($t = -0.280$, $P > 0.5$), although the slope of the regression of T_{ab} on T_a ($T_{ab} = 0.680\ T_a + 9.34$) was not significantly different from one ($t = -1.22$, $P > 0.2$).

Thoracic temperature excess ($T_{th} - T_a$) during feeding and walking was small in both species, and the slopes of the regression of T_{th} on T_a during these activi-

Table 8.5. Mean ± SE and sample sizes (in parentheses) of T_a, T_{th}, $T_{th} - T_a$ and T_{ab} (°C) during various activities, and walking speeds (ms^{-1}), of *Circellium bacchus* and *Pachylomera femoralis* in South Africa. ND = not determined. (After Chown *et al.* 1995).

Variable	*Circellium bacchus*	*Pachylomera femoralis*
Resting		
T_a	24.6 ± 0.6 (34)	26.8 ± 0.6 (19)
T_{th}	24.9 ± 0.7 (34)	27.8 ± 0.4 (19)
$T_{th} - T_a$	0.2 ± 0.3 (34)	1.1 ± 0.3 (19)
Ball rolling		
T_a	27.7 ± 0.5 (34)	ND
T_{th}	30.4 ± 0.6 (34)	ND
$T_{th} - T_a$	2.7 ± 0.4 (34)	ND
Pre-flight walking		
T_a	27.9 ± 0.6 (44)	24.8 ± 0.9 (9)
T_{th}	28.7 ± 0.5 (44)	26.8 ± 0.7 (9)
$T_{th} - T_a$	0.8 ± 0.4 (44)	2.0 ± 0.6 (9)
Post-flight walking		
T_a	ND	27.0 ± 0.2 (15)
T_{th}	ND	38.0 ± 0.5 (15)
$T_{th} - T_a$	ND	11.0 ± 0.5 (15)
Pre-flight warm-up		
T_a	ND	25.6 ± 0.3 (12)
T_{th}	ND	40.8 ± 0.4 (12)
T_{ab}	ND	37.1 ± 0.5 (12)
$T_{th} - T_a$	ND	15.2 ± 0.6 (12)
Flight		
T_a	ND	26.8 ± 0.2 (41)
T_{th}	ND	40.8 ± 0.2 (41)
T_{ab}	ND	36.5 ± 0.3 (41)
$T_{th} - T_a$	ND	14.0 ± 0.3 (41)
Walking speed		
Pre-flight	0.056 ± 0.003 (20)	0.070 ± 0.006 (9)
Post-flight	ND	0.112 ± 0.005 (15)

ties were much greater than zero, suggesting that they are ectothermic for these activities. However, immediately prior to flight, during flight, and during walking immediately after flight, temperature excesses were above 10°C in *P. femoralis* illustrating that it is endothermic. Furthermore, the slope of the regression of T_{th} on T_a during these activities was equal to zero suggesting that the species may be capable of thermoregulating. The slope of the regression of T_{ab} on T_a was never greater than one which implies passive cooling rather than active heat transfer. Consequently, *C. bacchus* is a strict ectotherm, and *P. femoralis* is facultatively endothermic as are all of the other winged rollers studied so far, and obviously very capable of successful competition at a dung source. The former, however, with a walking speed of 0.056 m s^{-1} and little means to elevate its thoracic temperature, would stand little chance in interspecific contests over dung, which has undoubtedly led to its restricted distribution to areas where large winged diurnal rollers are absent.

8.1.3 Behavioural thermoregulation

The mechanisms of thermoregulation discussed in this section have been fairly well studied and the processes appear broadly similar in all species. However, passive heat absorption during perching on foliage, which is typical behaviour of small forest dung beetle species while foraging for mainly monkey dung excreted in the forest canopy that sticks to foliage, has been described for *Canthon septemmaculatus* (Young 1984). *Canthon septemmaculatus* is a day-active, medium-sized (8.5 – 12.0 mm long, 0.152 g wet weight) dull black beetle with seven yellow spots (Young 1984). It is distributed from Panama to Argentina, in a variety of habitats, and feeds on carrion and dung. Young (1984) recorded 15 species of dung beetles known to "perch" on Barro Colorado Island (BCI), Panama. The diurnal species are usually light-coloured, or if dark, they are shiny. *Canthon septemmaculatus* was the one exception, being dull black. Young (1984) recorded that *C. septemmaculatus* was active for most of the daylight hours in the forest, but that it perched mainly on sunlit leaves between 09:00 – 11:00 when most sunlight fell on leaves at 1.0 – 2.0 m above the ground, which was its preferred activity stratum, and that it foraged during the hours after 11:00, with little evidence of perching behaviour then. The beetles also frequently shuttled between sun and shade. Although Young did not measure body temperature of any of the beetles, he felt confident that all evidence suggested that the mostly dull black beetles were controlling their body temperature behaviourally.

8.1.4 The use of light in competitive flight behaviour

Because African Onitini rapidly exploit the dung of various mobile herbivores, different flight behaviours result in spatial and temporal partitioning of species in the local dung community, and ambient light intensity appears to be the primary determinant of the onset of their daily flight period (Houston and McIntyre 1985; Caveney *et al*. 1995). The latter authors recorded the flight activity of 12 species of Onitini in Australia (introduced African and Mediterranean species) and in the field in South Africa, but since the patterns in all species were clearly cued by light intensity, only the results of the seven sympatric crepuscular/nocturnal species obtained under natural conditions in the field will be discussed. The species were either elephant or buffalo dung specialists, and were collected from fresh dung in the field. The beetles were kept under natural light and ambient temperatures, and flown within four days of capture. The flight experiments consisted of placing a known number of fed individuals of the appropriate species in clean lightly moistened soil a few hours before the known onset of flight. Light intensity and soil and air temperatures were recorded automatically at regular intervals by a multi-channel data logger, and thoracic temperatures of a representative sample of the beetles to be flown were measured with thermocouples glued into hypodermic needles, as discussed above under "endothermy". The beetles were allowed to fly in flight chambers and the time of flight of each beetle that flew recorded. Because it had been shown in a previous study (Houston and McIntyre 1985) that light intensity is the dominant cue triggering flight under favourable conditions, Caveney *et al.* (1995) plotted flight activity as a function of light intensity (Fig. 8.2).

The different species flew mostly for short periods during evening dusk, dark, dawn, or they had bimodal activity at dusk and dawn. Five of the species, *Onitis alexis, O. fulgidus, O. westermanni, O. pecuarius* and *O. viridulus* had crepuscular activity; *O. alexis*, *O. fulgidus* and *O. westermanni* flew only at dusk, whereas the other two species flew at dusk and dawn. Dusk activity coincided in all three species, flying during a narrow range of light intensity, but the onset of morning activity of *O. pecuarius* and *O. viridulus* was over a wider range of light intensities. *Onitis mendax* and *O. uncinatus* flew mainly at dusk, but individuals of both species also flew during the night. *Heteronitis castelnaui* was unlike any of the other species studied since it flew in the late afternoon, before sunset, and a second dawn activity peak extended well into the morning, up to two hours after sunrise.

Caveney *et al.* (1995) recorded that the thoracic temperatures of the beetles resting beneath or crawling on the soil surface, lay within 1°C of ambient soil or air temperature. However, in preparation for flight, the beetles raised their thoracic temperatures to between 35-40°C. *Onitis alexis*, the smallest species (live weight 0.36 ± 0.06 g, *n* = 40), tended not to fly at ambient temperatures of below 17°C, and was able to raise its thoracic temperature to a maximum of 34°C before flight. A larger species (an African species studied in Australia), *O. aygulus* (0.73 ± 0.016 g, *n* = 18) was able to warm its thorax to at least 19°C above an ambient soil temperature as low as 12°C. The largest species studied, *H. castelnaui* (2.77 ± 0.48 g, *n* = 20), had a constant pre-flight thoracic temperature of 40-42°C.

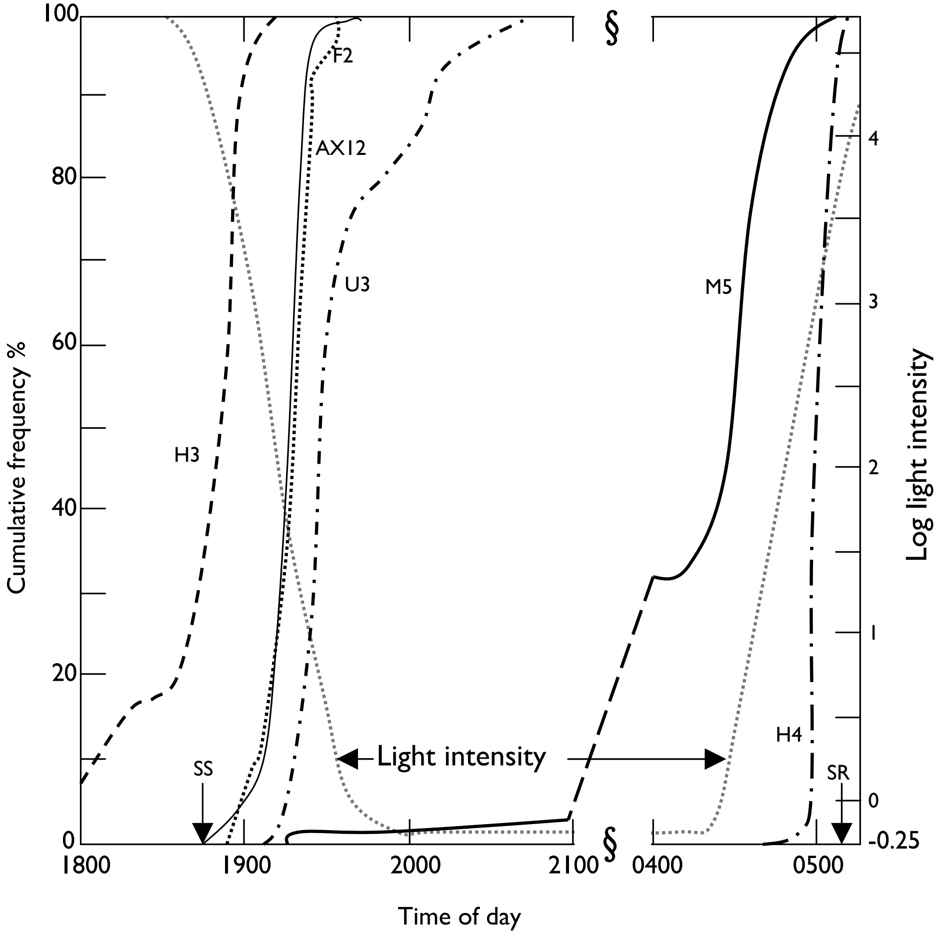


Fig. 8.2. Activity patterns of five sympatric onitine beetles flown on the same night in their natural habitat in South Africa. The dusk crepuscular flights of *O. alexis* (curve AX 12) and *O. fulgidus* (F2) coincided in time. The apparent lull in dung beetle flight activity during the middle of the night in this area is occupied by various coprine species, which are exclusively night-flying beetles. Sunset (SS) and sunrise (SR) times are marked by arrows. H = *Heteronitis castelnaui*; AX = *Onitis alexis*; F2 = *O. fulgidus*; U3 = *O. uncinatus*; M5 = *O. mendax*. (After Caveney *et al.* 1995).

Being an ephemeral and patchy resource, dung dropped throughout the day by various mobile mammalian herbivores provides opportunities for colonisation of different types of dung, in different habitats, and at different times of the day, to a host of specialised dung beetles. The onitines studied by Caveney *et al.*

(1995) partition the resource by dung type preference, and by often very subtle temporal shifts in their activity peaks. All of the species studied had crepuscular and early evening activity – none flew between about two hours after sunset or two hours before sunrise. This was the main activity period of a host of other tunnellers, mainly *Copris* and *Heliocopris* species.

Amongst the onitines that Caveney *et al.* (1995) studied, two species with very similar dung preferences and flight activity periods illustrate subtle differences in resource utilization that lead to spatial and temporal avoidance of competition. Both *Ontis mendax* and *Heteronitis castelnaui* feed on coarse dung of elephant and rhinoceros. *Ontis mendax* flew mainly about two hours before sunrise, while *H. castelnaui* had sunset and sunrise flight peaks. These flight periods coincide roughly with the times of day when elephants feed most actively, namely late afternoon, around midnight and early morning. Most dung is voided towards the end of the feeding periods (references in Caveney *et al.* 1995). Caveney *et al.* (1995) recorded that elephant dung voided at night contained only *O. mendax*, suggesting that large numbers of these beetles arriving before dawn pre-empt colonization by *H. castelnaui*. Elephant dung deposited at dawn contained both species while that voided around sunrise contained only *H. castelnaui*.

8.2 ORIENTATION AND AVOIDANCE OF COMPETITION

Ball rolling is considered to be a derived behavioural attribute that evolved under pressure from competitors and for space at the dung pat. Straight-line orientation away from the source of the competition after the acquisition of a suitable quantity of dung would be the most successful rolling strategy, and the use of a celestial cue would be the most dependable source of spatial information. Several recent studies by Marie Dacke and collaborators (Dacke *et al.* 2002; Dacke *et al.* 2003a; Dacke *et al.* 2003b; Dacke *et al.* 2003c; Byrne *et al.* 2003) have clearly demonstrated that the sun in a clear sky, and polarised light from the sun and moon respectively, at twilight and at night serve as cues for straight-line orientation away from the dung source while rolling a ball by both diurnal and nocturnal rollers.

The sun, in a mostly clear sky, is an obvious and dependable reference point for diurnal animals. However, under cloudy conditions when the sun may not be directly visible or when it is low on, or beneath, the horizon, polarised light indicating the position of the sun can be used. Likewise, when there is sufficient light from a bright moon, using polarised light offers nocturnal rollers a reliable orientation reference point.

When light from the sun or moon strikes the earth and its atmosphere, it becomes scattered and reflected by air molecules. As a result of this, a pattern of polarised light is formed across the sky (Dacke *et al.* 2002). This pattern varies in a systematic fashion over the day, both in the plane and degree of polarization, and consequently, it provides a cue with directional properties to animals capable of seeing it. Orientation with the use of celestial cues is widespread amongst animals and has been well studied in insects (see Wehner 1984). However, such navigation usually involves movement between a fixed position (often a nest) and feeding sites. Ball rolling by dung beetles is somewhat different since it is unidirectional, away from a food source, over unknown terrain, and towards an unknown destination where the ball is buried. This has some obvious advantages to the roller – it prevents accidental return to the source of the competition, and it ensures that the maximum distance is covered in the minimum time.

8.2.1 The sun as an orientation cue

Byrne *et al.* (2003) studied the role of the sun as an orientation cue in three *Scarabaeus* species (*S. rugosus, S. rusticus* and *S. (Kheper) nigroaeneus*), *Pachylomera femoralis* (all Scarabaeini), and *Garreta unicolor* (Gymnopleurini) at different sites in South Africa. All of the species are diurnal and were found to use the sun as a reference point for straight-line navigation. They found no evidence to suggest that the beetles used landmarks to any meaningful extent.

Byrne *et al.* (2003) performed various experiments to disrupt rolling beetles in the field by: placing various obstacles in their way; rotating rolling beetles on a round disc; and changing the direction of visible sunlight by shading the beetle and then reflecting the sun with a mirror at 180° from the actual sun position. They also tested whether the beetles showed a phototactic response to the sun. In the laboratory they substituted the position of a tungsten lamp as a proxy for the sun, and changed the position of the light instantaneously by switching to other lights at 90° or 180° from the original position.

i) Response to an obstacle

Two of the species, *P. femoralis* and *S. rugosus*, were obstructed by a 30 cm-wide transparent barrier being placed in front of rolling beetles, at right angles to the original direction of deviation. Differences between the original and final angles of rolling were measured with a compass and subjected to statistical analysis.

ii) Response to a fall and loss of contact with the ball

All five of the species were tested by placing a 5 cm-high ramp in front of rolling beetles. The fall from the ramp caused them to lose contact with the ball, and precipitated a brief "orientation" dance on top of the ball before the resumption of rolling. Differences between the original and final angles of rolling were measured with a protractor and subjected to statistical analysis.

iii) Response to induced rotation

Pachylomera femoralis and *S. rugosus* were tested for their ability to correct for a sudden 90° change in direction. This was achieved by placing beetles rolling balls onto a 42 cm diameter wooden disc covered with a thin layer of sand and then rotated by 90°. The authors measured the angular deviation from the expected reorientation of 90° with a protractor from the path left in the sand on the disc, and subjected it to statistical analysis.

The data were analysed according to statistical methods described by Zar (1996, according to Byrne *et al.* 2003). They calculated the mean resultant vector (α) for each distribution and used Rayleigh's test to ascertain whether the distributions differed from uniformity. Where there was an expected deviation from a particular orientation angle, the data were subjected to a modified Rayleigh test, and depending on the type of data, *t*-tests or ANOVA were used to compare between species (Table 8.6).

iv) Response to reflected sunlight

The sun's influence on *P. femoralis*'s orientation behaviour was tested by allowing beetles to roll in full sunlight for a distance of about 1 m, and then the sun was shaded from direct view of the beetle and reflected 180° from the opposite side with a mirror. The angular difference between the two paths before and after reflection was measured with a protractor and analysed. A mean deviation of 180° would be expected if the beetles were using the sun as an orientation cue.

v) Orientation to artificial lights

In the laboratory a single tungsten lamp was used to replace the sun. When a beetle had rolled for a few centimetres the position of the light source was switched to a second light at either 90° or 180° to the original position. The angle of deviation from the original path was measured with a protractor and tested as above. The expected deviation would be the angle between the first and second light.

vi) Orientation towards the sun

To determine whether ball rollers roll in a particular, set direction with respect to the position of the sun, the direction *P. femoralis* chose to roll balls was recorded. This was done on the same day between 14h00 and 16h00 when the sun azimuth moved between 272° and 260°.

The rolling beetles whose path was obstructed by a barrier turned left or right when they encountered the barrier, and continued rolling in the original

Table 8.6. Mean angles of re-orientation (∝), of ball-rolling beetles to a straight-line path after encountering an obstacle (*r* length of the mean vector, *n* sample size, *u* value of modified Reyleigh test; *P* level of significance of the modified Reyleigh result). The Reyleigh test was used to compare the mean angular correction obtained for each species, with that expected if the course correction was perfect. Statistical comparisons were used to compare results of different species and refer to data is the same columns. A *t*-test was used for two species comparisons, or ANOVA was used for several species.

Parameters	**Obstacle**		
	Barrier	**Ramp**	**Rotation**
Pachylomera femoralis			
∝ (°)	13.4	7.2	21.6[a]
r	0.966	0.992	0.99
u	8.299	6.960	5.82
P	< 0.001	< 0.005	< 0.001
n	39	25	20
Scarabaeus rugosus			
∝ (°)	16.8	13.8	8.7[a]
r	0.966	0.977	0.99
u	7.30	7.100	6.191
P	< 0.001	< 0.005	< 0.001
n	32	28	20
Scarabaeus rusticus			
∝ (°)	-	9.6	-
r		0.993	
u		4.379	
P		< 0.005	
n		10	
Garreta unicolor			
∝ (°)	-	6.4	-
r		0.995	
u		4.420	
P		< 0.005	
n		10	
Scarabaeus nigroaeneus			
∝ (°)	-	11.9	-
r		0.974	
u		4.669	
P		< 0.005	
n		12	

Parameters	**Obstacle**		
	Barrier	**Ramp**	**Rotation**
Statistical comparisons	*t* – Test	ANOVA	*t* – Test
	df = 69	df = 4,80	df = 38
	t = 0.820	F = 1.93	*t* = 5.174
	P = 0.45	*P* = 0.11	*P* < 0.001

[a]Means in the same column followed by the same letter are statistically different to P=0.05. (After Byrne *et al.* 2003).

direction. Angles of reorientation were not significantly different from 0° in either species (Table 8.6, *P* values). *P. femoralis* maintained a mean angle within 13.4° of its original path, and *S. rugosus* a mean deviation of 16.8°. There was no significant difference between the species (Table 8.6).

The mean deviation from the original direction of travel in response to a fall and loss of contact with the ball varied between 7.2-13.8° and was not significantly different from zero for any of the species (Table 8.6, *P* values).

The beetles tested for compensation of rotation all corrected for the rotation by turning in the opposite direction to that turned. *Scarabaeus rugosus* maintained a mean angle within 8.7° of its original path, and *P. femoralis*, within 21.6°.

All of the beetles tested in the field and laboratory responded to the sun and lights, respectively, clearly indicating that the sun is an important visual cue which beetles use to roll away from the dung source. All individuals also corrected for a 180° reflection of the sun's position, by a mean of 160.5°, but this did not differ significantly from 180° (ANOVA, *df* = 2, 34, *F* = 2.565, *P* = 0.85). This confirms that the beetles use the sun as an orientation cue. Beetles left to roll balls unhindered in the direction of their choice rolled balls at all angles from the dung, thus supporting the conclusion that their orientation is mainly menotactic (i.e. in relation to the sun) rather than phototactic (i.e. directly towards or away from the sun).

These results clearly demonstrate that rollers roll rapidly away from the dung source and try to maintain as straight a line as possible, even to the extent of rolling around obstacles, or recovering their ball lost in a fall. They have been shown to succeed admirably, using the sun as a celestial cue.

8.2.2 The use of polarised light for orientation

In the first study of the possible use of an area in the dorsal eye of a dung beetle for detecting polarised light, Dacke *et al.* (2002) described a special dorsal rim area (DRA) in the compound eye (see 5.2) of the diurnal South African coastal desert species, *Pachysoma striatum*. They also discussed its probable use in detecting polarised light for navigation, and although they did not determine experimentally whether the beetles could, actually, detect polarised light, the dorsal rim area of the eye is structurally ideally suited for it, and enough is known about *Pachysoma* foraging behaviour, and the environmental conditions to which the beetles are exposed (Scholtz *et al.* 2004), to safely assume that they use polarised light for navigation.

In a subsequent study, Dacke *et al.* (2003a) selected a crepuscular species (*Scarabaeus zambesianus*) to test for polarised light sensitivity, because during twilight the polarisation pattern is most simple, with the light of the whole sky polarised in one direction. The zenith of the sky at this time has the highest degree of polarisation of the day, reaching between 70% and 80% polarisation (references in Dacke *et al.* 2003a). This high degree of polarisation stretches in a band across the sky from south to north. The remainder of the sky is polarised in a parallel direction with falling degrees of polarisation towards the sun and anti-sun. On nights with a full moon, a similar pattern of polarised light also forms around this light source (Dacke *et al.* 2003a).

Scarabaeus zambesianus was active at the field site between about 10 minutes before and 10 minutes after sunset, which was between 18h58 and 19h00 at the time of their experiments. The sun set at 250° east of north. On dark nights the beetles were active for 40-50 minutes, while on nights with a high moon they stayed active for another 40-50 minutes. The authors undertook two experiments. The first was identical to that outlined above under "Response to an obstacle" from the paper by Byrne *et al.* (2003), in which a 30 cm obstacle was placed at right angles to the path of a rolling beetle, and the deviation after the obstacle, from the path taken before the obstacle, was measured with a protractor. In a second experiment, a polarising filter with diameter of 42 cm was placed 10 cm above the path of a rolling beetle, with its e-vector (electric vector) transmission axis orientated in a west-easterly direction (70-250° east of north, i.e. 90° to the plane of polarised light) (Fig. 8.3). Thus, as the beetle entered the area below the filter, the south-northerly orientated polarised light pattern of evening skylight appeared to switch by 90°. The authors repeated the experiment in the laboratory using an artificial light source as a substitute for the sun, and placed the polarising filter over a rolling beetle. After it had rolled 5 cm, the filter was rotated 90°, and the angle turned by the beetle in response to the filter being rotated, was measured.

In the first experiment, the beetles behaved as discussed above. They rolled until the end of the obstacle and then continued in the original rolling direction. Of 15 beetles tested, seven turned left and eight turned right, with no

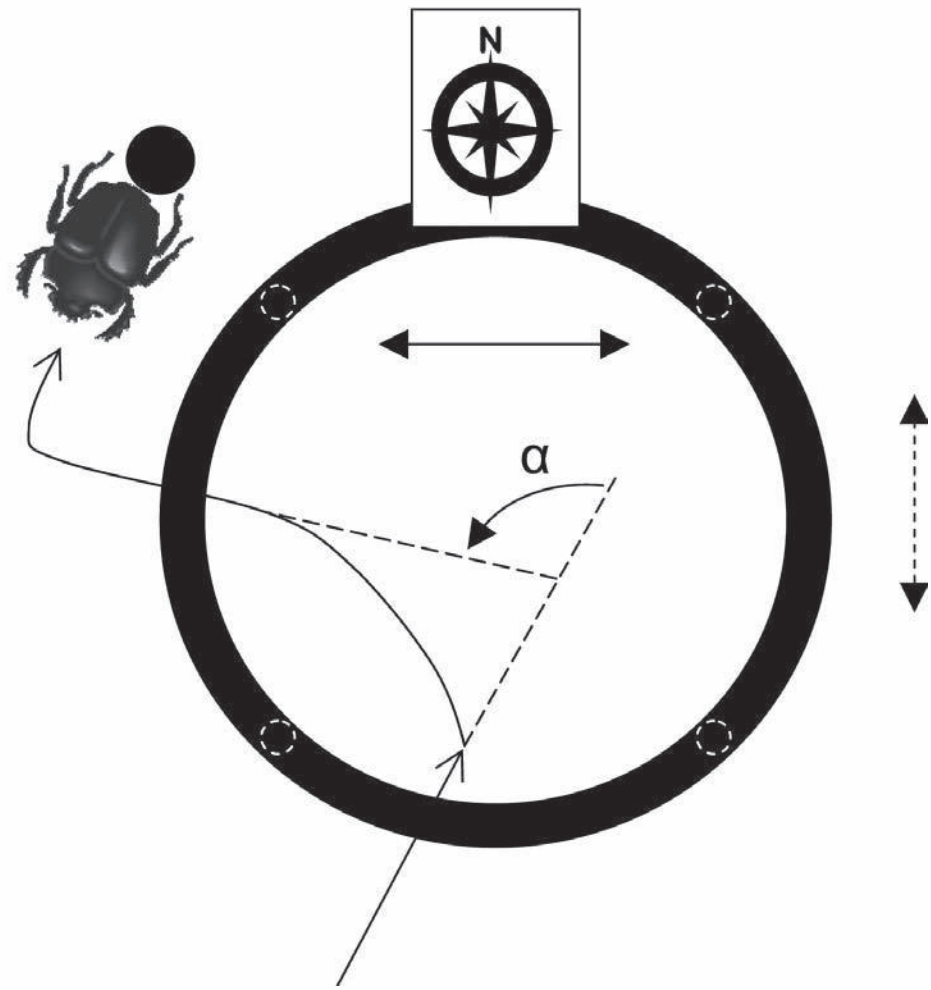


Fig. 8.3. Experimental set to determine orientation to polarised light by *Scarabaeus zambesianus*. The black open circle represents the polarising filter (shaded) in its holder, and the white dotted circles represent four symmetrically placed legs 10cm high. The set is equipped with a magnetic compass to orient the e-vector produced by the filter (double-headed arrow) in a west-easterly direction, 90° to the e-vector on the evening skylight (dotted double-headed arrow). The turn made by the beetle (a) in response to the shifted polarisation pattern experienced on entering the filter was measured from the track drawn after filming the beetle. Open arrows mark the direction of movement. Note that the beetle rolls head down and backwards. (After Dacke *et al*. 2003a).

preference indicated. The mean deviation from the original rolling direction was 16.9° ± 11.5°. In the second experiment, the deviation caused by the 90° switch in polarised light by the polarising filter in the field, resulted in a mean turn of 80.9° ± 15.8°. This was close to the expected 90°. In the laboratory, when the beetles were placed under the polarising filter which was then rotated, the beetles turned to a mean value of 61.4° ± 16.1°. The poorer response to the rotated filter in the laboratory was ascribed to possible loss of rolling precision by the beetles after two weeks in the laboratory, compared to those tested in the field.

Dacke *et al.* (2003a) concluded from their experiments that polarised light detection was most likely to be the primary cue that the crepuscular beetles used to orientate. In addition, the dance that these [and all other] rollers carry out on top of the ball at the start of rolling, after an induced direction change or after losing contact with the ball, is believed to recalibrate the beetles' polarization compass before starting or continuing their journey. Such rotations are well known in other insect species (references in Dacke *et al.* 2003a).

Dacke *et al.* (2003c) then posed the question whether *S. zambesianus* could use the light of a bright moon, albeit a million times dimmer than the sun, as a cue to continue foraging after the polarisation pattern of the afternoon sun is no longer observable. They followed this up with two studies (Dacke *et al.* 2003b,c) in which they demonstrated that *S. zambesianus* uses the polarised light in the form of a concentric pattern of polarised skylight centred on the moon disc, rather than the light from the moon itself, for orientation. The first of these was the first record for any animal using polarised light from the moon as a celestial cue for navigation.

Dacke and her colleagues studied the effect of moonlight on the activity of *S. zambesianus* at the same study site in South Africa where they undertook the study of its crepuscular activity. The methodology was basically the same, except that activity was studied on full moon nights, as well as four nights prior to this, and four nights after the event. The experiments were carried out after astronomical twilight, that is, when the sun was more than 18° below the horizon and no longer contributed to illumination of the sky.

Dacke *et al.* (2003c) repeated the experiment discussed above with a polarising filter held over a rolling beetle, but this time under direct moonlight and by shading the moon from sight of the rolling beetle. When the filter had its e-vector transmission axis orientated perpendicular to the dominant orientation of the e-vector present in the zenith, and along the lunar vertical, and it was rotated 90°, the beetles turned close to the expected 90°. Of 22 beetles tested, 12 turned left with a mean angle of 77° ± 14.7°, and 10 turned right (87.9 ° ± 9.3°; mean ± s.d.). As a control, they then repeated the experiment with the filter's e-vector orientation parallel to that of the sky. The beetles maintained their direction of rolling with an average deviation from the original angle of 6.7° ± 5.5°, so the authors were able to conclude that it was not the five-fold drop in light intensity experienced by the beetles covered by the filter that caused them to change direction but rather that it was the detection of the polarising pattern caused by the moon, that resulted in the specific rolling pattern.

Dacke (2003b) followed this experiment up with more field and laboratory experiments with *S. zambesianus* rolling balls, and by computing the polarisation sensitivity of individual retinal cells in the DRA of beetles' eyes.

In the laboratory they provided rolling beetles with a simple light source, to mimic the moon in the sky, by which to orientate. Lights were positioned around the arena in which the beetles were rolling, and then lights switched off and on simultaneously at either 90° or 180° from the original position. The beetles responded to 90° change in the position of the light source by turning 69.4° ± 1.9° (mean ± s.d.), and by 158.0° ± 7.2° when the light source was changed by 180°. These changes in direction of rolling did not differ significantly from the expected changes of 90° and 180° respectively.

In the field they provided rolling beetles with an artificial moon in the form of an electric light source with neutral density filters to adjust the intensity of the artificial moon to match that of the real moon. This was then switched on at 180° to the moon and the latter simultaneously shaded. In a second experiment, they moved the position of the moon 180° with a mirror while shading the real moon. They also repeated the "ramp" experiment discussed above, except that the beetles were allowed to roll up the ramp in full view of the moon, and then again with the moon shaded from their view.

Beetles rolling under the open sky were able to continue in their chosen direction when the moon was hidden, but the polarisation pattern of the sky was still visible. Providing them with an artificial moon as a possible cue was ignored in favour of the polarisation pattern. They were also able to continue in the original direction of rolling after a fall from a ramp with the moon shaded, further confirming that the moon itself is not the primary cue for orientating by. The deviations or non-deviations were all statistically significant compared to the expected.

Finally, Dacke *et al.* (2003b) were able to show with intra-cellular electrophysiological recordings that receptors in the DRA of the *S. zambesianus* eye are highly sensitive to polarised light. Polarisation sensitivity ratios (references in Dacke *et al.* (2003b) were 7.7 and 12.9 in two DRA cells while it was 1.5 in one and 1.6 in two others outside of the DRA.

Dacke and colleagues concluded from this set of experiments that the moon disc may be involved in orientation, but that the there seems to be little doubt that the polarisation pattern in the sky produced by the light scattering effects of moonlight reflecting off tiny particles in the sky, is the principal cue. The moon disc under natural conditions may often be obscured by clouds or trees, but the polarisation pattern is visible under all conditions except total cloud cover. As a result, the ability of this crepuscular / nocturnal species to use the polarisation pattern produced by a bright moon, enables them to extend their foraging activity deep into the night on several nights during each month. This spreads the activity period and lessens the competitive demand for limited food resources. Although this ability is only known from *S. zambesianus*, there is a host of other crepuscular to nocturnal rollers known, and it is quite likely that they have similar adaptations to those outlined by Dacke and her colleagues.

CHAPTER 9

THE LOSS OF FLIGHT

The enormous diversity and evolutionary success of insects can be attributed in part to the evolution of flight, which enables them to disperse widely and easily in search of mates, food, and new habitats. However, in spite of such seemingly obvious benefits some species in each of the major orders have become secondarily flightless, sometimes in only one sex. On the other hand, the presence of fully developed, seemingly functional wings is no indication that they are actually used.

In various parts of this book we have emphasised the ephemeral nature and mostly irregular occurrence of dung, the fierce competition amongst different species for this scarce resource, and the competitive advantages that the first-comers enjoy at a fresh dung source. Finding and competing successfully for dung is almost entirely directly (flight) or indirectly (endothermy) related to the ability to fly. Yet there are numerous species of dung beetles in various parts of the world that have successfully forfeited this significant evolutionary innovation under certain sets of selective pressures. In this section we deal with the morphological and behavioural changes that dung beetles undergo when they lose the ability to fly, and we discuss the higher than expected incidence of this phenomenon in certain habitats, and speculate on the reasons why some species of dung beetles have selected this evolutionary route.

Various hypotheses have been proposed for why pterygote insects have secondarily become flightless. Roff (1990, 1994) and Wagner and Liebherr (1992) cogently discussed the association between the frequency of flightlessness in insects in general and Scholtz (2000) discussed the phenomenon in Scarabaeoidea in particular. They also discussed various possible causes for it. Some of the possible factors which were reviewed that lead to increased flightlessness are: decreasing environmental heterogeneity; geographic variables; gender; alternative modes of migration; and taxonomic variation. One of the prime factors claimed to favour the evolution of flightlessness is that of increased environmental homogeneity. The incidence of flightlessness is also unusually high in forests, deserts, on the ocean surface, in specific habitats on the seashore, in aquatic habitats, in winter, in social insect nests and among ectoparasites of endotherms. It is low in riverine and arboreal habitats. The incidence of flightlessness increases with altitude and latitude and may be higher on oceanic islands than on comparable mainland areas.

Flightlessness is more frequent among parthenogenetic species and more frequent among females than among males. In some flightless species alternative means of dispersal such as phoresy have evolved but it appears to be relatively rare. Finally, flightlessness is common in some taxa and rare in others, implying a phylogenetic propensity toward loss of flight in some groups (also see Roff 1994).

Scholtz (2000) reviewed flightlessness in the Scarabaeoidea and recorded flightless species in most higher taxa from many of the habitats identified as selecting for, or maintaining, the loss of flight capability. He recorded that flightless species undergo predictable morphological changes after flight has been abandoned and that flightless dung beetles are more likely to occur in certain habitats than in others.

9.1 THE INFLUENCE OF HABITAT ON FLIGHTLESSNESS

Loss of flight capability in insects results in a significant decrease in dispersal ability and the consequent mobility to track habitat changes. Southwood (1962) proposed that the prime evolutionary advantage of migratory movement lies in enabling a species to keep pace with the changes in the location of its habitat. He confined his analysis of habitat to two categories, "temporary" and "permanent". He predicted that within a taxon one should find a higher level of migratory movement in those species associated with temporary habitats than in those with more permanent ones. Examples of what he considered to be permanent habitats are rivers, lakes, perennial plants including trees of climax communities such as woodlands, salt marshes, heath lands and marshes fringing lakes and rivers. Temporary habitats include dung, carrion, fungi, plant debris and annual and perennial plants of seral communities (Southwood 1962).

Various habitats prove to be ideal for the evolution of wingless forms in dung beetles and in most cases these coincide precisely with habitats in which other groups of flightless insects also occur. Flightless dung beetles are typically found in forest, desert, mountain and island habitats. There is also a distinct phylogenetic propensity among some groups toward flightlessness. However, flightless dung beetles are not well represented in tropical forests, at high altitude in the Holarctic, in association with social insects or in phoretic associations with other animals, although many species occur in these areas or in these associations.

Clearly the nature of the habitat has different significance for the various species associated with it and habitats that to us appear ephemeral may persist and be available for colonization for much longer than would ordinarily be expected. Southwood (1962), for example, considered dung, carrion, fungi, plant debris and perennial plants of seral communities to be "temporary" habitats. Of these, dung, carrion and plant debris have a host of flightless dung beetles associated with them although the distinction between them being used as "food" or "habitat" is tenuous. All of these habitats persist for long periods in particularly arid areas and consequently may be considered stable and dependable. Members of the Australian canthonine dung beetles and of the southern African scarabaeine genus *Pachysoma* feed on dry dung in arid areas and some species of the latter genus also feed on dry detritus.

Some of the major temporary habitat associations and food sources of dung beetle groups, according to Southwood's definition are: living and feeding in rotting wood (*Paraphytus*); feeding on carrion (many Scarabaeinae) or other animal remains (*Sceliages*); feeding on hypogeous fungi (*Coptorhina*); associating with social insects (*Ontherus*, *Megaponerophilus*); humus (*Bohepilisus*, *Cephalodesmius*, *Outenikwanus, Peckolus*); and herbivore dung (most species). In most cases adults feed in situations and on sources of food similar to those of the larvae.

9.1.1 Forest habitat

Forests are both persistent and, frequently, spatially extensive (Southwood 1962) and a higher-than-average incidence of flightlessness is found in them in several orders, including Coleoptera (Roff 1990). In spite of these general statements qualification is required in the case of dung beetles; altitude and latitude of the forests having an important effect on the incidence of flightlessness.

Lowland tropical forest supports very high dung beetle species richness in all regions, with several of the higher taxa being more or less restricted to these areas. Despite this high generic and species richness the incidence of flightlessness is very low. On the other hand, lowland subtropical forest areas in some regions, notably Australia, have a high incidence of flightless Canthonini, for example.

Temperate forests at high altitude in the tropics and subtropics present a very different situation to lowland forests, having low richness but fairly high incidence of flightlessness, as in various canthonine dung beetle groups in Africa, Australia and the Neotropics. On the other hand, temperate forests at high latitude in the northern hemisphere have few flightless species whereas those at low latitude in the southern hemisphere have fairly high incidence.

Many of the flightless forest dung beetles occur in stable and persistent microhabitats such as the litter layer, carrion or the dung of forest animals including mammals, birds, reptiles and various invertebrates. The highly unusual flightless canthonine dung beetle genus *Cephalodesmius* is found in wet coastal and montane forests along the south-east and east coast of Australia.

9.1.2 Desert habitat

There is a high frequency of flightless species in deserts in the Order Coleoptera, amongst others (Roff 1990). Due to the dryness in desert environments, rates of decay are slow and hence insects feeding on detritus, carcasses or on the persistent parts of plants, live in an environment that may be relatively persistent (Roff 1990). Some dung beetle taxa are restricted to desert areas or have a high proportion of the species living in a desert environment and, of these, a high percentage may be flightless. All but one species of the tribe Eucraniini in South America are flightless, as are all those of the south-western African genera *Macroderes*, *Pachysoma*, *Byrrhidium, Namakwanus* and *Dicranocara.* The monotypic south-east African *Circellium bacchus*, may also be considered an arid-adapted species (Duncan 2002: Kryger *et al*. 2006).

9.1.3 Mountains as habitat

Insect faunas of high mountains include a high proportion of wingless species and an increase in the incidence of flightlessness with increasing altitude has been observed both within and between insect species (Roff 1990). Mountains *per se*, with regard to dung beetles, are considered to be the high altitude alpine areas above the tree line and below the snow line. This “dung beetle” mountain zone varies on different continents and with latitude but lies on average at between about 2500m and 5000m above sea level. The generally lower plant biomass of often nutritionally poor quality, and climatic extremes, exclude all of those groups with an indirect dependence on plants, and due to an impoverished vertebrate fauna, limits the diversity of dung-dependent taxa. In spite of these limitations there is a fairly rich fauna of montane dung beetles, few of which, however, are flightless, and the tendency for increased incidence of flightless taxa at high altitude is higher in the subtropics and tropics and at low latitude than it is at high latitude. This incidence of flightlessness is low compared to other scarabaeoid beetle groups such as Geotrupidae and Trogidae, for example, (see Scholtz 2000).

9.1.4 Islands as habitat

Wollaston (1854) (cited in Roff 1990) pointed out the high incidence of flightless insects on the island of Madeira and his observations were central to Darwin's hypothesis that on oceanic islands a flightless morph would be more fit than a winged one because it would be less likely to be blown or fly from the island (Roff 1990). Since then there has been widespread acceptance of the notion that there is an increased incidence of flightlessness in insects on oceanic islands, although a number of authors have questioned both the hypothesis and the presumed correlation (Roff 1990). There are many problems with accepting this hypothesis, one of which is the problem of scale – environmental effects being very different on small and large islands and Roff (1990) concluded that flightlessness on oceanic islands should not, in general, occur because of the size of the island. Although Roff's (1990) arguments are convincing there are several scarabaeoid taxa with a higher than expected incidence of flightless species on oceanic islands although the question of scale and the other characteristics to which he refers appear inseparable. For instance, when is an island an island, what about the effects of cold and windy conditions on islands, or those in forests or on mountains on the island; which environment is exerting the most pressure on the species? Do New Zealand's two main islands as well as the smaller surrounding islands qualify equally as "oceanic islands" in the current sense? All of the dung beetles on New Zealand are flightless. There are flightless canthonines on Cuba, Puerto Rico, Mauritius and New Caledonia in greater proportion to winged species than is found, for example, in South and Central America with its very rich fauna, but in lower proportion than in Australia on the other hand. A complicating factor is that most of them occur in high altitude montane forests on the islands, both altitude and forest having independent, well documented, high incidences of flightlessness.

9.1.5 Association with social insects

Several taxa within the Scarabaeidae are more or less exclusively associated with ants or termites while some others appear to have opportunistically exploited this niche. Where known, these species appear to breed in the debris in social insects' nests (see 4.1.5.1). Some of these taxa apparently have an opportunistic association with the social insect host while others are clearly obligatory. Although there are a number of flightless scarabaeid species associated with social insects, this is almost exclusively restricted to the Aphodiinae, the purported sister group of the dung beetles, and is very rare in the Scarabaeinae with the only flightless genus thought to be a myrmecophile is the Australasian *Ignambia* (Matthews 1974).

9.1.6 Phoretic associations

Many flightless insect species have a phoretic dependence on other animals (Roff 1990) and although there are several highly unusual species of dung beetles which are morphologically and behaviourally adapted to, and which appear to have, a phoretic commensal association with various animals, there are no records of flightlessness amongst them. Three of the most unusual associations are between various dung beetle species and sloths in the neotropics, between several *Onthophagus* species and various Australian macropod marsupials, and between the Neotropical *Zonocopris*, and giant land snail species (see 4.1.5.2).

Species of *Pedaridium*, *Uroxys* and *Trichillum* have an intimate association with sloths, living phoretically in their fur until they descend from the trees at roughly weekly intervals to defecate and bury their dung at which time the scarabs leave the host to feed on and breed in the fresh dung. Only these specialised taxa indicate any interest in artificially exposed sloth dung (Ratcliffe 1980). One of the enigmas of the association is what becomes of the scarabs when the sloths defecate into the water covering the floor of the seasonally-flooded lowland forests in which they live.

Several Australian *Onthophagus* species have prehensile tarsal claws with which they grip the fur of the phoretic host (usually native macropod marsupials but also, occasionally, introduced eutherian mammals). Although they may occur on any part of the body they congregate near the anus or cloacal opening. During defecation the beetles converge on the emerging dung pellet, grip it and drop to the ground with it where they feed on it or breed in it. This behaviour is thought to be an adaptation to overcoming the rapid desiccation of dung in the arid areas of Australia where they occur (Matthews 1972).

The two known species of *Zonocopris* occur on the mantle of land snails where they feed on mucous (Vaz-de-Mello 2007). (See Chapter 2.1.1.4).

An obligatory phoretic association is only possible in host species with some sort of seasonal or permanent nest and clearly neither the scarabs' nor their hosts' biology permits such an intimate association. Even though these groups are morphologically and behaviourally adapted to their phoretic association they clearly need to locate hosts over some distance at various times and the only means of achieving this successfully is by flight, hence the retained flight capabilities.

9.2 THE EFFECTS OF HABITAT STABILITY ON FLIGHTLESSNESS

Flight is a major contributor to the success of insects; it aids insects in locating food and in distributing offspring among suitable sites. Yet in nearly every insect order there are species that have secondarily lost the ability to fly. Habitat stability is clearly a key factor favouring the loss of flight (Roff 1990; Scholtz 2000). However, even within stable habitats, most species retain the ability to fly; and often winged and flightless sister species may be found together which appear to have very similar environmental requirements and biological attributes. The question remains why some species should cease flying and others not.

One of the problems encountered with testing the hypothesis of habitat stability and persistence as major determinants of flightlessness is the lack of quantifiable characteristics of the habitat. As a consequence, habitats are usually only broadly categorised but in spite of this there is good evidence that flightless species are found at higher frequencies in some general types of habitats than in others. Furthermore, convergent evolution of similar traits in different lineages is considered strong evidence for adaptation to a particular habitat.

Within each of the stable habitats there may be a unique set of environmental pressures exerted on insects in that habitat and which contribute to the evolution of flightlessness. In some cases the primary cause of flightlessness is apparent, in others not. Compartmentalising environmental conditions in an attempt to deduce the most significant factors that select for flightlessness may lead to mistaken conclusions about the most important parameters since most of the environments in which there is a high incidence of flightlessness have a complex interplay between various strongly selective factors. For example, insects in high altitude island forests may be exposed to a multitude of selective factors such as island effects, those that prevail in the forest, or the effects of high altitude, or of cold.

The widespread occurrence of flightless insect species strongly suggests that "fitness costs" (Roff 1990; Zera and Denno 1997) are often associated with the ability to fly. The energy used to construct wings and flight muscles is simply not available for reproductive investment under some circumstances and there is strong support for a fitness trade-off between flight capability and reproduction provided by comparative studies across a wide range of insects (Zera and Denno 1997, and references therein). In isolated, stable habitats, for example, isolated mountain tops, the most likely explanation for the reduction of flight is that the leaving of dispersal genotypes causes a net loss because few or no immigrants arrive to replace the emigrants. The lowered numbers of winged dispersers are subsequently outbred by flightless non-dispersers in the relatively stable populations. Moreover, low temperatures or high winds, often encountered on high mountains and oceanic islands, may induce flight loss by increasing the energetic cost of flight. The same condition is also observed more generally among insects in cold climates. It has been suggested by several workers that flight in most insects is directly inhibited by cold temperatures because energy invested in wings and wing muscles may be wasted in cold regions such as high altitudes and high and low latitudes and consequently selection will favour the evolution of flightlessness in these areas (see Downes 1965; Roff 1990; Hunter 1995).

As early as 1945, Kalmus concluded that the distribution of ocelli in insects is correlated with flight ability. He suggested that in flying insects these may aid orientation, and showed that reduction or absence of ocelli in flightless species may extend to the level of the species, caste or even the somatic mosaic, and he pointed out that in *Drosophila* pleiotropic genes are known which affect eye and wing characters simultaneously.

Eye reduction occurs concomitantly with wing reduction in most dung beetles. Sight may assume less importance when wing reduction limits the habitat range available to the species that have a plentiful supply of readily accessible food such as in most species. In predatory Carabidae, however, which do not display eye reduction in flightless species, the capture of prey is a feature presumably unaffected by loss of ability to fly (Smith 1964).

In desert beetles the advantages of sealed elytra and the presence of a subelytral cavity into which spiracles open and which becomes filled with saturated exhaled air apparently outweighs the potential desiccatory effects of repeatedly opening the elytra as in winged beetles (see Chapter 10).

Large areas of typical historically persistent habitat with high incidence of flightless dung beetle species are to be found, for example, along the coastal strip of mainly eastern, northern and western Australia, the arid south-western region of southern Africa encompassing Namaqualand and the Namib Desert, the islands of New Zealand, isolated mountain peaks around the world, and temperate high altitude forests in tropical latitudes. Large historically unstable areas which have been greatly disturbed over time and which have a lower than expected incidence of flightlessness, can be found mainly in the northern hemisphere where the fauna was periodically decimated by Pleistocene glaciations. These north-temperate regions were drastically affected by the glaciations, with the vegetation zones repeatedly shifting, contracting and expanding according to the changing climate (Hanski 1991). Beetles provide good fossil material which shows that both in Europe and North America most insects "migrated" with changing climate and vegetation and so avoided extinction – for example *Aphodius holdereri*, a species now known only from the high plateau of Tibet, but which was by far the most abundant dung beetle in the

British Isles during the last glaciation (Coope 1973). However, these regions have not affected all beetle taxa equally since in the particularly well studied beetle family Carabidae, for example, there is a large body of quantitative data showing the strong dominance of flightless carabid beetles in north-temperate mountains (Nilsson *et al.* 1993).

Perhaps the most enigmatic regions in terms of flightless scarabaeoid taxa are the large tropical forested areas of South/Central America, Africa and South-East Asia, which, in spite of very high species richness have considerably lower than expected incidence of flightlessness.

The largest areas of land on earth are in the tropics and because of the peculiar set of environmental conditions there that lead to forest establishment and growth, these are the largest areas of forest on earth. Because of their large size they are the most species-rich areas, since there is a direct correlation between habitat area and species number (Rosenzweig 1995). Large forests also have various attributes which result in increased speciation events that contribute to the very high species richness found in the tropics. The first of which is that they have high levels of disturbance (Petraitis *et al.* 1989; Rosenzweig 1992). Diversity is the result of a balance between the frequency of disturbances that provides opportunities for species to recolonise, and the rate of competitive exclusion, which sets the pace of extinctions within patches (Petraitis *et al.* 1989). Large forest size, furthermore, leads to greater geographical ranges for species and consequently large population sizes which would result in: small accidental extinction possibility; more niche refuges – species with big ranges would be more likely to have some protected localised sites to lessen extinction rates; larger areas for geographical barriers to form in; population isolates to form and allopatric speciation to begin; higher speciation rates since a large population's chance to evolve a new gene function exceeds that of a small population. Consequently, large species ranges should reduce extinction rates and increase allopatric speciation (Rosenzweig 1995).

Central and South America enclose the largest expanse of tropical forests, with a long evolutionary history and rich dung beetle fauna. Lowland tropical forests covered much of South America by the close of the Cretaceous but Miocene and Pliocene orogenies fragmented lowland forest while giving rise to montane habitats (Gill 1991). Other types of forest as well as savanna probably developed in response to changes in topographic relief. Reduced rainfall resulting from lowered sea levels and lowered temperatures during the Pleistocene are thought to have shrunk the tropical forests into isolated refugia (see Gill 1991 for more detail and references).Tropical forests in South-East Asia are fragmented among the thousands of smaller and larger, and more or less isolated islands in the largest aggregation of islands in the world. The forests extend from the western Indo-Malayan region to the eastern New Guinean-Australian region; and while the large islands of the Sunda Shelf have been repeatedly connected and disconnected to the mainland and to each other, many of the central islands are oceanic. In spite of this the forests are currently fundamentally uniform (Hanski and Krikken 1991). The African rain forest, on the other hand, is a more or less continuous block of large size which has expanded and contracted during successive Pleistocene pluvial and interpluvial periods, the most recent pluvial peaking 9000 BP and ending by 5000BP (Cambefort and Walter 1991).

Since forests are claimed to be classical habitats in which flightlessness evolves (see Roff 1990; Scholtz 2000), why is it that tropical forests world-wide have such a depauperate flightless dung beetle fauna? The reasons may lie in the fact that environmental conditions that lead to high species radiation and richness are in strong contrast to the ones that lead to the evolution of flightlessness. Flightlessness requires high habitat stability and low levels of biotic interaction whereas high diversity requires environmental disturbance and high levels of biotic interaction (Petraitis *et al.* 1989, Rosenzweig 1992). Tropical forests clearly have been greatly disturbed over evolutionary time and are composed of complex multi-species communities which may explain the apparent dearth of flightless dung beetle species. On the other hand, temperate forests at high altitude in the subtropics and tropics support low species richness, which may be attributable to these forest areas usually being spatially small, but support a high incidence of flightless species.

However, some dung beetle taxa do have flightless tropical forest species although most do not. What possible conditions favour the exceptions? The explanation appears to lie in the question of scale. Some forest species have highly restricted microhabitats such as under bark or in litter where they may be less exposed to extreme conditions, and possibly, predation. Those which need larger or patchy, more exposed or more ephemeral resources, and are more likely to encounter adverse environmental conditions and predators, tend to retain flight capabilities.

In earlier reviews of flightlessness in insects, environmental stability was proposed as the major contributor to the evolution of flightlessness (e.g. Roff 1990) but these have considered only physical stability as the major factor and mostly ignored biological stabilty (such as reduced effects of predation, disease and competition). Scholtz (2000) added biological stability and generally simple biotic systems to the list of environmental factors that promote flightlessness.

It is clear from the evidence presented in this review that flightless dung beetles not only occur in environmentally stable habitats but that these habitats are relatively species-poor and lack complex biotic interactions. The flightless species is also often one of a relatively impoverished dung beetle fauna in that particular habitat. Most of the habitats in which flightless dung beetles have been recorded could be considered to be populated by relatively simple biotic communities, often under fairly severe environmental conditions such as those experienced in deserts, mountains and islands where aridity, cold or wind are extreme.

Based on examples of dung beetles discussed above, there appears to be one probable route to flightlessness. In suitably stable environments where males and females would encounter one another without having to cover large distances, or where population densities are such that there is a high chance of encounter between the sexes, the pressure to trade flight energy against reproductive investment or desiccation resistance, for example, would increase, and lead to behavioural flightlessness. This would give way to flight muscle reduction, decreased wing sclerites and reduced wings and ultimately to microptery and permanent winglessness.

9.3 TAXONOMY OF FLIGHTLESS DUNG BEETLES

Some taxa appear to have a phylogenetic propensity toward flightless species evolving while others may have large numbers of species of which some occur in apparently suitable environments for flightlessness to evolve but do not lose the ability to fly. Clearly taxa with exclusively flightless species must have evolved from a flightless ancestor but others, which are obviously derived from winged ancestors, with high proportions of flightless taxa indicate an increased tendency toward flightlessness under the appropriate conditions.

There is considerable variation in flight capabilities amongst different taxa – some have a high percentage of flightless taxa while others have few or no flightless taxa.

All but one species of the small tribe Eucraniini (16 species), are flightless (see Plate 12.15). Many genera have all species flightless, so there is clearly a phylogenetic element to this characteristic. Others have some winged and some flightless, indicating obvious selective environmental pressure to cease flying in the latter species. The other extreme, where a very large taxon has few flightless species, is the virtually cosmopolitan genus *Onthophagus* with only four flightless species (Zunino and Halffter 1988) out of about 1750 in the genus (Hanski and Cambefort 1991). Many species in the genus occur at high altitude; at 4000 m to 5200 m in the Himalayas, *O. cupreiceps*, (Halffter and Matthews 1966) for example, occurs higher than any other known species but flies, as do numerous island, forest and desert species (Matthews 1972). Three of the four flightless species occur in temperate forests at 2000 m to 3000 m altitude in Mexico and Central America. They are not closely related (Zunino and Halffter 1988). The fourth flightless species, *O. apterus* from Australia, occurs in relict patches of vine scrub in arid areas of inland Queensland where it probably feeds on macropod (for example wallaby) dung (G. Montieth, personal communication).

9.3.1 Canthonini

The Canthonini is the largest tribe and also has the largest proportion of wingless species (other than the much smaller Eucraniini). Of about 95 genera and 780 species (Cambefort 1991) recorded in the world about one-third of the genera and half of the species occur in the western Hemisphere (Halffter and Martinez 1966, 1967, 1968; Matthews 1966). Australia (Matthews 1974) and Africa (Howden and Scholtz 1987; Scholtz and Howden 1987a,b; Deschodt and Scholtz 2008) also have rich faunas, with about 30% and 25% of the generic diversity respectively (see Cambefort 1991). The incidence of wingless groups is much higher in Africa and Australia than it is in the New World, with about half of the genera and about 40-45% of the species wingless on those two continents.

Wingless canthonines are found in a variety of habitat types but all of them have persistence and stability in common. The species feed mostly on the dung of a wide variety of animals including mammals, reptiles and birds and, less commonly, also on plant matter (Halffter and Matthews 1966; Monteith and Storey 1981).

A typical example of a New World canthonine genus with flightless species is *Canthochilum* which is endemic to the islands of Puerto Rico and Cuba, with eight and five species respectively, of which one on each island is flightless. The species live in forested areas across a gradient of altitudes and habitats from lowland forest under fluctuating temperature and humidity conditions, through moderate altitudes under more humid and less variable montane forest conditions to the highest altitude in mesophytic forest with continuous low temperatures and high humidity (Matthews 1966). Both flightless species are restricted to the highest altitudes. *C. hispidum* occurs at 1000 m to 1300 m above sea level on some of the highest mountain peaks on Puerto Rico and; *C. guayca* at 1800 m on Pico Cuba peak in the Turquino massif, the highest peak in Cuba (Matthews 1965, 1966). *C. guayca* has only vestiges of the wings left, whereas *C. hispidum* has them reduced to about the elytral length. There are essentially four possible major complexes of habitat characteristics that may contribute individually or jointly to flightlessness in these species; the effects of an island environment, those of high altitude, leaf litter-inhabiting or other forest effects. However, the most plausible primary effect is probably that of high altitude since all of the *Canthochilum* species on these two islands are found in leaf litter in mature, climax forests, the only apparent major difference being that the flightless species occur at higher altitudes than the winged species.

The situation among Australian canthonines appears to be quite different to that elaborated above (Matthews 1974). The flightless species are concentrated along the east and west coasts of the continent, in a variety of woodland or forest biomes (Doube *et al.* 1991). South and central Western Australia and the east coast between 20°S and 35°S (Queensland and New South Wales) show an unusually high proportion of flightless species while the northern and southern coasts and the entire interior of the continent are devoid of them. The two major areas containing flightless species also display a high degree of endemism; the eastern area contains five flightless genera restricted to it while the western area contains four, plus wingless species of primarily winged genera. These two areas are quite different climatically, topographically, and therefore ecologically, the eastern one being mountainous and relatively wet, the western one largely flat and dry (Matthews 1974). In other words, it appears that flightlessness in Australian Canthonini is not correlated with present-day ecology or climate to any significant extent but with geography and faunal antiquity. This suggests a historical explanation; homogenous habitat and environmental (climate, predation and competition) stability over time. Portions of these two areas probably acted as refugia in the past during which time they would have provided stable conditions for relict species or for speciation events. Consequently, stability within limited areas is probably the only factor that these two regions of flightlessness have in common and this cannot be perceived from present-day climate or ecology.

The situation in Africa appears similar to that in Australia with most flightless species occurring in refugial areas with a long history of environmental stability (Howden and Scholtz 1987; Scholtz and Howden 1987a,b; Deschodt and Scholtz 2008). These are mainly the mountains and disjunct relictual forests of the southern Cape Province of South Africa, with cool temperate climate, the patchy south-eastern tropical lowland forests, and discontinuous temperate highland forests of the eastern escarpment of southern and central Africa. A number of species are also found along the arid west coast of southern Africa, a region with a high incidence of flightlessness amongst many groups of beetles.

Circellium bacchus is restricted to fragmented and disjunct patches of dense arid bush in south-eastern South Africa. It is among the largest of the African ball-rolling scarabs (see Plate 12.12) and depends on a constant supply of large herbivore dung on which to feed and in which to breed successfully. *Circellium bacchus* is thought to have evolved in forested areas in association with large forest specialist herbivores (possibly something like the black rhinoceros), and owes its survival, in part, to its dense stable habitat, its flightlessness and its large size which contribute to its more efficient energy and water utilisation than similar-size winged scarabs (Chown *et al.* 1995; Duncan 2002).

9.3.2 Sisyphini

A less clear-cut case of the reasons for flightlessness among species in high altitude environments on a tropical island can be found in the genus *Nesosisyphus* on the Indian Ocean island of Mauritius. There are four species in the genus, all of which occur in forests on mountain slopes at altitudes of between 350-750m above sea level. They have similar food requirements, feeding on dung of introduced monkeys as well as that of various birds. Two of the species are flightless and have restricted but more or less overlapping distribution which also coincides with that of the winged species (Vinson 1951, in Halffter and Matthews 1966). So here we have the enigmatic situation where closely related species with similar food and habitat requirements occur sympatrically in high altitude forests but only two of the species have lost, the other two retained, their flight capabilities.

9.3.3 Eucraniini and *Pachysoma* (Scarabaeini)

Dung is usually a scarce resource in desert areas because of a lack of herbivores, which is, in turn, as a result of a shortage of vegetation for food for them. When dung is available it is usually in the form of the small dry pellets of rodents and other small desert-adapted mammals. Various species have evolved to utilise this dry dung, or, in the absence of dung, some species are capable of collecting and feeding on plant detritus.

Two flightless dung beetle taxa with broadly similar and apparently convergent adaptations to a desert environment are the Argentine Eucraniini, with four genera (three with a few species each and all flightless, and one monotypic and winged) and about 16 species (Ocampo and Hawks 2006), and the southwest African *Pachysoma* with 13 species (Sole *et al*. 2005). The flightless species have evolved special foraging techniques to cope with an abundance of dry rodent and lagomorph dung pellets, or in some *Pachysoma* species, plant detritus. The pellets or detritus are collected and transported, by holding in the hind legs and dragging forwards in *Pachysoma,* (Fig. 9.1) or carried in the fore legs as in Eucraniini, (Fig. 9.2) to pre-prepared burrows in sandy soil where they are buried below the moisture line in the ground. The adults and presumably the larvae then feed on rehydrated dung or detritus (Scholtz 1989; Ocampo and Hawks 2006; Holter *et al*. 2009).

Fig. 9.1. *Pachysoma glentoni* (South Africa) dragging detritus to its burrow. (Photo Lena Stenseng).

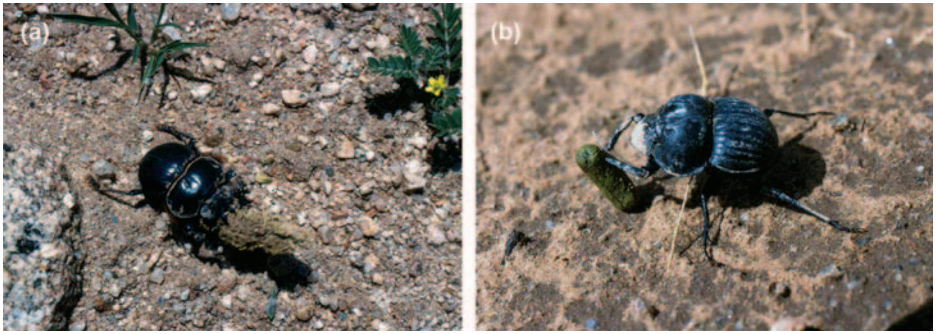


Fig. 9.2. (a) *Anomiopsoides* sp. and (b) *Glyphoderus* sp. carrying (a) a dung fragment, held with fore-legs and clypeus (b) a rodent dung pellet held in fore legs. (Argentina). (Photos Federico Ocampo).

CHAPTER 10

RESPIRATION AND WATER CONSERVATION

Most dung beetles fly strongly, a requirement for locating an ephemeral food source under conditions of often intense competition. Yet, despite the obvious advantages of flight ability for dung beetles, flightlessness is well documented in species living under particular sets of environmental conditions, and flightless species most commonly occur in desert regions, on high mountains, in forests and on islands (Scholtz 2000 – see Chapter 9). The environmental pressures contributing to the loss of flight have mainly been attributed to water- and energy-saving strategies, with the former the most important in desert regions, and the latter in cool or moist habitats. One of the characteristics of flightless beetles is the presence of a more or less sealed cavity under the fused elytra, the sub-elytral cavity into which the spiracles open. The physiological importance of the cavity has been the subject of considerable discussion by coleoptersists over the past 200 years. Some of these aspects are discussed below.

10.1 THE SUB-ELYTRAL CAVITY

The sub-elytral cavity (SEC) has been claimed to fulfil several functions in beetles. The first hypothesised function, and the one most thoroughly studied, is that most respiration take places through the spiracles that open into the SEC, which has also been hypothesised to have an atmosphere of high humidity, and consequently, breathing into the closed SEC, was proposed to lower the loss of respiratory water (Cloudsley-Thompson 1975; Crowson 1981; Zachariassen 1991). A second possible function of the SEC is that it allows the abdomen to extend upwards when expanded by the fat body or developing eggs (Halffter and Matthews 1966). A third is that the SEC of endothermically heated dung beetles forms an insulating air space which slows cooling after flight, and consequently, improves energy expenditure (Bartholomew and Heinrich 1978).

10.2 THE DISCONTINUOUS GAS EXCHANGE RESPIRATORY CYCLE AND WATER CONSERVATION

Respiratory airflow in insects is presumed to be from the anterior spiracles, where air is inspired, passed through the tracheae, and expired through the posterior spiracles. This causes fresh air to flow through the body (Chapman 1998). A similar pattern was proposed for flightless desert beetles, where the thoracic spiracles are used for inspiration and the sub-elytral spiracles for expiration (Ahearn 1970). Nicolson *et al.* (1984) proposed that the CO_2 that accumulates in the SEC is then expelled periodically through an opening created above the anus by lifting the elytra. This intermittent release of CO_2 results in the so-called discontinuous gas exchange cycle (DGC), which has been recorded in as many as 50 different species of insects, mostly ants and beetles (including several dung beetles – Chown *et al.* 2006; White *et al.* 2007).

The DGC is a cyclic discontinuity in external gas exchange which typically consists of three periods (Duncan and Byrne 2000; Chown 2002). The closed (C) period is when the spiracles are shut, which prevents both gas exchange and respiratory water loss. Oxygen levels in the tracheae drop, while CO_2 is largely buffered in the tissues and haemolymph. This is followed by the flutter (F) period, during which slight opening of the spiracles on an intermittent basis allows some normoxic O_2 uptake through the spiracles by diffusion and convection, but little CO_2 or water vapour is lost. The final period, the CO_2 burst (B) period, is triggered when the accumulation of CO_2 from respiring tissues causes some of the spiracles to open widely. This rapid unloading of CO_2 should minimise the time the spiracles are open and therefore reduce water vapour loss. Thus all periods, except the open period, are considered important to reduce respiratory water loss. It is well established that spiracular water loss in insects is high during activity as a result of elevated metabolic demand (Chown 2002), but the importance of respiratory water loss during periods of inactivity by way of the discontinuous gas exchange cycles, is contentious (Chown *et al.* 2006; White *et al.* 2007).

DGCs have been studied in a number of southern African dung beetle species, and all of the studies have attempted to determine the possible importance of respiratory water loss during the open and flutter phases (i.e. testing the hygric hypothesis – see below). The first of these studies (Lighton 1985) demonstrated that the south-west African *Pachysoma hippocrates* uses a discontinuous ventilation system. However, Lighton considered the species to be an active ball-roller requiring a respiratory system selected "for strength and high, consistent, work output during rolling and burying of dung balls" (Lighton 1985) so his assumptions should be treated with caution. Since that study Frances Duncan and Marcus Byrne in South Africa have studied one flightless species

(*Circellium bacchus*) in detail (Duncan 2002; Duncan and Byrne 2000; 2002; Byrne and Duncan 2003) and also compared DGCs in several other winged and wingless species (Duncan and Byrne 2005). Also in South Africa, Davis and colleagues recorded and compared DGCs in a number of species (Davis *et al* 1999; Davis *et al*. 2000; Chown and Davis 2003).

Duncan and Byrne (Duncan 2002; Duncan and Byrne 2000, 2002; Byrne and Duncan 2003) recorded, for the first time in a beetle (*C. bacchus*), that airflow during respiration is, in fact, predominantly anterograde (or tidal) when the beetles are at rest. They recorded that the DGC in *C. bacchus* was found only at one, anterior, mesothoracic spiracle (outside of the SEC), and it showed only the closed and burst periods (Fig. 10.1). The flutter period was largely reduced or absent. They detected no large, intermittent CO_2 bursts from outside the elytral case, which would correspond to the lifting of the elytra to expel accumulated CO_2. Ninety per cent of the CO_2 was expelled through the mesothoracic spiracle and most of the water lost during respiration was also via this spiracle (Duncan 2002).

In a subsequent detailed study of respiration, the SEC, and its role in water retention in a dung beetles, Byrne and Duncan (2003), cogently discussed the processes involved in *C. bacchus*. They drilled holes in beetles' elytra and sampled gases at different stages of the DGC and were so able to measure, by infrared gas analysis, the role of the sub-elytral spiracles in respiration. They simultaneously measured respiratory gas exchange from the anterior and posterior half of beetles at rest. When they continuously sampled gases from the SEC, they observed a reversal of the pattern of CO_2 emission they previouly recorded from the mesothoracic spiracle in which the majority of CO_2 emitted was from the sub-elytral spiracles (Fig. 10.2), which clearly exhibited a flutter period before the burst period. They concluded that: gas emission from the SEC is synchronised to that of the mesothoracic spiracle; that the sub-elytral spiracles play an active part in respiration of beetles at rest; and strongly suggested that the SEC has a role in respiration in accordance with its hypothesised function as a water conservation adaptation (Byrne and Duncan 2003). The total CO_2 emitted that they recorded from the two halves of a beetle was similar to that recorded from a single beetle. They found no evidence to suggest that the beetles lift their elytra at any stage to expel CO_2.

Circellium bacchus has an SEC tightly sealed by microtrichia (Byrne and Duncan 2003), in common with many other groups of flightless beetles (Crowson 1981). At any time the air inside the SEC was high in CO_2 and water vapour, while the concentration of O_2 was lower than atmospheric (Table 10.1). [Although in a recent, unpublished study, Frances Duncan, personal communication, found that the SEC is not completely air-tight but appears "selectively leaky"]. The air was kept at high humidity regardless of the stage of the DGC cycle at the mesothoracic spiracle. Their data (Byrne and Duncan 2003) indi-

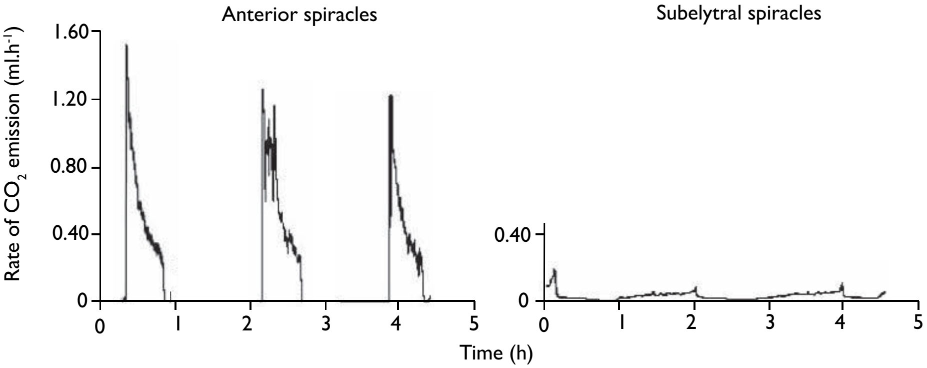


Fig. 10.1. Recordings of CO2 emissions of *Circellium bacchus* (mass 7.122g) from the anterior and posterior spiracles when air was drawn through a respirometer chamber and over the elytral case. (After Byrne and Duncan 2003).

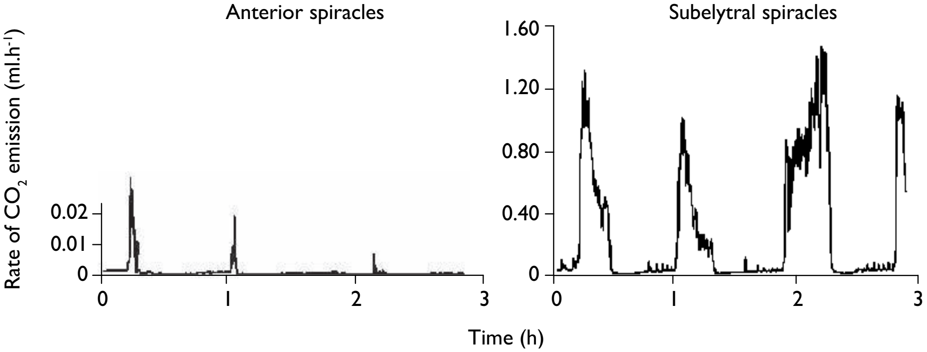


Fig. 10.2. Recordings of CO2 emissions of *Circellium bacchus* (mass 7.122g) from the anterior and posterior spiracles when air was drawn through a respirometer chamber and over the elytral cavity i.e. over the the subelytral spiracles. (After Byrne and Duncan 2003).

cated that should the elytra be opened, the proportional increase in water lost would be approximately 74%. By restricting CO_2 exchange with the atmosphere to only one mesothoracic spiracle, which is only open for short periods during the burst phase, water loss is minimised. The burst period of the mesothoracic spiracle was preceded by the burst period of the sub-elytral spiracles, but with considerable overlap. Very little CO_2 was recorded outside the elytra, further emphasising the almost airtight nature of the seal. Therefore CO_2 must be moved forward through the body as demonstrated for O_2 by Duncan and Byrne (2002), and be expelled by the mesothoracic spiracle during the burst period. The mesothoracic spiracle is then shut during the closed period, while

Table 10.1. Composition of air within the sub-elytral cavity, when sampled at different times during the discontinuous gas exchange cycle of CO_2 emission from the meso-thoracic spiracle. (After Byrne and Duncan 2003).

Period of DGC cycle	***N***	**Volume of CO_2 (µl.g $^{-1}$)**	**Maximum V_{CO2} (µl.g $^{-1}$)**	**Percentage increase in water loss rate* (%)**
Before burst period	9	16.19 ± 6.98[a]	211.46 ± 72.96[a]	75.6 ± 8.4[a]
During burst period	11	18.71 ± 10.27[a]	269.19 ± 141.86[a]	75.9 ± 4.4[a]
After burst period	18	8.24 ± 5.38[b]	97.5 ± 34.01[b]	71.2 ± 1.8[a]

Values represent means ± S.D. *N* = number of samples taken during each period from recordings from five different beetles. Values in the same column followed by the same letter are not significantly different at $P = 0.05$.
*Percentage increase = (highest water loss rate sampled from sub-elytral cavity – water loss rate sampled from outer elytral case) / (highest water loss rate sampled from subelytral cavity) x 100.

the subelytral spiracles progress from being closed to rapid fluttering. The flutter period lasts about 20 minutes, during which O_2 diffuses from the SEC to the tracheal system. However, this introduces a complexity to the process – for O_2 to continue diffusing into the tracheae it needs to be replenished in the SEC by atmospheric oxygen, which necessitates allowing oxygen in but retaining water vapour and CO_2. Retention of high levels of CO_2 [although O_2 may enter due to the leaky SEC – F. Duncan, personal communication] in the SEC then serve a dual function: CO_2 can be sequestered in the SEC which increases the overall CO_2 capacity of the body, which in turn lengthens the DCG period and reduces respiratory water loss, and; contributes to a diffusion gradient that draws atmospheric O_2 into the SEC. Water vapour in the SEC also contributes to water conservation during the flutter period, by reducing its concentration gradient between the tracheae and ambient air.

In a later study, Duncan and Byrne (2005) compared respiratory patterns in three species of dung beetles from other regions of South Africa, with those recorded for *C. bacchus* (distributed along the south-eastern seaboard). These were two flightless species from the arid west coast (*Pachysoma striatum* and *P. gariepinum*) and one winged species from the mesic savanna interior of the country (*Pachylomera femoralis*). *C. bacchus* belongs to the Canthonini, the other three species to the Scarabaeini. The authors predicted that the species from similar environments would show similar respiratory adaptations, and that these would be linked to water conservation strategies.

Duncan and Byrne (2005) found that the basic CO_2 release pattern for the species differed: *Pachylomera femoralis*, *Pachysoma striatum* and *P. gariepinum* all emitted CO_2 using a combination of both the mesothoracic and sub-elytral spiracles, while *C. bacchus* used the anterior spiracles almost exclusively (Fig. 10.3). However, the relative contribution of the mesothoracic spiracles ranged from about 80% in *C. bacchus*, to 46% in *P. striatum*, to 20% in *P. gariepinum* and finally, to only about 7% in *P. femoralis* (Table 10.2). Consequently, the inverse applies to CO_2 emitted from the sub-elytral spiracles.

The authors concluded that their study supported the assumption that dung beetles from distant, yet similar, physical environments, have similar respiratory patterns involving increased use of the mesothoracic spiracles for CO_2 emission, and that the trend grades from mesic to arid habitats, but Duncan and Byrne (2005) were equivocal about these mechanisms being as a consequence of an adaptation for water retention.

Table 10.2. Comparison of the mean rate of CO_2 emission from the mesothoracic spiracles and elytral case in four species of dung beetles (*Pachylomera femoralis*, *Pachysoma gariepinun*, *P. striatum* and *Circellium bacchus* (mean ± S.D.). *N*, number beetles measured. Means in the same row, followed by the same letter are not significantly different ($P < 0.05$; ANOVA with LSD range test). (*From Duncan and Byrne 2002; rest of data after Duncan and Byrne 2005).

Species	***P. femoralis***	***P. gariepinum***	***P. striatum***	***C. bacchus****
N	**5**	**7**	**6**	**6**
Mass (g)	5.117 ± 0.62^{a}	1.716 ± 0.35^{b}	0.742 ± 0.20^{b}	7.427 ± 1.86^{c}
Rate of CO_2 emission ($\mu l\ h^{-1}$)				
Mesothoracic spiracles	35.53 ± 28.7^{a}	24.88 ± 19.2^{a}	27.68 ± 19.7^{a}	258.2 ± 118.2^{b}
Posterior spiracles	468.39 ± 97.13^{a}	121.45 ± 75.3^{b}	28.56 ± 11.0^{b}	119.5 ± 123.6^{b}
Ratio of CO_2 emission				
Mesothoracic: elytral case	0.083 ± 0.07 (range 0.019 – 0.22)	0.31 ± 0.3 (0.11 – 1.06)	1.56 ± 2.1 (0.22 – 5.9)	3.47 ± 2.0 (042 – 6.81)
% total CO_2 emitted through mesothoracic spiracles	7.31 ± 6.5	20.07 ± 15.05	46.23 ± 22.9	79.4 ± 4.48
Frequency (mHz)	0.73 ± 0.3^{a}	0.33 ± 0.2^{b}	0.42 ± 0.2^{b}	0.26 ± 0.05^{b}
DGC cycles per hour	2.6 ± 1.1^{a}	1.2 ± 49.80.6^{b}	1.5 ± 0.8^{b}	0.94 ± 0.2^{b}
Total rate of CO_2 emission				
($\mu l\ h^{-1}$)	503.92 ± 87.5^{a}	146.03 ± 87.2^{b}	56.24 ± 11.5^{b}	377.74 ± 138.7^{c}
($\mu l\ h^{-1}\ g^{-1}$)	98.66 ± 13.2^{a}	80.53 ± 39.6$^{a,\,b}$	80.19 ± 25.4$^{a,\,b}$	51.52 ± 18.12^{b}

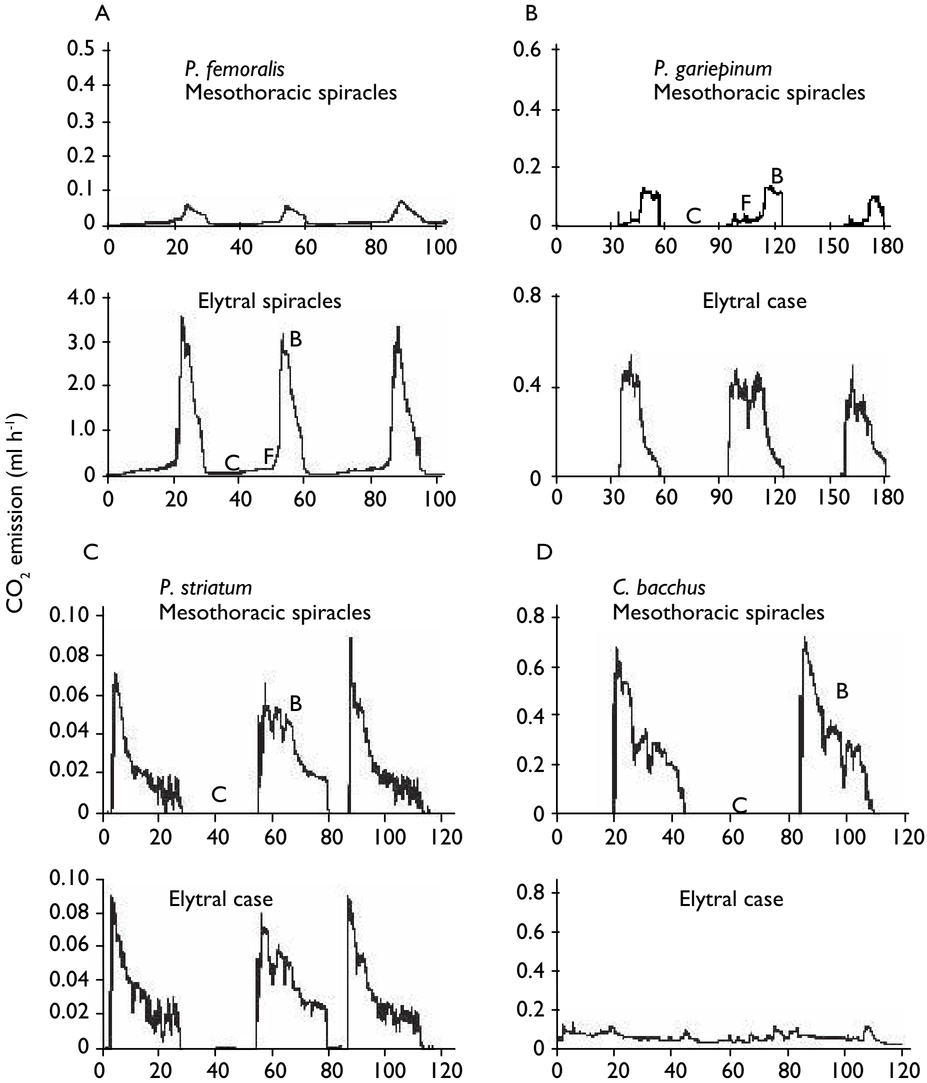


Fig. 10.3. Recordings of CO2 emission from the anterior mesothoracic spiracles and the posterior elytral case in four species of dung beetles. (A) *Pachylomera femoralis* (5.530g), (B) *Pachysoma gariepinum* (1.475g), (C) *P. striatum* (0.487g) and (D) *Circellium bacchus* (4.859g).

Note the different scales on the axes. C, closed period; F, flutter period; B, burst period. (After Duncan and Byrne 2005).

10.2.1 Hypotheses of the genesis of discontinuous gas exchange cycles

Although various studies have provided evidence that the DGC in insects is maintained for adaptive reasons, the evolutionary origin thereof remains unresolved (White *et al.* 2007). The DGCs in different insect groups have clearly evolved polyphyletically and various dung beetle groups could be under pressure to develop DGCs independently from one or several selective forces.

Several hypotheses have been postulated to explain the evolution of the discontinuous gas exchange cycle in insects, but only two have been considered in dung beetles, while the third, though untested, is also worth considering in dung beetles. The first has been termed the hygric hypothesis (see Chown *et al.* 2006; White *et al.* 2007). The second hypothesis is that the main driving force for the evolution of the system may be to compensate for anoxic and hypercapnic conditions experienced by geophilic insects – the chthonic hypothesis (or elaborated as the hygric-chthonic hypothesis – see Chown *et al.* 2006 and White *et al.* 2007 for details). The quaintly-termed "strolling arthropods hypothesis" suggests a third possible process – evolution of DGCs to ensure irregular spiracular opening to exclude parasites.

10.2.1.1 Hygric hypothesis

Respiration by wingless beetles with a sealed SEC has long been thought to be intimately associated with water conservation strategies. Expelling air into the SEC was assumed to be an adaptation to arid areas by wingless beetles, because the air in the cavity is maintained at high humidity, so water lost by respiration would be minimised because the tracheae are not exposed to dry air. The discovery of discontinuous gas exchange cycles much later was thought to be the mechanism by which resting insects could restrict respiratory water loss. This led to the formulation of an hypothesis which was later termed the "hygric hypothesis" (see Chown *et al.* 2006 for a review of the origin and history of the hypothesis). A detailed analysis of the different models by White *et al.* (2007) supported it as the most likely model of the evolution of DGCs. It is also the hypothesis that enjoys the most support amongst dung beetle researchers. White *et al.*'s (2007) best model incorporated phylogeny of the insects studied, and included the significant effect of habitat ambient temperature, a non-significant effect of habitat precipitation, and an important interaction between temperature and precipitation.

10.2.1.2 Chthonic hypothesis

Most adult dung beetles spend a large part of their active periods either submerged in wet dung, or in a burrow under the soil where an atmosphere low in oxygen and with excessive carbon dioxide is likely, although CO_2 travels readily through sand (F. Duncan personal communication), so this may not apply to all species under all conditions. Although intuitively appealing as an evolutionary model for DGCs in dung beetles at rest in hypoxic or hypercapnic conditions in underground burrows, the second hypothesis of the evolution of the DGC, the chthonic origination hypothesis (Lighton 1996) hasn't been seriously considered. Lighton and colleagues (see Lighton 1996) proposed that the DGC may have originally evolved to enhance gas exchange efficiency under hypoxic and hypercapnic conditions as an alternative to continuous respiration and possible excessive loss of respiratory water, but Lighton (1996) concluded that there are insufficient data to support this model as the origin of the DGC.

Although studies of respiration by scarabaeine dung beetles under conditions of low oxygen and high CO_2 concentrations are lacking, Holter and colleagues have studied respiration in Aphodiinae in Denmark which live under broadly similar conditions to many scarabaeine species, so comparisons between them are reasonable.

Intense metabolism of dung microflora may lower the O_2 in cavities in the dung to 1-2% and elevate the CO_2 to 20 – 30% (Holter 1994; Holter and Spangenberg 1997). Methane may constitute 30 – 50% of the same air, which increases the anoxic conditions in the dung even more. Conditions close to the surface or at the bottom of the pat, however, are less extreme, with higher levels of oxygen and less carbon dioxide and methane (Holter 1991). Conditions in underground burrows excavated by dung beetles are also likely to be extremely hypoxic and hypercapnic, since the entrance to the burrows is usually plugged with soil and some individuals, such as brooding females, may spend months inside them.

Chown and Holter (2000), working on the aphodiine, *Aphodius fossor*, in summer in Denmark, set out to test whether the DGC in this species may have originated in response to hypoxic and hypercapnic conditions, rather than as a strategy to reduce water loss. *Aphodius fossor* is a widespread Holarctic species inhabiting fresh cattle dung. In Denmark the species is most active in late spring and early summer. They fly mostly in the evening and at night when ambient humidity is high. When foraging and breeding they occur in dung pats with moisture content of around 80% and high microbial activity, with resultant lowering of the O_2 concentration and increasing the CO_2 concentration.

Chown and Holter (2000) experimentally recorded respiration rate and gas exchange characteristics for *A. fossor*, first in ambient air, after which the O_2 percentage was progressively lowered, and the experiments repeated at four lower values. They recorded that under normoxic conditions gas exchange in *A. fossor* was characterised by typical DGCs. As ambient O_2 concentration declined, mean CO_2 release rate remained constant, except at the lowest level (2.84% O_2), at which CO_2 release rate increased significantly, and by approximately 23% over the mean CO_2 release rate value ($\dot{V}CO_2$) combined over all the higher O_2 concentrations (Table 10.3). As the O_2 concentration declined, DGC frequency increased and duration declined (Table 10.3). The CO_2 release rate declined in importance during the open-phase of the DGC as a consequence of declining open-phase volume and duration, while the rate of F-phase CO_2 release increased, despite declining F-phase duration.

Cuticular water loss by *A. fossor* under normoxic conditions was 95%, whereas respiratory water loss made up the remaining 5%.

Chown and Holter (2000) concluded that, in response to declining oxygen levels, *A. fossor* switches from a DGC pattern to one of continuous diffusion / convection, and although this is likely to lead to increased water loss rates, the loss is unlikely to be severe. This is because the species loses most of its water through the cuticle rather than via respiration, and furthermore, it lives in a virtually saturated environment where lost water is easily replenished. However, they were unable to explain from their data why *A. fossor* exhibits a DGC at all,

Table 10.3. V_{CO2}, discontinuous gas exchange cycle (DGC) duration and frequency, and open phase peak height in *Aphodius fossor* under normoxic and declining ambient O_2 concentrations.

O_2 concentration (%)	*N*	V_{CO2} (ml.g $^{-1}$ h^{-1})	DGC period (s)	DGC frequency (mHz)	Open phase peak height (ml.g $^{-1}$ h^{-1})
20.47	10	0.165 ± 0.007	999.4 ± 115.4	1.146 ± 0.144	0.673 ± 0.028
16.55	9	0.203 ± 0.015	514.6 ± 69.9	2.271 ± 0.312	0.659 ± 0.041
11.28	10	0.195 ± 0.014	285.0 ± 16.7	3.615 ± 0.208	0.468 ± 0.032
6.13	10	0.203 ± 0.016	218.4 ± 21.9	5.080 ± 0.568	0.406 ± 0.031
2.84	10/3[a]	0.236 ± 0.013*	216.2 ± 49.8	5.275 ± 0.974	0.307 ± 0.024

[a] Sample size at 2.84% was 10 for V_{CO2} and 3 for all other variables.

An asterisk denotes a significant difference from all other values at the 5% level using a Tukey HSD test ($F_{2,42}$ = 4.171, P = 0.006). (After Chown and Holter 2000).

since water retention appears relatively unimportant, and the DGC is not used to enhance gas exchange under hypoxic / hypercapnic conditions, the basic tenet of the chthonic hypothesis. They suggested instead that the DGC may be the default state of a system regulated by two interacting feedback loops that regulate a single function when demands are absent. Chown *et al*. (2006) proposed a new hypothesis, the "emergent property hypothesis" to explain the situation in *A. fossor*, and stated it as follows: "DGCs are a non-adaptive outcome of interaction between the O_2 and CO_2 set points that regulate spiracle opening and closure".

10.2.1.3 Strolling arthropods hypothesis

Early beetle researchers (see Crowson 1981) postulated that migration of the metathoracic and abdominal spiracles to positions beneath the elytra in fossorial beetles, and the evolution of various spiracular structures such as sieve plates, may have evolved to prevent dust and/or parasites from entering the tracheal system.

The strolling arthropods model is appealing because of the preponderance of mites, including parasitic mites, which live in dung and soil and are a potential threat to invade open spiracles of dung beetles (see Halffter and Matthews 1966 for lists of mites associated with dung beetles). Tracheal mites in honey bees have been shown to reduce the safety margin for oxygen delivery in flying bees (Harrison *et al.* 2001), so similar effects on dung beetles are quite probable.

10.3 WATER LOSS IN DUNG BEETLES

As discussed above, water retention during respiration is inextricably linked to respiration itself, and to the function of the SEC during respiration in dung beetles, although the interrelationships between gas exchange and water balance in insects remain controversial (Chown and Davis 2003). Furthermore, the significance of the contribution of respiratory transpiration to total water loss (which includes cuticular loss) in insects is also contentious (Chown and Davis 2003). Those studies that have examined this proportional contribution mostly concluded that respiratory water loss is low (3-15% of the total), and bears little relationship to the physical environment in which the insect occurs (references in Chown and Davis 2003). Duncan (2002) and Zachariassen and colleagues (e.g. Zachariassen 1996), however, working mainly on flightless beetles from arid areas are of the opinion that respiratory water loss is nevertheless an important proportion of total water lost and that adaptations to meliorate this loss would be selected for.

Chown and Davis (2003) studied water loss in five South African scarabaeine species known to exhibit DGCs. Two of the species are flightless, arid, west coast endemics (*Pachysoma gariepinum* and *P. striatum*, the same species studied by Duncan and Byrne 2005 – see above). The other three are members of the genus *Scarabaeus* and were collected from lowland savanna (190 m asl – *S. galenus*), highveld savanna (1260 m asl – *S. rusticus*), and montane grassland (1900 m asl – *S. westwoodi*). The authors tested for: the proportional contribution of respiratory water loss to total transpiration; the relationship between metabolic rate and respiratory water loss rate; and the contribution of variation in components of the DGC to water conservation. In all the beetle species studied, variation in respiratory water loss was related to variation in total water loss, and both cuticular and respiratory water loss contributed significantly to total water loss rate. Variation in spiracular water loss rate was best explained by a combination of CF-period duration, B-period duration and $\dot{V}CO_2$. Decreasing rates of water loss were associated with an increase in the duration of the CF-period, a decline in the B-period, and a decrease in metabolic rate, thus providing strong support for the hypothesis that alteration of metabolic rate can be used by insects to control change in water loss rate (references in Chown and Davis 2003). Chown and Davis' (2003) results also provided support for the hypothesis that modulation of DGC characteristics and metabolic rate can be used to change water loss rates, and that the changes imply a relationship to changes in environmental water availability. In other words, species from arid areas have lower metabolic rates, shorter B-periods, and longer CF-periods than species from more mesic environments, thus strongly implying that the DGC is an adaptation for water conservation.

10.4 WATER CONSERVATION IN DUNG BEETLES

Most adult dung beetles feed on the liquid components of fresh dung which may consist of up to 85% water by weight so presumably water is not a limiting factor for most species. The situation in desert species, however, is vastly different. They feed on dry dung or detritus under dry conditions so water is undoubtedly a limiting factor for species such as those belonging to the genus *Pachysoma*.

The only species in which water acquisition by dung beetles in desert areas has been studied is in *P. glentoni* (Holter *et al.* 2009; and unpublished). Its possibilities of gaining water will be briefly discussed. Although remarkable examples of nocturnal drinking based on condensed fog are known in tenebrionid beetles from the Namib (Seely 1979), this is not an option for *P. glentoni* whose above ground activity is in the middle of the day when all condensed water has evaporated. Other sources of liquid water are not available. Water absorption from air in their rather dry underground chamber seems equally improbable. In beetles, this ability is usually associated with a so-called rectal (cryptonephric) complex (e.g. Chown and Nicolson 2004), particularly known from tenebrionid larvae. However, no sign of this structure in *P. glentoni*'s hindgut was found (P. Holter, University of Copenhagen, personal communication), leaving water uptake by feeding and metabolic water as the remaining possibilities. As to feeding, the approximately 0.5 g of water lost from the detritus (see Table 6.2) is the only available estimate (probably a maximum value) of the amount potentially extracted by the beetle. Most of the assimilated 0.66 g organic matter was probably carbohydrate yielding 0.56 g water per g metabolised food (e.g. Willmer *et al*. 2000 in Holter *et al*. 2009). Lipids and proteins, with higher and lower water yields, were also present, but use of the carbohydrate factor for the entire assimilation means that roughly 0.4 g metabolic water was produced. If so, the total weekly water gain was 0.4-0.9 g.

The weekly water uptake of *P. glentoni* is probably somewhere between 0.4 and 0.9 g. What makes survival of a large (4-5 g) beetle in an arid ecosystem possible with this modest water supply? As food collection seemed to take only a few hours, the animals spend, say, 95-98 % of the time underground at a moderate, and probably constant (Seely and Mitchell 1987), temperature of about 20°C. As the water percentage of stored detritus did not change, the atmosphere may be near-saturated. Apart from feeding, activity is probably low, and the flightless beetles have practically no wing muscles that must be metabolically maintained (e.g. Chown and Nicolson 2004). Moreover, *P. glentoni* may, like its congeners *P. striatum* and *P. gariepinun*, use a water-saving ventilation pattern (Duncan and Byrne 2005) while underground. All this is likely to minimise water loss by respiration and cuticular evaporation.

CHAPTER 11
SEXUAL SELECTION IN DUNG BEETLES

Sexual selection has two basic components, mate choice and competition for mates (Trivers 1972). In general, mate choice occurs more often in females than in males, and the competition for mates is more intense among males than among females. This sexual asymmetry is considered to be because parental investment is usually larger in females than in males (Trivers 1972). Males generally invest relatively little energy in reproduction because of the low energetic cost of sperm production and their mostly minor contribution to care of offspring. They are, therefore, limited by the number of copulations only, and increase their fitness by increasing mating frequency. Females, on the other hand, invest heavily in egg production, gestation, lactation, brood care, or combinations of these and are expected to enhance their reproductive fitness by selecting superior males to fertilize her eggs (Trivers 1972). This discrimination may be based on either direct benefits, such as protection, or in response to food provided by the males, or on indirect benefits for her offspring, such as parental care or good quality genes (Le Roux *et al.* 2008).

Mate choice can be divided into pre- and post-copulatory mate choice. Pre-copulatory mate choice consists of two mechanisms – active female choice and competition between males, with the outcome of the latter sometimes resulting in passive female "choice". Active choice of a potential suitor among several contestants by the female entails discrimination between them based on some observable morphological or behavioural trait that emphasises their quality. Of these, body size and various body structures such as antlers and horns, have been shown to be important in female choice (see references in Emlen 1997a). Male-male competition occurs when males contest for reproductive access to the females. This often takes the form of fighting and body size and / or horn size are important determinants of the outcome of a contest and successful access to the female. The good-genes hypothesis (Zahavi 1975), predicts that only males of superior genetic quality will be able to develop and maintain exaggerated features that enable females to assess male quality.

Post-copulatory mate choice requires selection after mating has occurred, and involves cryptic female choice and sperm competition (Le Roux *et al.* 2008, and references therein; Simmons, Emlen and Tomkins 2007, and references therein). Cryptic female choice may involve processes such as the interruption of copulation, differential sperm retention, abortion of a particular embryo or preferential allocation of parental care (Birkhead 1998). Females may also assess the quality of a copulating male by assessing the size of his penis – males with bigger reproductive organs theoretically translate to superior partners (Eberhard 1985).

Dung beetles have been the subject of numerous sexual selection studies, of which most have revolved around male-male competition between horned and hornless morphs, and larger- or smaller-bodied individuals. Horns are almost exclusively restricted to tunnelling species, and it is these that have been subjected to most study. It is mostly males that bear horns, although in some groups they may be borne by males and females, and occasionally, they may be found exclusively in females. Examples of early studies were by Otronen (1988), Cook (1990) and Rasmussen (1994). These were followed by a number of papers by Douglas Emlen and various collaborators (mostly Hunt, Moczek and Simmons, but they have also independently, and jointly, published on various aspects of sexual selection in dung beetles) and interest in the field continues to develop (e.g. Le Roux *et al.* 2008; Parzer and Moczek 2008; Pomfret and Knell 2008).

Horns are found in males of some genera, at least, of all groups of tunnelling dung beetles, whereas rollers very seldom bear horns, and have been subjected to fewer studies of sexual selection than have tunnellers (Sato and Hiramatsu 1993; Le Roux *et al.* 2008). They are widespread in Coprini, Phanaeini, Oniticellini and Onthophagini. Although the function of these has only been studied in a small fraction of these groups, the general patterns in those studied appear to be broadly similar (Emlen and Philips 2006; Oniticellini – Lailvaux *et al.* 2005; Pomfret and Knell 2006, 2008; Onthophagini – Cook 1990; Hunt and Simmons 1998; Moczek 1998; Phanaeini – Otronen 1988; Rasmussen 1994). Females usually excavate the breeding tunnel and provision the burrow with dung (sometimes assisted by the male). Large-horned males (= guards) guard the burrow entrance against intruding males, while small-horned males use a sneaking tactic (= sneaks) to access the females, which are mostly unselective in their acceptance of mates. There is an obvious mechanical advantage to horned males being able to block a tunnel and keep rivals at bay in order to have exclusive access to the female behind it (Emlen 2000). Because success in these encounters depends on horn size relative to that of rival males, the population they form part of probably experiences continuous directional sexual selection for increased investment in weapons (Emlen *et al.* 2005b). Males of these species are likely to benefit from raised structures that provide traction or add leverage during contest, or simply increase the circumference of the beetle to physically block the tunnel. And, because larger or longer horns are more effective than smaller or shorter horns for fighting rivals and blocking tunnels, pressure to enlarge these is likely to increase.

Horns, however, are physiologically expensive to produce and physically difficult to bear, but males with horns undoubtedly have increased reproductive access to females, so the reproductive benefits gained by having large horns presumably outweigh the costs of producing them. Growth of horns prolongs beetle development, with concomitant increase in larval mortality, for example, from soil nematodes (Hunt and Simmons 1997). Furthermore, because developmental resources are finite, shunting nutrients from other areas to favour horn development impedes development of the former (Nijhout and Emlen 1998). Species with large horns often have smaller than normal structures that develop adjacent to them, principally antennae and eyes but also testes and wings (Kowano 1997; Nijhout and Emlen 1998; Emlen 2000, 2001; Knell, Pomfret and Tomkins 2004; Emlen *et al.* 2005b; Tomkins *et al.* 2005; Simmons *et al.* 2007). Horns developing on the thorax reduce development in wings, and consequently, flight capability; those developing on the middle or front of the head probably impact on antennal development and olfactory capabilities; and those developing on the back of the head reduce the size of eyes and likely impair vision. However, males must still be able to mate successfully, see, smell and fly in order to functional normally.

Sperm competition, which is a special form of sexual selection, was defined by Parker (1970), as competition among the ejaculates of two or more males for the fertilization of a female's ova. It is now widely recognised as a pervasive force of sexual selection (Simmons *et al.* 2007). Multiple matings and sperm storage in insects have favoured the mixing and preservation of sperm which promote sperm competition (Parker 1970). In insects, the sperm that ultimately fertilize the female's eggs may range from that of the first mated male to the last, with some degree of sperm mixing. However, the sperm of the last male to mate usually achieves more than 50% of fertilization (Simmons 2001). In species with high paternal investment, males should have evolved adaptations to reduce sperm competition (Trivers 1972).

Although monogamy is uncommon in insects, pair-formation is common amongst many groups of dung beetles. Males of these species invest varying amounts of energy in mate-guarding to prevent females from mating with other males, and brood care, which ranges from helping to collect food, forming and rolling brood balls, and even to spending long periods in the nest with the female and brood.

11.1 SEXUAL SELECTION IN TUNNELLERS

11.1.1 Phanaeini

Otronen (1988) studied the very large carrion-feeding *Coprophanaeus ensifer* in Brazil. The species is unusual in that both males and females bear large head horns and several processes in a generally concave pronotum (Otronen 1988).

Otronen (1988) tested: how the beetles use their horns; whether males and females use their horns in a similar way; whether anything in their biology could explain horn presence in females; whether different-sized individuals behave in different ways, and; that large size differences might indicate alternative mating strategies.

There was large variation in body and horn size in both sexes although body size did not differ between males and females. Horn size correlated well with individual size in males and females, and although relative horn size (horn length divided by elytral width), was larger in males than in females (Mann-Whitney *U*-test, $z = 3.06$, $P < 0.01$), the increase in horn size with body size did not differ between males and females.

The author observed three different types of fights between individuals, male-male, male-female and female-female. Fights between males involved considerable pushing and lifting and the bigger male always won. Fights between males and females were usually not reciprocally aggressive, one of the combatants (of either sex) being fairly passive. In fights between females, 51.5% of the fights were won by the largest female, but 33% ended without a clear result indicating less motivation amongst females than males to fight.

So, why large horns in *C. ensifer* females? Otronen (1988) argued that because the species is very large (up to about 60.0 mm long) and breeds in a scarce and very ephemeral resource, large amounts of the resource are required for successful reproduction. This necessitates females being able to defend the resource against other females, and if already mated, against other males (but see below under "Onthophagini" for other interpretations of possible reasons for horns in females). Males, in addition to defending a food resource, need to fight for access to females. This extra component in fighting behaviour in males would select for relatively larger horns in males than in females. The author found no evidence of discrete male size compartments with different reproductive strategies.

In a study of another phanaeine species, *Phanaeus difformis*, Rasmussen (1994) investigated the influence of horn and body size on the reproductive behaviour of the species. As with the previous species discussed, males and females of *P. difformis* are horned, but female horns are shorter and much less variable than those of males. In contrast to the previous species, however, female *P. dif-*

formis are, on average, significantly larger than males (Rasmussen 1994). Horn size is significantly correlated with body size in both sexes.

When males and females encountered other individuals during burrow construction and provision, same-sex encounters resulted in conflict, whereas encounter between members of the opposite sex usually led to pairing. Male-male contests were mostly won by larger-bodied males, but if they were of roughly equal size, the one with the longest horn invariably won (17 *vs* 3; Sign test, $P < 0.05$).

Females defended their burrows from other females attempting to steal dung fragments from the burrow, or from females attempting to take over the burrow. Larger females were more likely to win encounters than smaller females although the effect of body size on the outcome of female-female contests was weaker than for male-male contests (52 *vs* 34; $x^2 = 3.77$, $P = 0.05$) (Rasmussen 1994).

Rasmussen's (1994) study was the first to record that one of two discrete male morphs in horned beetles has a "sneaking" reproductive strategy. The phenomenon was subsequently studied by various other authors, most notably Emlen, who elegantly elaborated, in various papers, on the occurrence of the two discrete forms (guards being the other) and their very different reproductive strategies.

11.1.2 Onthophagini

Most of the published studies of various aspects of sexual selection have considered members of the Onthophagini (*Onthophagus*). There are probably several reasons why this is so: it is the largest tribe and its members are fairly ubiquitous; the species are small and reproductive episodes are relatively short; some of the species are widely distributed across different biogeographical regions, making comparisons possible; and many species are typically r-selected, breeding often. Furthermore, the presence of two discrete male morphs (horned and hornless) with different reproductive behaviours is common amongst the species.

Horn size is determined by the amount of food available to the developing male larva – larvae destined to grow horns need more food than those that aren't, and the developmental switch between horn growth and hornlessness occurs abruptly around a threshold body size (Emlen 2000). (See Fig. 11.1).

Emlen *et al*. (2005b) undertook a molecular phylogenetic analysis, using partial sequences from four nuclear and three mitochondrial genes of 48 species of Onthophagini, from all of the geographical regions where they occur. They then used these data to test for the evolutionary origin of horns, and to characterize their evolutionary radiation. Although they sampled only about 2% of the world's species of Onthophagini, they recorded a staggering minimum of 25 separate gains and losses of different horn types at five developmental locations that they identified in five classes (see section on Morphology). They eloquently explained this extra-ordinary lability of these exaggerated structures in terms of sexual selection and ecology.

Emlen *et al.* (2005b) hypothesised that a horn extending from the base of the head (the vertex) of males was ancestral to this genus, and that their data suggested multiple losses of these horns and several possible regains. They postulated that this type radiated at least seven times into different forms, and that these subsequently radiated into several more (see Fig. 5.5). Their most parsimonious reconstruction of horns on the thorax suggested that the central horns had evolved independently nine times, and the lateral horns, twice. Apparently, once additional horn types were acquired, the ancestral horn type was sometimes lost, but tended to occur only after additional, alternative weapons had been gained. Their combined data suggest a total of 25 changes in the physical location of horns, 15 gains of novel horn types and one regain of the ancestral head horn.

Emlen *et al.* (2005b) speculated on the possible environmental pressures that may have selected for horns in males, and predicted that increasing popu-

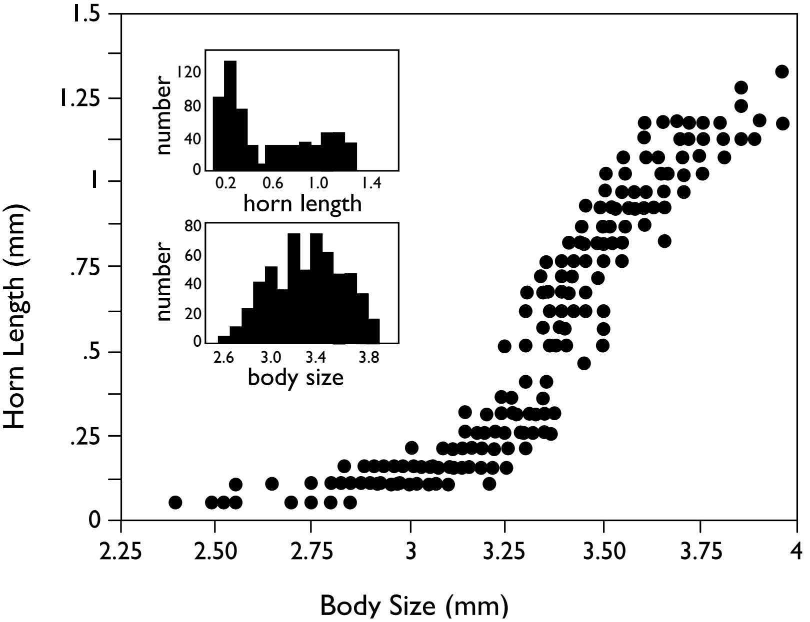


Fig. 11.1. Scaling relationship between horn length and body size (prothorax width) for 500 male *Onthophagus acuminatus* from Panama. The sigmoidal relationship (top) is associated with a bimodal frequency distribution of horn lengths in natural populations and separates males into hornless and horned adult shapes. (Based on Emlen 2000).

lation density would affect the numbers of encounters between rival males, and consequently, the intensity of natural selection for weapons. They analysed independent contrasts of continuous horn traits, and found that total horn number and total horn length were significantly correlated with evolutionary increase in population density (horn number *vs* population density: $r = 0.448$, $F = 10.545$, $P = 0.002$, $N = 43$ contrasts; horn length *vs* population density: $r = 0.362$, $F = 29.518$, $P = 0.000$, $N = 29$ contrasts). Then, using high and low density as separate two-state characters, they tested for correlations with gains and losses of specific horn types. They found that gains of thoracic horns were positively correlated with high population densities (concentrated change test: seven of 11 gains, $P = 0.003$), but that gains of head horns were not (one of five gains, $P = 0.762$). Emlen *et al.* (2005b) postulated that only the ancestral horn type had been lost (nine separate times), and that these losses were correlated with behavioural shifts from diurnal to nocturnal activity (seven of nine losses, $P = 0.000$). They also detected two additional patterns that led to horn loss: the evolution of high population densities in open habitat (see also Pomfret and Knell 2008) and more generalized dung diet, and; extreme diet specialization, such as rotting fruit in forest, and low population densities.

The study by Emlen *et al.* (2005b) represented a broad survey of the diversity of horn presence and location in a number of *Onthophagus* species across five continents and numerous habitats. Pomfret and Knell (2008) presented a finer-grained survey of ecological factors associated with horn presence and absence in a savanna community of 14 South African onthophagine dung beetle species. They collected all species during both years of their two-year study. Nine of the species have horned males and five do not. One of the species (*Onthophagus vinctus*) has both horned males and females, although the female horn is very small (average length for males 0.19 mm, for females, 0.05 mm). They controlled for habitat, time of year, location and dung bait used in their experiments, and were thus able to concentrate on the influence of mean male crowding and the operational sex ratio (OSR) on horn presence in the community.

Pomfret and Knell (2008) calculated mean crowding as the arithmetic mean number of male beetles per trap per day adjusted by the variance to mean ratio minus 1:

$$\bar{x}^{*} = \bar{x} + \left(\frac{\sigma^{2}}{\bar{x}} - 1 \right)$$

An aggregated distribution has a variance to mean ratio of >1, so mean crowding was greater than the arithmetic mean. An over-dispersed distribution, on the other hand, has a variance to mean ratio of <1, so mean crowding was less than the arithmetic mean.

Mean crowding was considered by Pomfret and Knell (2008) to be a better estimate of crowding than simple abundance because it includes a measure of how aggregated the population is; individuals from more aggregated populations are more likely to encounter conspecifics than are individuals from more evenly dispersed populations.

The OSR can be calculated as the ratio of the number of sexually active males to the sum of sexually active males and receptive females at a given time in a population (Pomfret and Knell 2008). It is usually expressed as a percentage, ranging from 0%, when only females are prepared to mate, to 100% when only males are prepared to mate. The authors claimed that this method of measuring competition is preferable to using simple sex ratios because it takes the proportion of each sex that is not available to prospective mates into account. Because the OSR can determine the strength of competition for mates, it is considered an important factor in determining the nature of sexual selection. Biased OSRs have been shown to drive sexual selection for secondary sexual traits in many organisms (see references in Pomfret and Knell 2008) and they can influence both male-male competition and female mate choice.

When Pomfret and Knell (2008) entered log mean crowding +1 and OSR into a general linear model (GLM), both partial correlation coefficients were statistically significant, and both explanatory variables were also significantly correlated with horn presence when fitted as single explanatory variables. Operational sex ratio was positively correlated with horn presence, and log mean crowding was negatively correlated (Fig. 11.2).

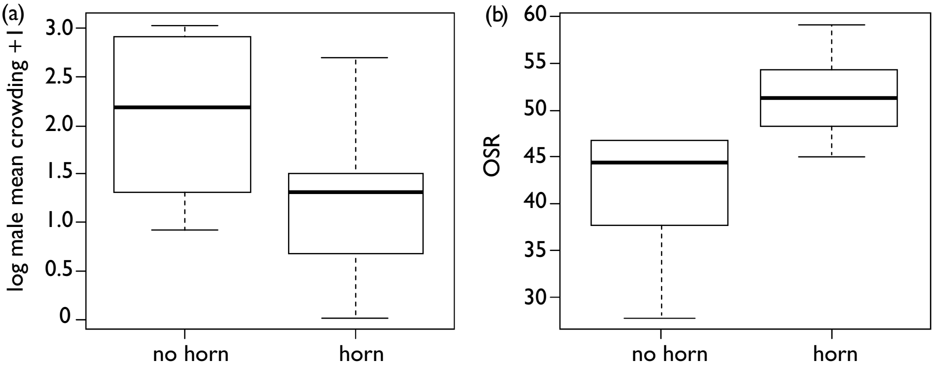


Fig. 11.2. Boxplots showing (a) log male mean crowding C1 and (b) operational sex ratio (OSR) for horned and hornless Onthophagine species in South Africa. The bold line is the median, the box the interquartile range and the whiskers extend to the furthest point less than 1.5 times the interquartile range from the box. (After Pomfret and Knell 2008).

Although it has been argued that increased crowding should select both for and against the evolution of male weapons, Pomfret and Knell's (2008) results appeared to support a case for "scramble" competition between males because crowding reduced levels of direct competition since females are not defendable. An alternative hypothesis suggests that an increase in total number of individuals in an area could lead to an increase in the intensity of male-male competition, which could aggressively monopolise females. They concluded, however, that their data support a role for both crowding and OSRs in determining horn diversity in the dung beetle community they studied – hornless beetles appeared to experience high levels of crowding and to have female-biased OSRs.

Pomfret and Knell (2008) proposed that if the males of "high density" species compete for matings via scramble competition, then high fitness would be related to mobility, to the ability to find females quickly, and to successful sperm competition.

Sperm competition theory predicts that across species, male expenditure on the ejaculate should increase with the probability of a sneak mating, and within male dimorphic species, sneaks should have greater expenditure on the ejaculate than guards (Simmons *et al.* 2007). In the male dimorphic species of *Onthophagus* studied, sneaks, because of their mating tactic, are always subject to sperm competition, whereas guards are subject to sperm competition with average probability determined by the frequency of sneaks in the population (Simmons *et al.* 2007). Horned males have been found to have smaller testes than similar-sized hornless males (Simmons and Emlen 2006), produce less sperm, and less often successfully fertilize females (Simmons *et al.* 2007). Major males (guards) assist females by collecting and carrying dung from the surface to the underground brood mass, while minor males (sneaks) do not assist in brood provisioning. Females readily mate with both major and minor males, and in those species studied, sperm numbers in the oviduct at the time of egg-laying appear to be an important determinant of competitive fertilization success (Tomkins and Simmons 2000; Simmons, Beveridge and Krauss 2004).

The local populations of the southern European species, *O. taurus*, which has been introduced into Australia and the USA, have undergone significant evolutionary divergence in the position of the switch point that delineates alternative mating tactics (Simmons *et al.* 2007). Minor males are more common in the high-density populations in Australia than in the low-density populations found in the USA (see Moczek *et al.* 2002). This suggests that the likelihood of male-male encounters is driving the evolution of horn investment (Parzer and Moczek 2008).

Weapons are rare in female beetles, but there are some ecological situations where competition for food is especially intense, and it is possible that these situations may favour the expression of weapons in females as well as males (Emlen *et al.* 2005). Horned females are found only in the same tribes as are males with horns. Emlen *et al.*'s (2005) phylogenetic reconstruction of 48 *Onthophagus* species yielded a most parsimonious hypothesis of 13 gains of female horns, of which 10 occurred on the same branches as corresponding gains of the same horn type in males (concentrated changes test: 10 of 13 gains, $P < 0.000$), two occurred on lineages where the particular horn type had been long expressed in males, and in only one, *O. sagittarius*, did horns develop independently in females.

Various hypotheses have been proposed for the reasons for horn development in females (see above under "Phanaeini"; also Emlen *et al.* 2005), but the most likely explanation appears to be that larger (and by implication, because of the apparent increase in body size that horns cause) females are more attractive to males as potential mates, especially in those species where males are also involved in provisioning of brood burrows. If males assess these females during contests, larger or horned females might be chosen over those without. If that were so, it would be expected that females with horns would occur in species where males invest substantially in brood care, or where males pair preferentially with larger females (Oniticellini – *Attavicinus monstrosus*, Emlen and Philips 2006; Onitini – e.g. *Heteronitis castelnaui*, personal observation, C.H. Scholtz; Onthophagini – e.g. *O. sagittarius*, Emlen and Philips 2006; Phanaeini – e.g. *Coprophanaeus ensifer*, Otronen 1988; *Phanaeus difformis*, Rasmussen 1994).

The next question needs to be why some species that evolved from a horned ancestor have lost the horns that evolved at such evolutionary cost? In all dung beetle species with horn-dimorphic males studied to date (seven species of *Onthophagus* – Cook 1990; Emlen 1997; Kotiaho 2000; Moczek and Emlen 2000; Hunt and Simmons 2002; *Euoniticellus intermedius* – Lailvaux *et al.* 2005; Pomfret and Knell 2006; *Coprophanaeus ensifer* – Otronen 1988 and *Phanaeus difformis* – Rasmussen 1994), males with the longest horns won disproportionate access to females. Yet, in their phylogenetic study of *Onthophagus,* Emlen *et al.* (2005b) recorded complete loss of horns three times. Their explanation was that these losses might be because the costs of horn production become prohibitive under certain changed ecological circumstances – extreme crowding, for example, might make guarding impractical, and very low population densities, on the other hand, might render it unnecessary.

11.1.3 Oniticellini

The only species of the Oniticellini that has been studied in a sexual selection context is the African *Euoniticellus intermedius* (Lailvaux *et al.* 2005; Pomfret and Knell 2006). It is a small (<10 mm) tunneller with horned males and hornless females, and although there is variation in male size, there is no evidence of the two distinct morphs with alternative mating strategies such as described for several onthophagines (sneaks are unknown). All males will fight, using their horns either to push rival males out of the tunnel if defending a female, or, if an intruder, to push a defender backwards until the intruder is able to pass him in the tunnel (Lailvaux *et al.* 2005).

Also in contrast to onthophagines, Pomfret and Knell (2006) recorded that horn size is the most important predictor of contest outcomes between larger males in *E. intermedius*, and body size is weakly negatively correlated to the probability of victory.

Lailvaux *et al.* (2005) tested the hypothesis that relative horn size in *E. intermedius* also predicts relative whole animal performance ability, as would be expected if performance capabilities were related to the outcome of male contests. They measured two types of performance: net pull resisting force (pulling force); and maximal exertion. The former represents the force required to push a beetle out of a tunnel, and the latter is a measure of locomotor effort expended before the onset of exhaustion.

Pulling force was measured by attaching a small pot to individual beetles in artificial burrows and then water was slowly added to the pot. When the beetle was no longer able to advance, the critical threshold was considered reached. The mass of the pot and water was then converted to Newtons as the measure of force. Maximal exertion was measured by forcing individual beetles to run until exhausted, and the distance they covered was considered to be the measure of locomotor effort.

Both measures of performance, maximum force (endurance), that Lailvaux *et al.* (2005) used were correlated with each other both before (df = 30, $P < 0.001$, $r^2 = 0.539$), and after, statistically accounting for body size (df = 30, $P < 0.001$, $r^2 = 0.293$). Table 11.1 gives summary statistics for the two measures of beetle morphology retained (mass was excluded because it was particularly closely related to horn length), and for the two measures of performance used.

Horn length in *E. intermedius* is a strong predictor of victory in male fights (Pomfret and Knell 2006) and Lailvaux *et al.* (2005) showed that it is strongly

Table 11.1. Summary statistics for morphology, exertion and pulling performance for male *Euoniticellus intermedius* beetles ($N = 32$). (After Lailvaux *et al.* 2005).

	Mean	Range	Standard deviation
Body length (mm)	6.556	5.2-8.4	0.937
Horn length (mm)	0.711	0.56-0.96	0.112
Endurance (m)	17.383	14.2-20.8	1.553
Pulling force (N)	0.182	0.128-0.35	0.029

correlated with two measures of whole-animal performance, which are independent of body size, namely the force to pull a beetle out of a hole and the distance a beetle is able to walk before reaching exhaustion.

Lailvaux *et al*. (2005) concluded that the connection between horn length and victory in male-male fights in *E. intermedius* is mediated by physical performance – male beetles with relatively long horns are stronger and have greater endurance, and consequently, win fights. Furthermore, horn size probably acts as an honest index of male performance ability which signals the strength and fighting ability of the individual to other males.

11.2 SEXUAL SELECTION IN ROLLERS

11.2.1 Canthonini

Circellium bacchus

The south-east African *Circellium bacchus* is one of the largest African ball-rollers. It is monotypic and biologically unusual in many respects (see Sections on breeding, respiration, conservation etc). This extends to mate selection (Le Roux *et al*. 2008).

The females expend a significant amount of energy in reproductive episodes. They roll a large brood ball, unaided by males, but which is often fiercely contested by other females. Males follow a rolling female and fights between competing males are frequent and fierce (Kryger *et al*. 2006; Le Roux *et al*. 2008). Involvement by males in breeding is of brief duration, starting with the male that succeeds in contesting for the female climbing onto the ball as it is being buried by the female, mating in an underground chamber, and then departure, all within a few days (Kryger *et al*. 2006). The female then re-models the ball, lays an egg and broods the immatures, eventually emerging with the teneral adult 4-5 months later. Females may, under ideal conditions breed twice per year, but once is most likely in the semi-arid areas where they occur. They probably live for 3-5 years, but their lifetime fecundity is still amongst the lowest for any insect species (Kryger *et al*. 2006).

Female lifetime reproductive success is, consequently, limited by considerable environmental and biological constraints, so one would expect them to exhibit extreme mate choice to ensure maximum reproductive success.

Le Roux *et al*. (2008) investigated mate selection mechanisms that operate within the *C. bacchus* mating system. They investigated potential pre-copulatory mechanisms of mate choice in the field, and possible post-copulatory mechanisms based on genital allometry, in the laboratory.

All interacting beetles (n = 313), during about a month spent in the field in early summer were collected and information on sex (n = 162 males, n = 151 females; 0.93:1.0, although the ratio becomes more male-biased later in the season – Kryger *et al.* 2006), mass, and several size measurements were recorded (see Table 11.2).

In the laboratory, Le Roux *et al.* (2008) measured 20 individuals of either sex to examine genital allometry. In males, aedeagus width, length and hook length were measured, as were width and length of the reproductive tract, as well as the length of the ovary in females. They normalised their data by log transformation and applied two different regression methods: linear ordinary least squares (OLS) and reduced major axis regression analysis (RMA). If the former indicated relationship (i.e. whether slopes deviated significantly from zero – β_0) between log (length of body part) on log (length of body-size indicator) then the latter was used to determine the allometric relationship (full details of the analyses, and justification for using two methods in Le Roux *et al.* 2008).

Table 11.2. Summary statistics for ordinary least squares (OLS, testing for a significant deviation from a slope of zero, β_0) and reduced major axis regression (RMA, testing for a significant deviation from a slope of one, β_1) for male *Circellium bacchus* of all traits on body size. The percentage coefficient of variation (%CV) and the sample size (n) are also shown. RMA analysis was carried out only if a relationship was shown by the OLS regression. The CV of body length is 10.53%. *P<0.05; **P<0.01; ***P<0.001. (After Le Roux *et al.* 2008).

Trait	**Sample size *(n)***	**ß$_o$**	***t* Value**	**ß$_1$**	***t* Value**	**Allometry**	**%CV**
Elytra width	20	1.05	23.26***	1.07	1.51	Isometric	11.18
Head length	20	0.79	18.95***	0.81	-4.57***	Negative	8.33
Head width	20	0.85	18.04***	0.88	-2.64*	Negative	9.03
Pronotum length	20	1.06	22.53***	1.08	1.73	Isometric	11.26
Pronotum width	20	1.07	22.76***	1.09	1.92	Isometric	11.38
Pygidium length	20	0.54	5.58***	0.68	-3.29**	Negative	6.98
Pygidium width	20	0.77	9.03***	0.85	-1.76	Isometric	8.90
Aedeagus length	20	0.27	3.89***	0.40	-8.67***	Negative	4.08
Aedeagus width	20	0.29	5.18***	0.37	-11.38***	Negative	3.79
Aedeagus hook length	20	0.43	5.32***	0.55	-5.55***	Negative	5.63

Females of *C. bacchus* rolling balls appear oblivious of males following and fighting, and accepted whichever male won the fights, which were significantly the larger males in the contests (Mann Whitney, $U = 295$, $n = 34$, $P < 0.001$).

Summary statistics for the males are provided in Table 11.3 – OLS regression of all variables measured, against body length, were statistically significant. In the subsequent RMA all three genital morphological characters measured were found to be significantly lower than a slope of 1, indicating negative allometry.

Female *C. bacchus* react aggressively towards other females when rolling a ball but ignore males following her and interacting with each other, which suggests that females do not discriminate actively between potential mates, and that aggressive interactions between males play a central role in the species' mating system (Le Roux *et al.* 2008). This system is typical of a male-biased operational sex ratio (see above) which results in greater competition among males, and suggests a refined form of passive female choice. Males would be selected for based on their size and fighting ability.

The negative male genital allometry recorded for this species may be explained by the "one size fits all" hypothesis, which holds that sexual selection might benefit males that possess intermediate-size genitalia, since this would enable them to mate with females of average size which can be expected to be the largest category of potential mates. Furthermore, males potentially have many mating opportunities since they spend little time below ground.

Finally, interactions between males appear to be an adequate strategy to ensure that the superior males in terms of competitive ability are the most likely ones to mate successfully, and this mechanism enables females to conserve energy for brood care and not spend limited energy reserves on the costly activities associated with active mate choice.

Canthon cyanellus cyanellus

Favila *et al.* (2005) studied the Neotropical canthonine species, *Canthon cyanellus cyanellus*, which has very different reproductive behaviour to that of *Circellium bacchus*. It is a ball-rolling carrion-feeding species, in which the male participates with the female in brood care (Favila 1993; Favila *et al.* 2005; see Chapter 3.2). They tested for: sperm storage in wild-captured females; sperm precedence in controlled matings with two genetically colour-determined males; and uncontrolled mating by a second male.

Of the wild-caught females, 90% produced brood balls, from which adults emerged in 72.36% of them. This clearly demonstrated that free-roaming females had been inseminated before capture.

To determine sperm precedence, Favila *et al.* 2005 used a visible genetic marker. The cuticular colour of the genetic marker is red, and it behaves as a homozygous recessive character with regard to the wild green colour (Favila *et al.* 2000). Thus, when a female of recessive genotype mates with males of different genotypes, the offspring will exhibit the father's phenotype (Favila *et al.* 2005). Males of both colours were bred in the laboratory and the reciprocal double mating method (references in Favila *et al.* 2005) used to determine sperm competition between males. They mated virgin red females once, either to a red male (Mr) or to a green wild-type male (Mg), and later, once to a male of the alternative genotype.

The third aspect of their study was to mate a red female once to a red male, after which she was left with a green male and allowed to mate repeatedly.

The results of the sperm precedence experiment from the double matings indicated that the two colour morphs have similar fertilizing capabilities (P_2 [proportion of eggs fertilized by the second male to mate] of MrMg mating = 55.25±37.59%, P_2 of MgMr mating = 43.35±31.09%, Mann-Whitney $U_{(19,18)} = 149$, $P = 0.52$), and considering the two sequences, the second male fertilized 49.46±36.01% of the eggs. It is clear from these results (Favila *et al.* 2005), that the paternity obtained after one mating with a second male is no greater than that of the first male, although the authors recorded that there was considerable individual variation, and that 15.62% of all double matings resulted in sperm precedence by the last male.

Sperm precedence from double matings in which the second male was allowed to mate repeatedly with the female, resulted in 86.5% brood survival, and the second male obtained a high paternity level (median = 83%, range 50-100%), which differed significantly from that obtained after a single mating ($U_{(19,17)} = 95.5$, $P = 0.03$).

Favila *et al.*'s (2005) results, consequently, strongly suggest that sperm competition occurs in this species and that in the field, males have a high probability of beginning a nest with a previously mated female. However, while constructing a nest and before brood ball formation and oviposition, the male is able to mate repeatedly with the female, assuring him of a higher probability of fertilizing the female's eggs.

11.2.2 SCARABAEINI

Scarabaeus (Kheper) platynotus

Sato and Hiramatsu (1993) studied mating behaviour and sexual selection in the diurnal African ball-roller *Scarabaeus platynotus* in Kenya.

Adults of *S. platynotus* are active during the two rainy seasons (April-May and November-December). They make both food and brood balls of chiefly elephant dung. Brood balls are occasionally made by single female, but more usually by a male-female pair. When a brood ball is made by a pair, it is usually rolled and buried by the male with the female clinging to the ball. After burying the ball, copulation takes place and the male abandons the nest. The female then refashions the dung ball into from 1-4 brood pears, oviposits in them and then cares for the brood until emergence of the young adults.

However, there is some variation in male breeding behaviour and in female investment in brood ball construction. Of 55 brood balls made by beetles in the field, 11 (20%) were by single females, and the rest by male-female pairs.

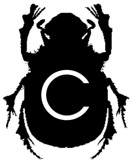
Males exhibited two different mating behaviours. In one type, a male approaching a female on or in the dung, or fashioning a ball, would attempt to force a copulation. Females mostly repulsed these attempts, although 21% were successful. The more common type was a male approaching a ball-constructing female who almost always accepted the male. The male then usually rolled and buried the ball, although males sometimes attempted to mate with the female during ball-making. This was successful in 75% of cases. Of these, 22% then abandoned the female and brood ball, while the remainder stayed with the female and ball until after burial and copulation.

During forming and rolling of balls, both males and females were attacked by other individuals of the same sex, who tried to dislodge them from the ball. The larger individual was most successful in repelling these attempts, as was the resident on the ball.

Sato and Hiramatsu (1993) interpreted the different male mating patterns as follows: males that stayed with the ball and female and fought off intruders, mated underground, and then abandoned the nest immediately, were indulging in pre-copulatory mate guarding; those that stayed with the female for a few days after mating were performing post-copulatory mate guarding. The authors explained the behaviour in terms of seasonal phenology: during early season males attempted to mate with any female, whether wandering, food- or brood ball forming. Although results were low, some males were successful and investment was minimal. Thereafter, as the season progressed and fewer and fewer females were available (because many are underground brooding in mid to late season), males invested more and more heavily in reproduction, although at greater cost. Males that remained with the female and brood for the longest had the best chances of successful fertilization.

Females were in all cases prepared to mate with any male when in possession of a brood ball, so their choice of mates was always passive, whereas males always competed strongly for females. This is similar to the case of *Circellium bacchus* discussed above, and the advantages that accrue for the females of the two species are likely to be the same.

Section C



PHYLOGENY OF THE SCARABAEINAE

Clarke H. Scholtz

Early dung beetle taxonomists appear to have had a good intuitive grasp of the fact that major taxonomic groups of dung beetles that were separated by morphological and behavioural gaps reflected the evolutionary results of shared ancestry and, by implication, supposed monophyletic lineages. Janssens (1949) first articulated this understanding of the various groups by dividing the Scarabaeinae into six tribes: Coprini (with subtribes Coprina, Dichotomiina, Ennearabdina and Phanaeina); Eurysternini, Oniticellini, Onitini, Onthophagini; and Scarabaeini. The latter included all the rollers in the subtribes Canthonina, Eucraniniina, Gymnopleurina, Scarabaeina and Sisyphina. His system was followed by Halffter and colleagues (e.g. Halffter and Matthews 1966; Halffter and Edmonds 1982) who were the only major dung beetle researchers for many years, and who attempted to interpret and compare most aspects of dung beetle biology in terms of evolution and implied phylogeny.

Balthasar (1963) presented a classification of the Scrarabaeoidea that was followed by many, particularly European, contemporary dung beetle workers, and which formed the basis for the "phylogenetic" classification presented by Hanski and Cambefort (1991e) that was subsequently followed by most dung beetle researchers until recent evidence of the polyphyly of major groups and of the basic patterns of breeding behaviour indicated that this system, although appealing, was simplistic. Balthasar divided the Scarabaeidae into the subfamilies Coprinae and Scarabaeinae. He excluded the other major groups that are currently recognised as subfamilies equal to the Scarabaeinae (to which he accorded family status as Aphodiidae, Geotrupidae, Melolonthidae etc.). He divided the Coprinae and Scarabaeinae into six tribes of tunnellers, and six tribes of rollers respectively.

It was, however, only after Willi Hennig in the 1960's provided a method for deducing shared characteristics of taxonomic groups and emphasising the importance of shared derived characters in hypothesising relationship, that questions about "phylogeny" of taxa were actually articulated. In spite of the revolution in insect systematics that Hennigian cladistics stimulated, it was 20 years before the Scarabaeinae were subjected to phylogenetic analysis, albeit very superficially (Zunino 1983), and it took another 20 years before the first comprehensive cladistic analysis that treated a suite of multiple morphological characters and representatives of all major groups, was undertaken (Philips *et al.* 2004b). The rapidly increasing and widespread use of molecular techniques to test relationship amongst organisms towards the close of the 20th century heralded a new phase of phylogenetic study in the Scarabaeinae with the first study, on a subset of [Iberian] taxa, published in 2002 (Villalba *et al.* 2002).

Cambefort (1991b) eloquently introduced the appealing but phylogenetically untested and cladistically unacceptable grouping of tribes of rollers and tunnellers into "ancient", "intermediate" and "modern" groups. According to his system, the cosmopolitan Canthonini and Dichotomiini are ancient, and gave rise to all tribes of rollers and tunnellers, respectively. Intermediate tribes of rollers are the Neotropical Eucraniini and Eurysternini and the Afro-Eurasian Gymnopleurini and Scarabaeini. Intermediate tribes of tunnellers are the Afro-Eurasian Onitini and New World Phanaeini. The only modern roller tribe is the widespread Sisyphini, and modern tunneller tribes are the widespread Coprini and Oniticellini and the virtually cosmopolitan Onthophagini. The Oniticellini are divided further into the nominal subtribe as well as the Madagascan endemic Helictopleurina and the widespread Drepanocerina.

Several recent studies have indicated that the group of dung beetles classified as Scarabaeinae is monophyletic (Villalba *et al.* 2002; Philips *et al.* 2004b; Ocampo and Hawks 2006, Monaghan *et al.* 2007), and sister to the Aphodiinae (Browne and Scholtz 1998; Philips *et al.* 2004b; Ocampo and Hawks 2006; Monaghan *et al.* 2007) although at least some of the tribes currently included in the subfamily, are clearly poly- or -paraphyletic.

Philips *et al.* (2004b) also questioned, based on their empirical analyses, the widely-held view (e.g. Hanski and Cambefort 1991e; Villaba *et al.* 2002) that the evolution of groups using rolling and tunnelling behaviours was of approximately equal age and that each evolved only once, so consequently, the six tribes of rollers and six tribes of tunnellers represented monophyletic groups. Monaghan *et al.* (2007), concur with Philips' *et al.*'s (2004b) conclusions that rolling had several origins and that the currently-recognised Canthonini and Dichotomiini each consist of multiple paraphyletic lineages.

Sole and Scholtz (2009) tested the hypothesis that dung beetles evolved in Africa and that the basal-most groups are still found there. Although some of these groups had been assigned to the Canthonini in the taxonomic studies that have dealt with them, it was always with reservation (see Scholtz and Howden 1987a; Davis *et al.* 2008b) since only very superficial morphological characters indicated their possible placement there. It was only recently established that some of these basal groups, although putatively belonging to the rolling Canthonini, actually behave as tunnellers, dragging dung fragments backwards into burrows (Deschodt *et al.* 2007).

Although there is considerable doubt about the validity of the currently-recognised tribes, we discuss them here in their historical context to avoid introducing even more confusion. The 12 tribes currently recognized obviously relate to very different hierarchical levels, with some of the smaller tribes confirmed to be monophyletic terminal groups whereas the Canthonini and Dichotomiini each consist of multiple lineages at hierarchical levels equivalent to the smaller tribes (Monaghan *et al*. 2007). There is now sufficient phylogenetic evidence to not only seriously question the monophyly of Dichotomiini and Canthonini but also that of Coprini, Onthophagini and Oniticellini. By contrast, there appears to be little doubt that the Onitini, Phanaeini, Gymnopleurini, Scarabaeini, Sisyphini, Eucraniini and Eurysternini are monophyletic groups although it has become questionable in the light of some of the recent phylogenetic analyses whether tribal status of each of them can still be justified. There are now also strong cases to be made for the consideration of some newly-discovered phylogenetic entities such as "the" basal southern African group that could justifiably be considered as distinct supra-generic taxa (Sole and Scholtz 2009).

CHAPTER 12
CURRENTLY-RECOGNISED TRIBES OF SCARABAEINAE

Monophyly of several tribes has been tested over the past 20 years (Dichotomiini and Coprini – Montreuil 1998); Scarabaeini (Mostert and Scholtz 1986; Forgie *et al*. 2005; Forgie *et al*. 2006; Sole *et al*. 2005); Phanaeini (Philips *et al*. 2004a); Eucraniini (Philips *et al*. 2002; Ocampo and Hawks 2006); Helictopleurina (Orsini *et al*. 2007); Onitini (Cambefort 1995), but with the exception of the changes to the tribal classification proposed by Montreuil (1998 – see details below) none of these studies has significantly changed the traditional classification, nor have any of these researchers expressed any serious reservations about the validity of current tribal composition.

12.1 TUNNELLERS

12.1.1 Dichotomiini

Taxonomy and morphology: The Dichotomiini comprise shiny or matte black species ranging in average body size from smallish to very large (5.0 mm – 47.0 mm long see Plate 12.1). Body shape varies from elongate to oval, approaching hemispherical in some species, but it is always strongly convex both ventrally and dorsally. As in the Coprini, the second article of the labial palps is shorter than the first and the third article is always clearly visible but, unlike the Coprini, the species lack external ridges on the short mid and hind tibiae. Recent studies suggest that the characterization, generic composition, and the nomenclature used to define the tribe, require revision, as its present membership is probably polyphyletic. These studies are discussed below.

Diversity and distribution: As traditionally constituted, the Dichotomiini comprise about 750 species in about 40 primarily tunnelling genera and are

Plate 12.1. Tribe Dichotomiini; *Heliocopris neptunus*, male, Botswana, 35 mm.

considered to show a Gondwana distribution centred on southern land masses (South America, Africa, Australia). The tribe is still prominent in the dung beetle fauna of South America (about 25 genera, and 580 species) where it comprises around 30% of the genera and 55% of the species. However, at 0-7%, it forms a much smaller proportion of the species in the faunas of other regions where it may have been replaced or partly superseded by other dung beetle groups with similar habits. The Afrotropical fauna has the largest number of representatives outside of South America (9 genera, 126 species) with smaller numbers in the faunas of the Oriental region (6 genera, 31 species), the Caribbean and North America (2 genera, 5 species each), and Australia (1 genus, 14 species). They are absent from Madagascar and absent or poorly represented in the Palaearctic, depending on the adopted classification system (either integrating the Coprini into the Dichotomiini or retaining them as two tribes in which case *Synapsis*, with one species in arid, Palaearctic, southern Central Asia, remains in the Coprini).

Several of the the New World genera are very speciose, with more than 30 species (*Anomiopus, Ateuchus, Canthidium, Dichotomius, Ontherus* and *Uroxys*) and are widespread in the region. A number of others is monotypic (*Chalcocopris, Deltorhinum, Hypocanthidium, Pseuduroxys* and *Pteronyx*) or consist of fewer than five species (*Aphengium, Bdelyropsis, Bdelyrus, Holocephalus* and *Isocopris*). The monotypic genera or ones with few species are usually the ones which have highly specialised and atypical biology. Most species of the bigger genera, however, feed on dung although carrion-feeding is common and an association with leaf-cutting ants (Attini, e.g. *Atta* and *Acromyrmex* species) appears more common than previously thought (Halffter and Edmonds 1982; Vaz-de-Mello *et al.* 1998).

In Africa, the genera may show either restricted or widespread distributions and some have highly specialized feeding biology such as the Afro-Oriental rainforest genus that feeds and breeds in rotting tree trunks (*Paraphytus*). Another three genera may be specialized to feeding and breeding using fungi. One is intertropical with an Afro-Oriental distribution (*Delopleurus*). Another is widespread in moist African savanna (*Coptorhina*) but with a centre of diversity towards the cooler, higher-lying regions of the south and east. The third is restricted to South Africa in the forest and highveld grassland of the summer rainfall region and the shrub/woodland of the winter and bimodal rainfall regions (*Frankenbergerius*). A further two widespread dung-eating genera are found in forest, moist to dry savanna and highland grass. They are either very large-bodied tunnellers with few competitors within their size range and an Afro-Oriental distribution (*Heliocopris*), or they are considered to be kleptocoprids (*Pedaria*) using the dung buried by large African tunnellers, particularly *Heliocopris*. Three other coprophagous genera are primarily restricted to south-east Africa. They comprise a flightless genus endemic to the winter and bimodal rainfall regions of South Africa (*Macroderes*), a forest and grassland genus in the eastern highlands of South Africa and Zimbabwe (*Xinidium*), and a genus of unknown habits distributed from the winter rainfall shrubland of the Western Cape to the summer rainfall savanna of northern Tanzania (*Sarophorus*).

Phylogeny and evolutionary history: It is difficult to provide an entirely acceptable account of evolutionary history for the Dichotomiini owing to differing opinions on its validity and composition. These differences stem from four recent evolutionary studies, which are discussed in detail below. The first phylogenetic study (Montreuil 1998) was restricted to an examination of 26 out of 40 genera in the Dichotomiini and Coprini and 42 morphological characters indicated two principal lineages (Fig. 12.1). On the basis of the two principal lineages indicated by his study, Montreuil (1998) suggested some fairly profound changes to the classification of the Scarabaeinae. Because one lineage expanded the former membership of the Coprini by adding Coprini-like genera from the Dichotomiini the other lineage comprising the depleted membership of the Dichotomiini had to be renamed the tribe Ateuchini according to the international rules of nomenclature because the type-genus of the Dichotomiini, *Dichotomius*, now resides in the reconstituted Coprini. In this system, the Ateuchini are hypothesised to be basal but that both tribes are represented on all major land masses except Madagascar.

In a second relevant study, Philips *et al.* (2004b) examined relationships between 47 genera that represent all 12 tribes composing the subfamily Scarabaeinae based on 200-odd morphological characters. This study indicated complex relationships between genera from three tribes (Dichotomiini, Canthonini, Coprini) occurring primarily on a series of basal lineages (Fig. 12.2). The intermingled scatter of genera from the three tribes suggested the advisability of revision of current tribal level classification and its generic composition. In Philips *et al.*'s (2004b) phylogeny, members of the redefined Ateuchini were biased towards occurrence on more basal lineages than those of the redefined Coprini.

The third, a molecular, study (Ocampo and Hawks 2006), used two gene regions and a subset of mainly New World taxa for their analyses. They included 10 dichotomiine taxa, one Australian, the rest Neotropical. Their analyses returned a polyphyletic Dichotomiini and even when there was some structure in the tree topology indicating relationship, it was weakly supported (see Fig.12.6).

The fourth study, Monaghan *et al.*'s (2007), and the first using a large matrix of molecular characters and taxa, yielded a Dichotomiini mostly without any phylogenetic structure (see phylograms below). The taxa (27 species of 14 genera) were selected from all the major regions where Dichotomini occur. Their

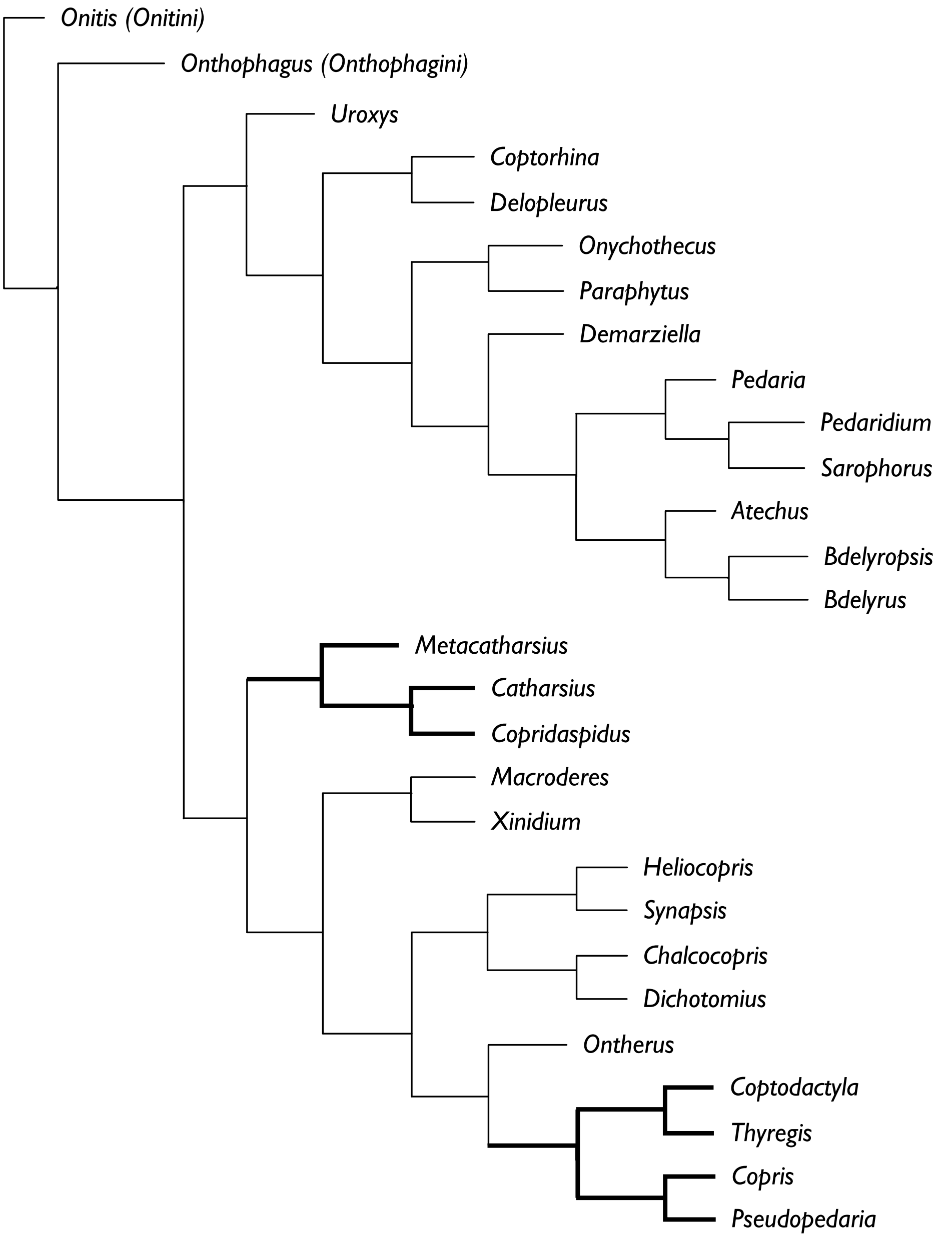


Fig. 12.1. Tree of a subset of Dichotomiini-genera based on the morphological dataset from Montreuil (1998) as re-analysed by Philips *et al.* (2004b). The non-monophyly of the Coprini, as indicated in bold, is readily apparent.

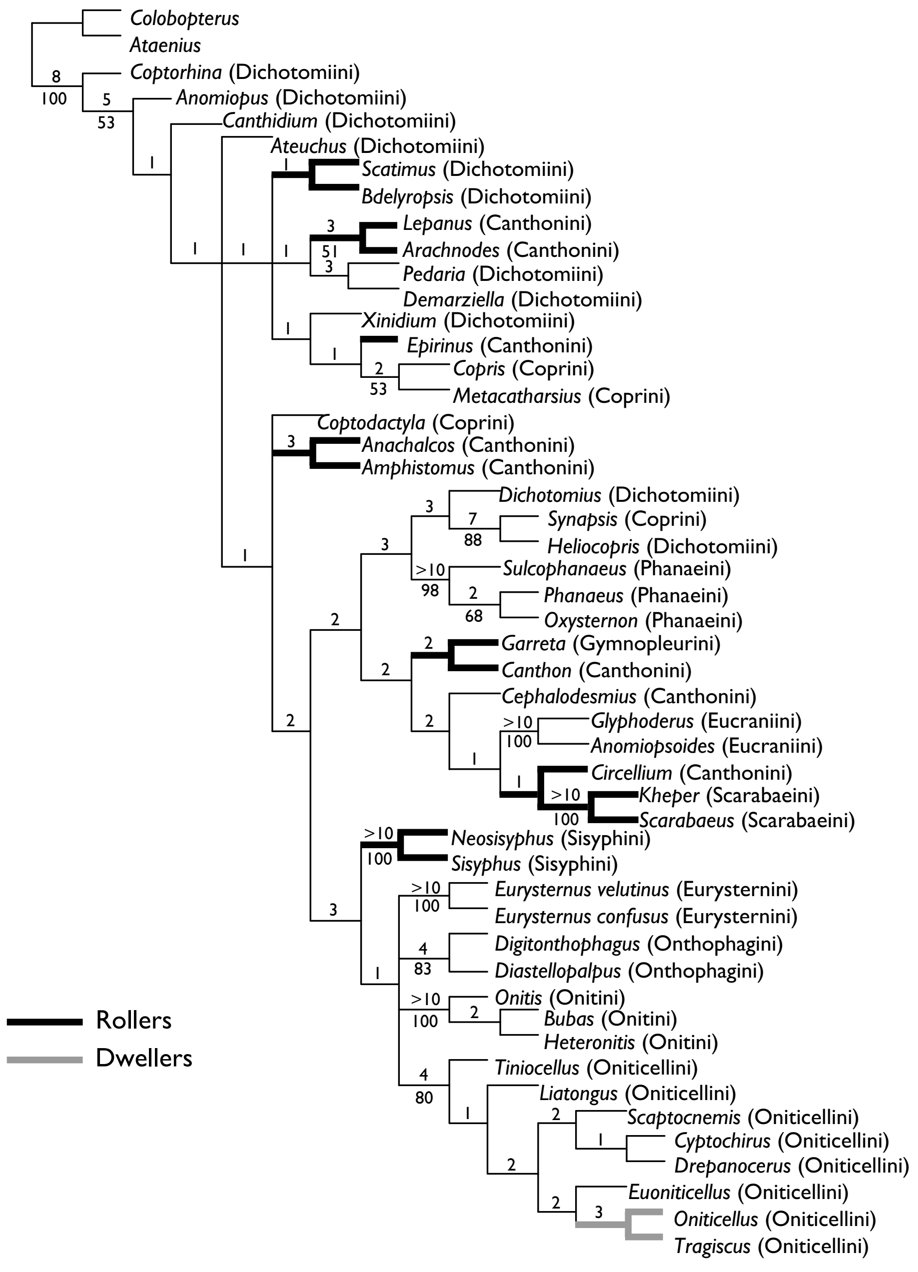


Fig. 12.2. Unweighted consensus. Tree branch pattern coded for behaviour (rollers and dwellers, all other tunnellers). Bremer support values are above each node and bootstrap values are below each node. (After Philips *et al.* 2004b).

preferred tree returned a strongly-supported basal clade of the African *Coptorhina* + *Sarophorus* [+ *Macroderes*] but virtually all other clades (10 of them), with the possible exception of the small group of Neotropical genera [and the Australian canthonine, *Boletoscapter*], sister to the Australasian clade that included dichotomiines, were weakly, or not at all, supported. Virtually every other major clade had at least one, often poorly-supported, dichotomiine nested in it, often at the root (also see Sole and Scholtz 2009).

Interestingly a common feature among the phylogenetic studies was the basal placement of the African dichotomiine, *Coptorhina*, in Philips *et al.* (2004b), Monaghan *et al.* (2007), and the much earlier but very superficial study by Zunino (1983). In the most recent study of the basal African dung beetle groups, Sole and Scholtz (2009) convincingly confirmed this placement. However, with the exception of this common pattern, the Dichotomiini is the tribe that suffers the poorest phylogenetic resolution in all of the studies since there is virtually no coherent pattern in any of the generic groupings.

Geographical origin: The Dichotomiini have long been considered to be one of two tribes (with the Canthonini) to show an ancient Gondwana distribution pattern that has its origin in the fragmentation of the southern super-continent of Gondwana commencing in the Mesozoic Period. Genera of both the ateuchine and expanded coprine components occur in each of three major southern land mass fragments of West (South America, Africa) and East Gondwana (Australia), suggesting a separation between the two lineages that pre-dated the fragmentation of the super-continent (Montreuil 1998). However, the ateuchine component allegedly forms the basal lineage in the phylogeny of the subfamily. As the western ateuchine elements are more basal (*Coptorhina* in Africa, followed by *Ateuchus* in the Americas) than those in Australia (*Demarziella*), this may or may not indicate an origin in the western Gondwana fragments. However, in view of the recent detailed phylogenetic study by Monaghan *et al.* (2007) it is doubtful whether any of these relationships can still be justified. It may be possible to justify ancient origins of some 'dichotomiine" taxa in view of the basal positions they occupy on various lineages of the phylogeny for the subfamily, but doubt has certainly arisen about tribal relationships between continents.

The Dichotomiini are represented by different genera between southern land masses whereas they are mostly represented by different species within the same genera between southern and northern land masses. Most generic level differences are thought to emanate from the older separation of southern continents due to the breakup of Gondwana in the Mesozoic Period (over 100 mya) whereas species-level differences are thought to result from the more recent radiation of species between southern and northern continents after continental drift led to land re-connections. These were respectively, between South and North America in the Pliocene (±3 mya), between Africa and Europe in the Eocene (±40 mya) and the Miocene Epoch (±15 mya), between Europe, Asia and North America in the Miocene and the Pleistocene Epochs (± 1 mya), or between India and the rest of Asia in the Miocene Epoch which caused the later virtual isolation of the Oriental region through uplift of mountain ranges. The patterns are similar whatever the adopted classification system. In a membership of 34 genera in the old Dichotomiini, five genera showed shared distributions with northern land masses and one (*Onychothecus*) was endemic to the Oriental region. When classification is revised as the Ateuchini or expanded Coprini, the Ateuchini comprise only slightly fewer genera shared with, or endemic to, the northern land masses (3 + *Onychothecus*) than the revised Coprini (5 + *Synapsis*, endemic to the Oriental and Palaearctic regions).

Biological and ecological notes: The larger New World genera demonstrate the general lack of specificity and phylogenetic signal in feeding behaviour, with dung, carrion and debris-feeding being common amongst the species. *Ateuchus* and *Canthidium* are typical in this respect: *A. histeroides* is a typical dung-feeder and *A. granigerum*, *A. viridimicans*, *A. carcavalloi* and *A. myrmecophilus* breed in the debris of attine nests (as do some species of *Anomiopus*, *Ontherus* and *Uroxys* – Vaz-de-Mello *et al*. 1998). *Canthidium puncticolle* is a necrophagous species from tropical southern Mexico that deposits carrion in a single vertical tunnel, lays an egg in an egg chamber, and fills the tunnel in with soil. *Canthidium granivorum*, on the other hand, was recorded to feed on seeds of a legume in the field in Mexico, although they accepted dung in the laboratory (Halffter and Edmonds 1982). In the field, the female breaks up the plant fragments with her clypeus and front tibia and these, mixed with her faeces, are compacted into a tunnel to form the brood mass. An egg is laid in an egg chamber at the top of the mass and during the time that the egg takes to develop microbial action transforms the brood mass into an orange substance which continues to darken and decompose as the larva develops. *Bdelyrus* is often common in decomposing accumulations of debris at the base of bromeliads (Halffter and Matthews 1966) although their biology in unstudied.

Some species of the genera *Pedaridium, Uroxys* and *Trichillum*, which otherwise have more typical species, have very unusual biology – they have an intimate association with sloths (see Chapter 9.1.6).

The African Dichotomiini comprise primarily tunnellers although at least one coprophagous genus (*Pedaria*) has been reported to show kleptocoprid behaviour. The genera variously show coprophagous (*Heliocopris*), mycetophagous (*Coptorhina*), or possibly even sapro-xylophagous habits (*Paraphytus*). Some genera appear to comprise day-flyers whereas others are entirely night-flying. There are published accounts of nesting in *Heliocopris* (expanded Coprini, e.g. Klemperer and Boulton 1976), *Paraphytus* (Cambefort and Walter 1985) and *Coptorhina* (Ateuchini; Frolov *et al.* 2008). *Heliocopris* shows Type 2 nesting in which dung is buried rapidly into a tunnel under the dung. Adults of *Paraphytus* species may feed on soft rotten wood although they may equally feed on fungi and other micro-organisms occurring in the rotten logs in which they occur. Nests and larvae have been described for the African species, *P. aphodioides* (Walter and Cambefort 1985). Nests are located in rotten logs and comprise a single, soft and fragile, brood ovoid constructed from the debris and digested droppings remaining after activity by xylophagous insects, including those of their distant relatives, the Passalidae, with which *Paraphytus* co-exist in the logs. Each single brood is tightly housed in a poorly delimited cavity or chamber created by the female drawing materials together for brood construction. Throughout periods of observation, the female was always found in attendance, suggesting that the species cares for its brood during larval development. It was confirmed that the ovoids contained larvae.

Coptorhina is a genus of obligate basidiomycete fungus-feeding dung beetles. The highly unusual (for a dung beetle) trophic association between members of the genus and mushrooms was first recorded during the 19th century. *Coptorhina* specimens have been observed feeding on mushrooms with two types of fruit-body. In the case of "puff-ball" mushrooms the adults burrow into the fruit-body, detach pieces and drag them into their burrows. In "parasol" mushrooms, the beetles climb the stalk and detach pieces of the gills, which they then drag into their burrows. Beetle activity is correlated with the availability of the fruit bodies of mushrooms and is mostly limited to periods after rain. Generally similar behaviour has been observed in three South African species (*C. auspicata, C. klugii* and *C. nitidipennis* – Frolov *et al.* 2008).

Specimens of *C. auspicata* and *C. klugii* have been bred in the laboratory in containers with sandy soil collected in their habitat and fed on commercial mushrooms (*Agaricus* species) from a grocery store. The beetles made brood balls about 2 cm in diameter and covered these with a layer of soil. Typical coprine-like 3rd -instar larvae were found in the brood balls after three weeks. The larvae were observed to eat the macerated mushroom substance along with sand particles. The smaller size of brood balls (compared to those of dung feeders like *Copris* or *Catharsius* with similar sized larvae) is probably due to the higher nutritive value of mushrooms compared to dung. As the larvae progressively consume the brood ball contents and repeatedly re-ingest their own faeces, it is likely that bacteria and fungi inhabiting the brood ball substance become the main nutritional component of the larval food (Frolov *et al.* 2008).

12.1.2 Onitini

Taxonomy and morphology: The Onitini are characterized by antennae with nine articles, four teeth on the fore tibiae, and by a visible scutellum. The body shape is elongate and flattened in most genera (Plate 12.2), tapering posteriorly in some genera, but almost rectangular in some others. All species show moderate to large body size averaging from 14.0 mm to 37.0 mm long. The mid and hind tibiae are short in all species. Generic and species separation is based on dorsal sculpturing of the head (spines, horns and ridges), on both dorsal and ventral sculpturing of the thorax (keels, ridges, rugosity, granulation, punctuation), and on striation, granulation or punctuation of the elytra. Other useful diagnostic characters include body shape, mouthparts, presence or absence of tarsi or spurs at the tips of the legs, and armament on the femora, especially in male *Onitis*.

Diversity and distribution: This tribe of about 210 tunnelling species comprises 18 entirely coprophagous genera. Of these, two genera are relatively species-rich (*Cheironitis*, *Onitis*) with distributions extending beyond Africa into the Palaearctic and Oriental regions, whereas 16 are species-poor, comprising one Palaearctic (*Bubas*) and 15 African endemics. Of the African endemics, two monotypic genera (*Allonitis**, *Lophodonitis*) are restricted to West and Central African tropical rainforests. The other 13 comprise from 1-5 species each and mostly show restricted distributions, nine of them in peripheral savanna woodlands of West, northeast and/or southern Africa with species of at least one genus (*Gilletellus*) recorded from the arid southwest of Africa. Although *Heteronitis** (five species) and *Neonitis** (four species) are represented in the southern, eastern and western African savannas, the remainder (1-3 species each) is restricted to southern Africa (five genera – *Kolbeellus*, *Anonychonitis**, *Tropidonitis**, *Megalonitis**, *Gilletellus*), southern to East Africa (two genera – *Platyonitis**, *Pseudochironitis**), East Africa (one genus – *Acanthonitis*), East to West Africa (one genus – *Aptychonitis**), or West Africa (two genera – *Pleuronitis*, *Janssensellus*). Although *Lophodonitis* is attracted mainly to primate dung, at least nine of the remaining 14, species-poor, genera (those marked by an asterisk*) are known primarily from the coarse-fibred dung of large non-ruminant herbivores, particularly that of elephants and rhinoceros. Some of these species-poor genera are poorly represented in collections, which may be related to the disappearance of large non-ruminants and associated dung beetles from much of their former

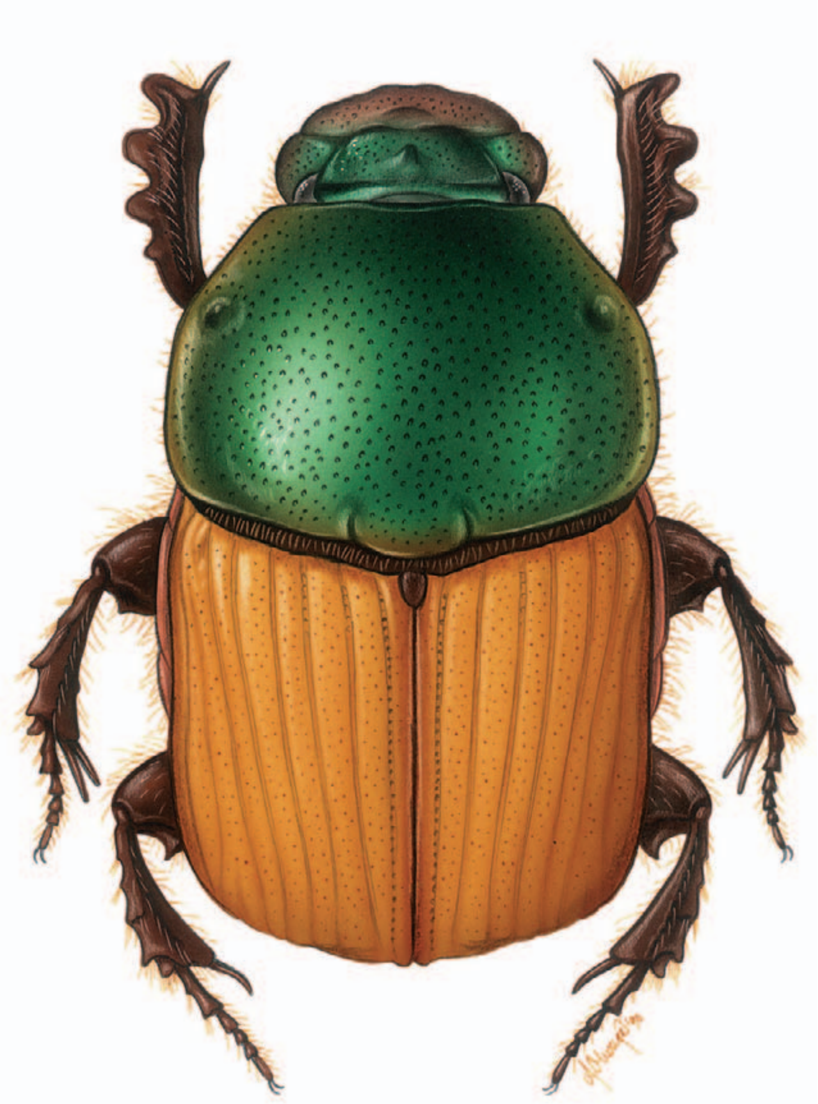


Plate 12.2. Tribe Onitini; *Onitis alexis*, South Africa, 13 mm.

ranges. However, recent collecting, using quantitative methods, suggests that some of these species-poor genera are uncommon even in the game reserves where they are still known to exist. Dung associations of the more species-rich genera differ as they include non-ruminant dung specialists and herbivore dung generalists, as well as species found predominantly in the dung pats of large ruminant herbivores of the ungulate mammal tribe, Bovini (buffalo and cattle).

Phylogeny and evolutionary history: The Onitini have been included in four recent phylogenetic analyses of the Scarabaeinae, one using morphological (Philips *et al.* 2004b) and three (Villalba *et al.* 2002; Ocampo and Hawks 2006; Monaghan *et al.* 2007), molecular characters. The Philips *et al.* (2004b) analyses returned a tree with a monophylum of the genera sampled (*Onitis, Bubas* and *Heteronitis*), sister to a clade of Onthophagini and Oniticellini. Villalba *et al.* (2002) also sampled the same first and second two genera as in the former study but added *Cheironitis*. Their single most parsimonious tree yielded a monophyletic group, with strong support for a sistergroup relationship to Oniticellini and Onthophagini. Ocampo and Hawks (2006) only used two African *Onitis* species in their analyses, although the *O. alexis* they sampled were from an introduced population in the USA. They also returned a monophylum for the two species that was, as with the analyses mentioned above, sister to the Oniticellini and Onthophagini. Monaghan *et al.* (2007) sampled the same four genera included in the previous studies; *Onitis* (four species – three from South Africa, one from Hong Kong), *Bubas* (two species from Spain), *Heteronitis castelnaui* from South Africa and *Cheironitis hoplosternus*, also from South Africa. Monophyly of the group was strongly supported, and it too was sister to the Oniticellini and Onthophagini. Consequently, all of these studies provided a strongly monophyletic tribe, with clear sister-group relationships.

It has been suggested (Cambefort 1995) that the many species-poor genera within this tribe that are associated with the dung of non-ruminant herbivores represent an early radiation since elephants have an African origin (fossils from Eocene Epoch deposits of roughly 45 mya) whereas rhinocerotids and equids have a northern origin and are known as fossils from deposits of similar age. Radiation in some of the species-rich taxa may represent a much later event since the Bovini only enter the African fossil record at 10 mya, in the late Miocene Epoch, and the Asian record in deposits of comparable age. However, Cambefort's (1995) phylogeny for the tribe (Fig. 12.3), albeit based on only 23 morphological characters and with no statistical support indicated, suggests that there is no direct sequential congruence between dung association and evolutionary age. On this phylogeny, *Cheironitis* is second only to the basal element whereas *Onitis* lies in the middle of the hierarchy of derived genera. It shares

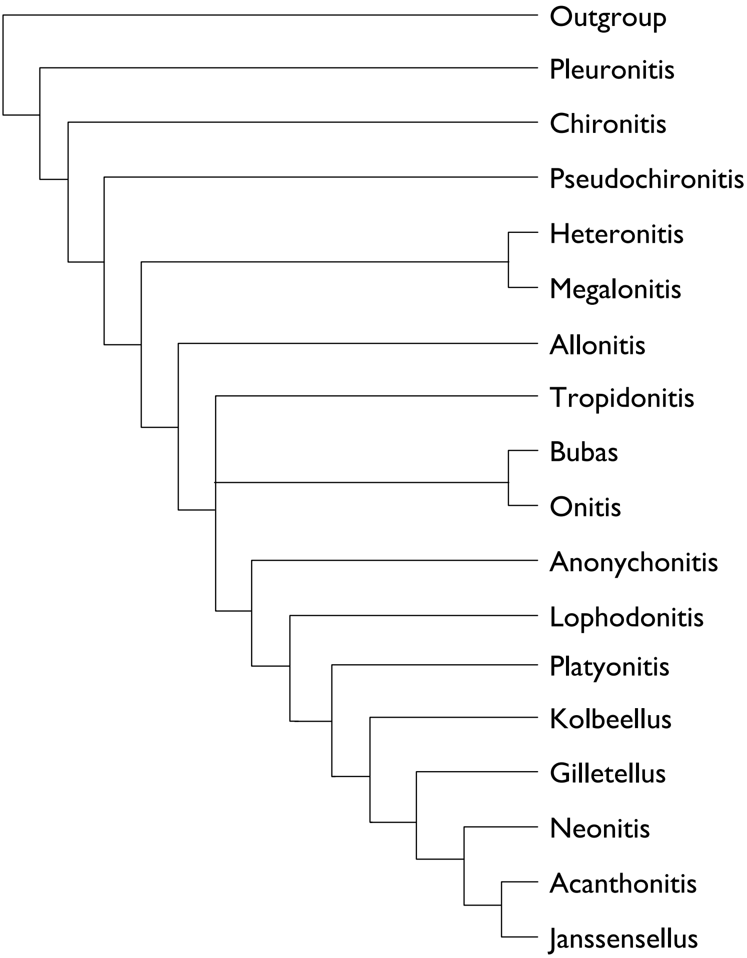


Fig. 12.3. Phylogeny of the Onitini genera (redrawn from Cambefort 1995).

a common ancestor with about half of the remaining genera showing associations with non-ruminant dung. This may mean that the near basal *Cheironitis* has undergone radiation on both the coarse-fibred dung of large non-ruminants and on the pats of large ruminants whereas some derived coarse dung taxa, with restricted distribution, have radiated coeval with *Onitis*, which also show both non-ruminant dung specialists and species which have radiated on bovine dung.

Geographical origin: There are two principal viewpoints concerning the origin of the Onitini (Cambefort 1995; Davis *et al.* 2002a). Although the basal genus *Pleuronitis* is endemic to West Africa, it has been suggested that the tribe originated in the Palaearctic region owing to the joint African / Eurasian occurrence of the near basal genus, *Cheironitis* (Cambefort 1995). Alternatively (Davis *et al.* 2002a), an African origin has been suggested due to the overwhelming dominance of generic level endemism to Africa. As regards the possible Eurasian origin of *Cheironitis,* and the tribe in general, a species level phylogeny is required to determine the direction of radiation, whether from Africa to Eurasia, Eurasia to Africa or, even a dual origin, as faunal exchanges occurred between the Palaearctic and Africa in the Eocene Epoch and between Eurasia and Africa in the Miocene Epoch. Although many genera show a specialist association with non-ruminant herbivore dung, this is not necessarily useful in pinpointing their geographical origin as the earliest fossil record of elephants is in Africa whereas that of rhinoceros and horses is in the Northern Hemisphere.

As a further complication concerning the geographical origin and biogeography of the tribe, historical studies suggest a trend towards drier climate over the 65 million years of the Cenozoic Period. This has led to the retreat of forests and the expansion of drier vegetation types in Africa, so that the arid areas in which many *Cheironitis* occur might be interpreted as younger than many moister areas. Thus, although *Cheironitis* is sub-basal on the phylogeny of the Onitini (Cambefort 1995), radiation of the present species may be more modern than the phylogenetic position of the genus would suggest. Whatever the historical details, the recurring trend in association of species-poor genera with coarse-fibred dung may be a relict of greater past diversity of non-ruminant mammals.

Biological and ecological notes: Feeding and nesting behaviour are unknown for most genera. Thus far, only Type 1 nesting behaviour has been observed but this is probably characteristic for the entire tribe. It ranges from the production of single broods in simple nests in *Anonychonitis* and *Cheironitis*, to that of several broods in compound nests at the branched tips of a tunnel in some *Onitis*. In other *Onitis*, the compound nests comprise dung sausages with eggs in series in a single tunnel or in branches at the tip of a tunnel. Onitini are mostly slow tunnellers although at least one species of *Onitis* has been recorded to bury dung fairly rapidly (*O. deceptor*). Most, though not all, *Onitis* species are night-flyers, while the members of several species-poor genera are active by day.

12.1.3 Phanaeini

Taxonomy and morphology: The tribe comprises the following 12 genera: *Bolbites, Coprophanaeus, Dendropaemon* (Plate 12.3), *Diabroctis, Gromphas, Homalotarsus, Megatharsis, Oruscatus, Oxysternon, Phanaeus* (Plate 12.4), *Sulcophanaeus*

Plate 12.3. Tribe Phanaeini; *Dendropaemon denticollis*, Brazil, 8 mm.

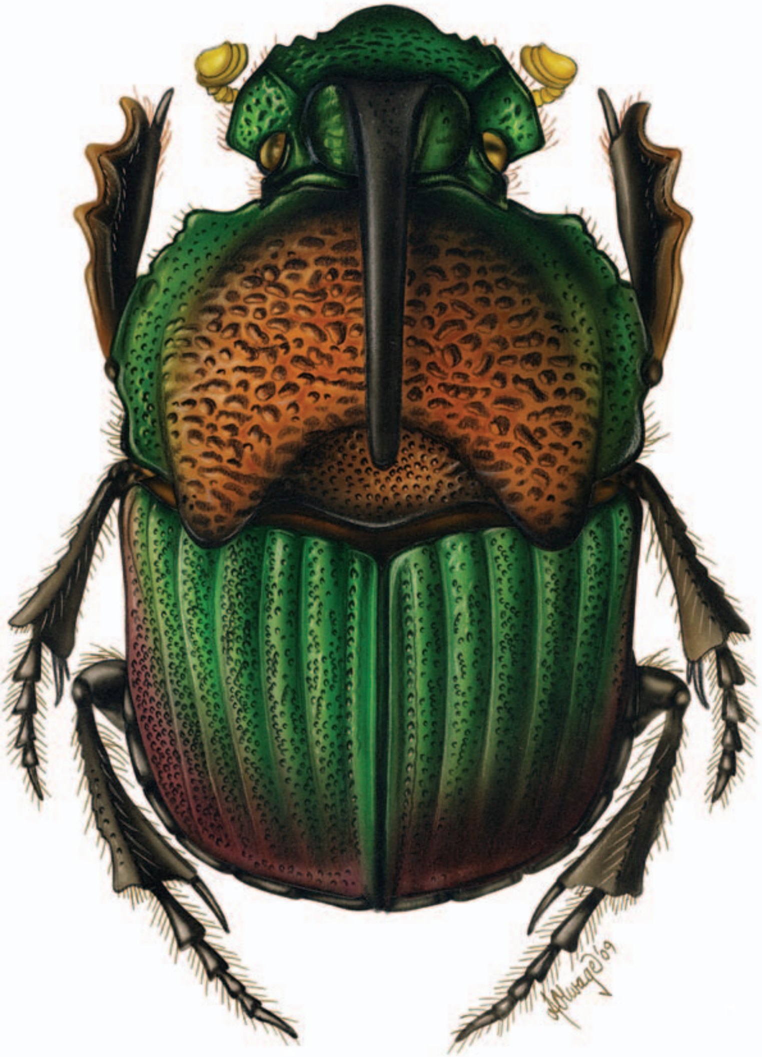


Plate 12.4. Tribe Phanaeini; *Phanaeus difformis*, male, Texas, USA, 22 mm.

and *Tetramereia*. *Bolbites, Homalotarsus, Megatharsis* and *Tetramereia* are monotypic. The other genera have between two (*Oruscatus*) and about 50 species (*Phanaeus*). The genera consist of groups of very different appearance. Some are squat and short-legged and generally flattened (*Dendropaemon*), others are robust, convex and long-legged (*Bolbites*). They may be brightly metallic-coloured (*Phanaeus*) or dark matte and range in average body size from moderate to quite large (10.0 – 35.0 mm). Males and females of some groups are horned. Some of the easily visible external characters that are more or less unique to the Phanaeini are: the mesosternum with a median T-shaped ridge; absence of hind tarsal claws; width of third labial palpomere much narrower than the second; seventh antennomere short and rounded or cup-shaped; posterior margin of metascutellum with abundant long setae. Species of some of the genera have reduced tarsomeres on the middle and hind tarsi (to four in some *Tetramereia* and to three in some *Dendropaemon*).

Diversity and distribution: The Phanaeini consist of 12 genera and about 150 species, all in the New World. Its members are prominent in the dung beetle fauna of the region, comprising about 8% of the species.

Phylogeny and evolutionary history: Most of the genera are well defined and there has been little disagreement among dung beetle researchers about the definition of the genera, but, by contrast, there has been little consensus over some of the genera that constitute the tribe (see Philips *et al.* 2004a). At various times the eucraniine *Ennearabdus* and the dichotomiine *Pteronyx* have been included in the tribe, and Edmonds, the leading authority on the group (Edmonds 1972, 1984, 2000) excluded *Bolbites, Gromphas* and *Oruscatus* from the group because they were considered (see Halffter and Edmonds 1982) to belong to the Dichotomiini (which they treated as a subtribe of the Coprini).

Edmonds (1972) published the first, albeit highly unresolved tree, with hypothesised generic relationships within the group. It excluded the three genera mentioned above but illustrated that all the other genera, except for *Sulcophanaeus* (Edmonds 2000) are probably monophyletic (four are monotypic). This study was followed by that of Zunino (1985) who attempted to place the Phanaeini in the broader context of relationships in the Scarabaeinae and concluded that they are sister to the Old World Onitini.

Philips *et al.* (2004a) undertook a comprehensive morphological phylogenetic study of the tribe. Their analyses included representatives of all of the genera (except for the very rare *Homalotarsus*), the three *Dendropaemon* subgenera, and of each of the five *Sulcophanaeus* species groups identified by Edmonds (2000), and 137 morphological characters. They rooted the analyses with representatives of several New World as well as Australian (*Thyregis*) and African (*Xinidium*) dichotomiine genera, the eucraniine *Ennearabdus* and an African onitine (*Onitis fulgidus*) because of the past implied relationships to these groups. The analyses returned a monophyletic Phanaeini (none of the outgroup taxa was found within the ingroup) with a strict consensus tree of 601 steps, CI of 0.43 and RI of 0.68 (Fig 12.4). The coprophagous genera *Bolbites, Gromphas* and *Oruscatus*, which had been excluded from the Phanaeini in the past, were basal on the tree and the myrmecophile, *Dendropaemon*, terminal. The sister group relationship of the phanaeines, however, was not quite as clear but Philips *et al*. (2004a) concluded that it was unlikely to be the Onitini as proposed by Zunino (1985) but rather the Eucraniini, and that they, together with the Phanaeini, appear to be derived from a dichotomiine-like ancestor. This hypothesis was supported by a molecular phylogenetic analysis of a large data set using two gene regions and 45 taxa (Ocampo and Hawks 2006) and another using three gene regions and 214 taxa (Monaghan *et al*. 2007).

Geographical origin: It is apparent from their current distribution, that the Phanaeini probably evolved in South America from an ancient Gondwanan ancestor and that they probably entered North America after the Panamanian land bridge reopened in the Pliocene (Philips *et al*. 2004a). Since phanaeines are amongst the largest New World tunnelling dung beetles, it is tempting to speculate that they may have evolved in response to the abundance of dung produced by the Miocene Neotropical mega-mammal fauna and that the extinction of the latter in the Pleistocene may have caused phanaeine extinctions too, or prompted the switch to carrion, mushrooms and myrmecophily found in the group. The basal taxa in the Philips *et al*. (2004a) phylogeny are coprophagous while the intermediate species are carrion- or mushroom-feeders, and the terminal taxa, myrmecophiles.

Biological and ecological notes: Phanaeines have fairly diverse biology; many are coprophagous but carrion-feeding is common and mushroom-feeding has been recorded. Members of the *Phanaeus* subgenus *Megaphanaeus*, which, as implied by the name are large – they are almost exclusively carrion-feeders and Martinez (quoted in Halffter and Matthews 1966) reported that four individuals of the very large species *Phanaeus* (*Megaphanaeus*) *ensifer* buried the carcase of a 10 kg dog in one night. The most unusual biology recorded for phanaeines is an association with leaf-cutter ants (*Atta* sp.) by *Dendropaemon* and *Tetramereia* (Vaz-de-Mello *et al*. 1998), and although the biology of *Homalotarsus* and *Megatharsis* is unknown, they are also suspected to be associated with leaf-cutter ants (Philips *et al*. 2004a). Phanaeine breeding biology has been fairly

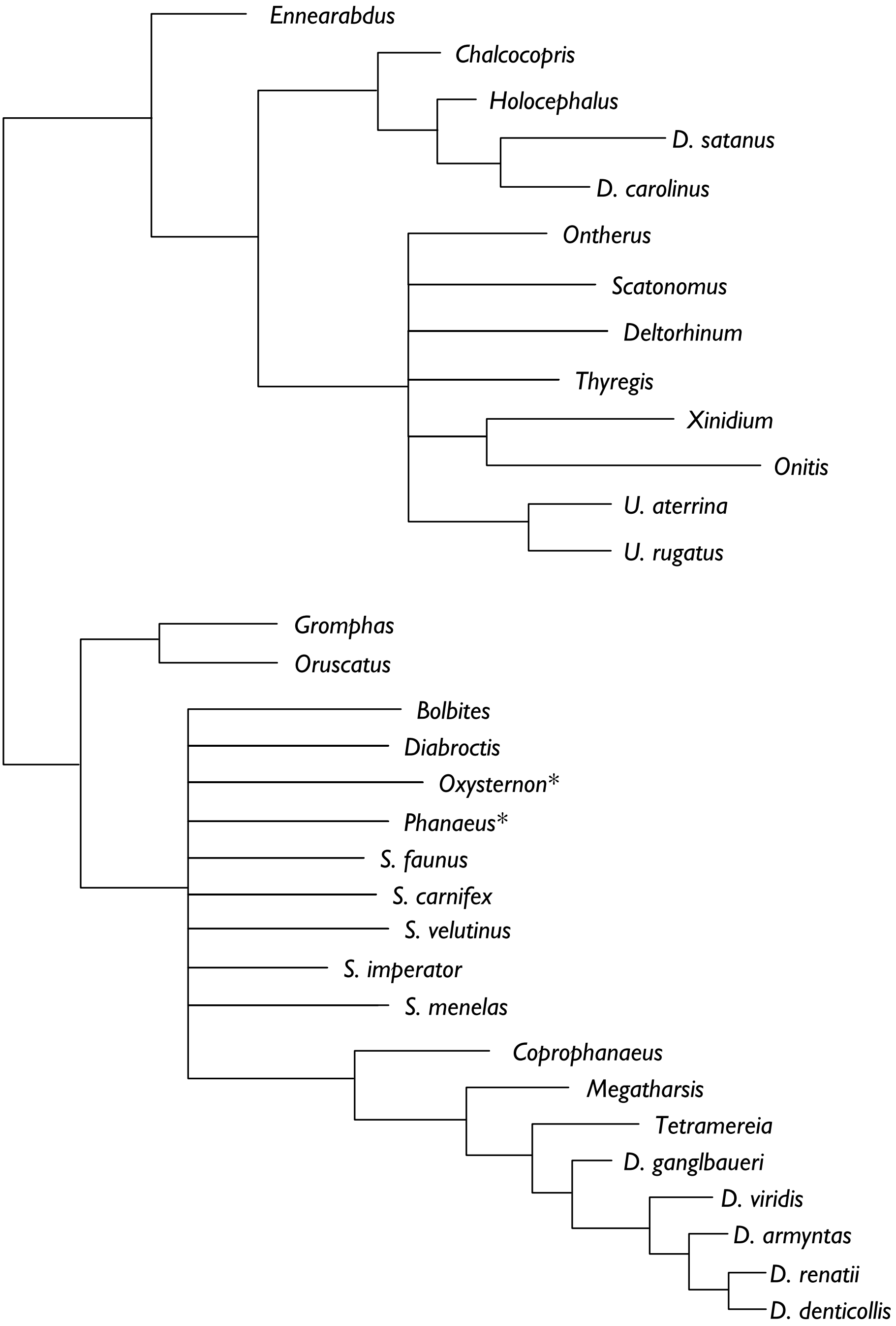


Fig. 12.4. Tree after Philips *et al.* (2004a) indicating monoplyly of the Phanaeini and sister to a group of Eucraniini and Dichotomiini.

well studied (see Chapter 4.1.5.1, Halftter and Edmonds 1982; Cabrera-Walsh and Gandolfo 1996) and varies from simple nests in which a vertical gallery is packed with a cylindrical brood mass of dung by the female and an egg laid in an earthen cell at the upper end (*Gromphas*) to a situation where nests containing one or more brood balls are constructed and placed in separate galleries by a co-operating pair of beetles (*Phanaeus*).

12.1.4 Coprini

Taxonomy and morphology: The Coprini comprise shiny black, medium- to large-bodied species averaging 9.5 mm to 30.0 mm long (Plate 12.5). Body shape is mostly elongate but tends to oval in *Metacatharsius*, although it is always strongly convex. The mid and hind tibiae are short in all species. There are from 8 to 10 elytral striae. As in the Dichotomiini, the second article of the labial palps is shorter than the first and the third article is always clearly visible. Although the Coprini are characterized, especially, by an external ridge on at least the hind tibiae, this is often very short, with a subterminal tooth. Recent studies suggest that the characterization used to define and separate this tribe from the Dichotomiini does not have any phylogenetic validity. Current arguments revolve around absorbing the Coprini into the Dichotomiini or redefining their characterization to retain two tribes but with different generic membership. These findings are discussed below and also in the section on the Dichotomiini.

Diversity and distribution: As traditionally constituted, this tunnelling tribe comprises a total of about 400 species in 10 valid genera. Three of these genera comprise two Australian endemics (*Coptodactyla* and *Thyregis*) and a genus that shows a combined Palaearctic/Oriental distribution (*Synapsis*). Of the remaining seven genera, four are species-poor Afrotropical rain forest or moist savanna woodland endemics (*Copridaspidus*, *Litocopris*, *Pseudocopris*, *Pseudopedaria*). The other three are species-rich and widespread. *Metacatharsius* is regionally restricted in Africa owing to its association primarily with deep sands, in arid or moist savanna, although a single species is shared between Africa and the arid south of the Palaearctic region from Arabia to western Pakistan. The other two genera are widespread throughout the moister regions of Africa south of the Sahara with *Catharsius* also occurring in the Oriental region and *Copris* (Plate 12.5) also in the Palaearctic, Oriental, and Nearctic regions, just penetrating the Neotropical region through Central America as far as the northern part of South America to the west of the Andes.

Plate 12.5. Tribe Coprini; *Copris elphenor*, male, South Africa, 21 mm.

Phylogeny and evolutionary history: It is difficult to provide an entirely acceptable account of evolutionary history for the Coprini as presently constitued owing to differing opinions on its validity and composition. These differences stem from several recent phylogenetic studies. One study (Montreuil 1998), used 42 characters to analyze relationships between 26 genera of Coprini and Dichotomiini (out of 40 worldwide). This analysis produced two large clades, one named as the Coprini and one as the Ateuchini (Fig. 12.1). The Ateuchini comprised only former dichotomiine genera whereas the new Coprini comprised both genera of the former Coprini and Dichotomiini. The included five genera of the original Coprini formed two groups separated by two lineages of former dichotomiine genera, which included the African *Macroderes*, *Xinidium* and the Afro-Oriental *Heliocopris*. Another study (Philips *et al*. 2004b) of the Scarabaeinae used 200 characters to analyze relationships between 47 genera, including 14 Coprini and Dichotomiini. In this study, the Coprini were embedded within and indistinguishable from the basal Dichotomiini and Canthonini (Fig. 12.2). This suggests a history apart from the remaining tribes, which were mostly grouped together in derived and terminal positions on the evolutionary tree. The Coprini were also shown to be polyphyletic since the Australian *Coptodactyla* and the Palaearctic / Oriental *Synapsis* each showed sister relationships with different sets of genera to the two studied African taxa (*Copris*, *Metacatharsius*). This arrangement was not supported by the Montreuil (1998) phylogeny where *Copris* and *Metacatharsius* were sister genera and *Heliocopris* and *Xinidium* occurred on more distant lineages. Three recent molecular studies have yielded yet different hypotheses on the Coprini. Villalba *et al*. (2002), using only European taxa, returned a phylogeny with *Copris* as the only genus sampled, sister to the sisyphine genus *Sisyphus*, and they, in turn, were sister to a clade composed of *Gymnopleurus* and *Scarabaeus* species (Fig. 12.5). However, support for these clades was weak. Ocampo and Hawks (2006) also used a subset of scarabaeine taxa, albeit with broader representation than Villalba *et al*. (2002), and they recorded strong support for relationship between *Copris* (one North American, and one South African species) and the Scarabaeini, represented by three South African species of two genera (Fig. 12.6a,b). This is somewhat congruent with Villalba *et al*.'s (2002) results. Monaghan *et al*. (2007) sampled 14 taxa (4 genera) from a wide geographical area – *Copris* was represented by species from Costa Rica, Indonesia and South Africa, *Catharsius* from Indonesia and South Africa, *Metacatharsius* from South Africa and *Coptodactyla* from Australia. *Catharsius* and *Metacatharsius* formed a monophyletic clade, with strong support for a sister relationship to the Gymnopleurini. *Copris* was monophyletic on a distant but more basal clade, sister to the dichotomiine, *Heliocopris*, and the canthonine *Panelus*. *Coptodactyla* lay in the Australian clade

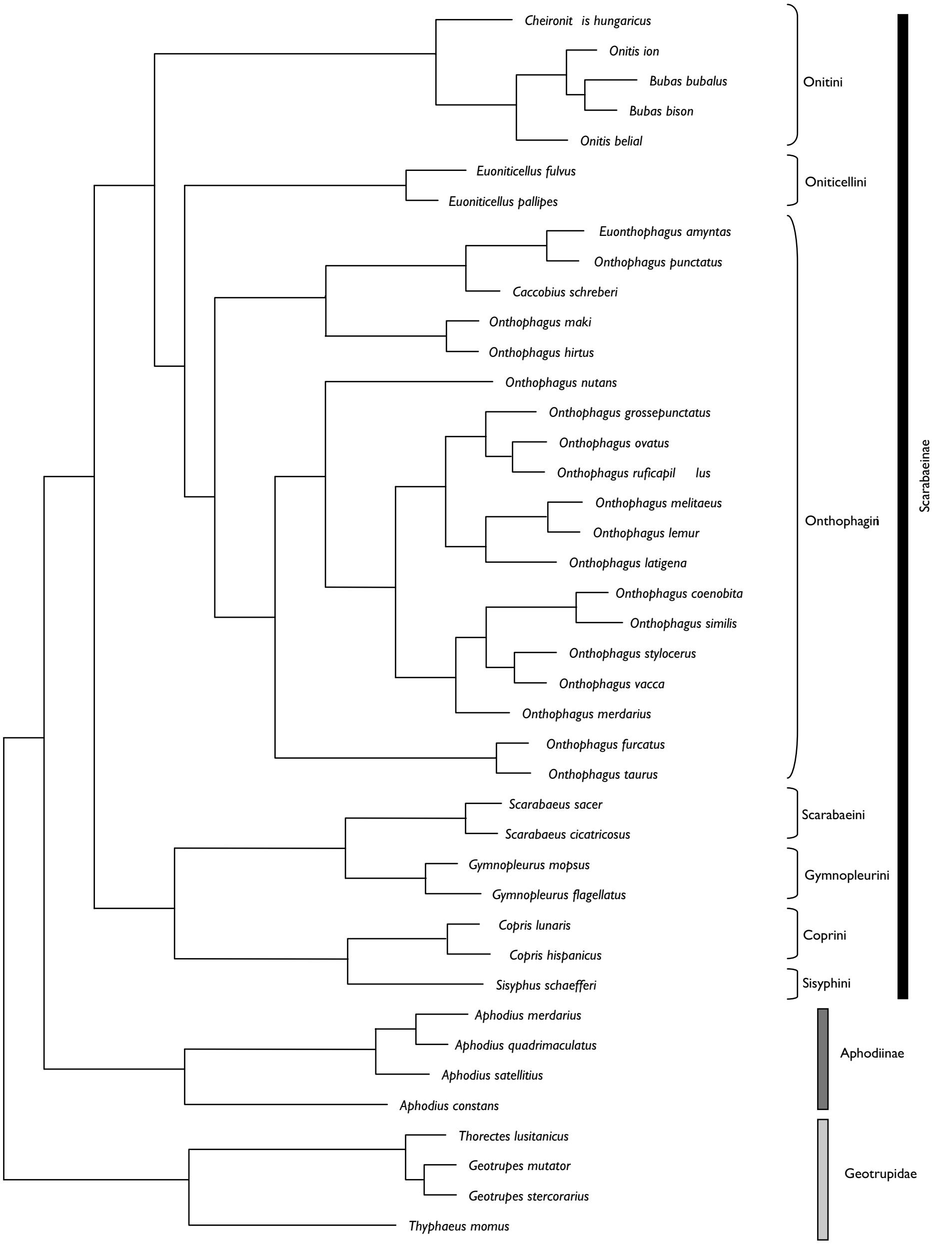


Fig. 12.5. Molecular phylogeny of Iberian Scarabaeinae. (After Villalba *et al.* 2002).

consisting of representatives of all the Australian tribes except Onthophagini (Fig. 12.7). Philips *et al.*'s (2004b) study was the only one to include the Palaearctic/Oriental *Synapsis*, and their analyses suggested a sistergroup relationship with the dichotomiine *Heliocopris*. Consequently, for the size of the tribe, it is the one with least phylogenetic structure and, based on all the recent studies, is undoubtedly polyphyletic. There is, consequently, no justification for retaining it – the question, however, remains of where to place the disparate genera?

Geographical origin: It is difficult to discuss the origins of the genera of the original Coprini considering the unresolved arguments on generic affiliations and tribal level systematics. However, it is possible to question their origin without resolving their classification. The observation that their greatest overall species endemism is in the Afrotropical region would strengthen hypotheses for an African origin. Whereas the four species-poor genera (*Copridaspidus*, *Litocopris*, *Pseudocopris*, *Pseudopedaria*) are endemic to the region, diversification of two species-rich genera (*Metacatharsius*, *Catharsius*) has also been predominantly within Africa with few species in the Palaearctic or Oriental regions. Although the large genus *Copris*, is represented in five biogeographical regions with less than half of the species occurring in Africa, species level relationships suggest that this distribution results from relatively recent range expansion, although the historical details of species diversification are not known. As there are two taxonomic groups within Nearctic *Copris* that are not duplicated in Afro-Eurasia, it appears that the American *Copris* fauna originates from two separate range expansion events. This evidence is suggestive of range expansion into North America from the direction of Afro-Eurasia, perhaps coeval with the Miocene and Pliocene Epoch land links between the regions at Beringia. A period of intervening geographic isolation in America would account for the taxonomic divergence between species groups of the first and second waves of immigration. The Australian genus *Coptodactyla* apparently evolved in Australia from an endemic ancestor unrelated to any modern coprines (Monaghan *et al.* 2007), and although untested, the same probably applies to the other Australian coprine genus, *Thyregis*.

Biological and ecological notes: The Coprini are primarily coprophagous although there are also necrophagous species showing specialist association with carrion. There are, however, insufficient quantitative data to determine dominant trends in dung associations, if any. There are quantitative records of omnivore dung specialists, herbivore dung specialists, and dung generalists on both ruminant herbivore and omnivore dung. Further species have been observed to show associations with elephant or rhinoceros dung. A minority of species has been

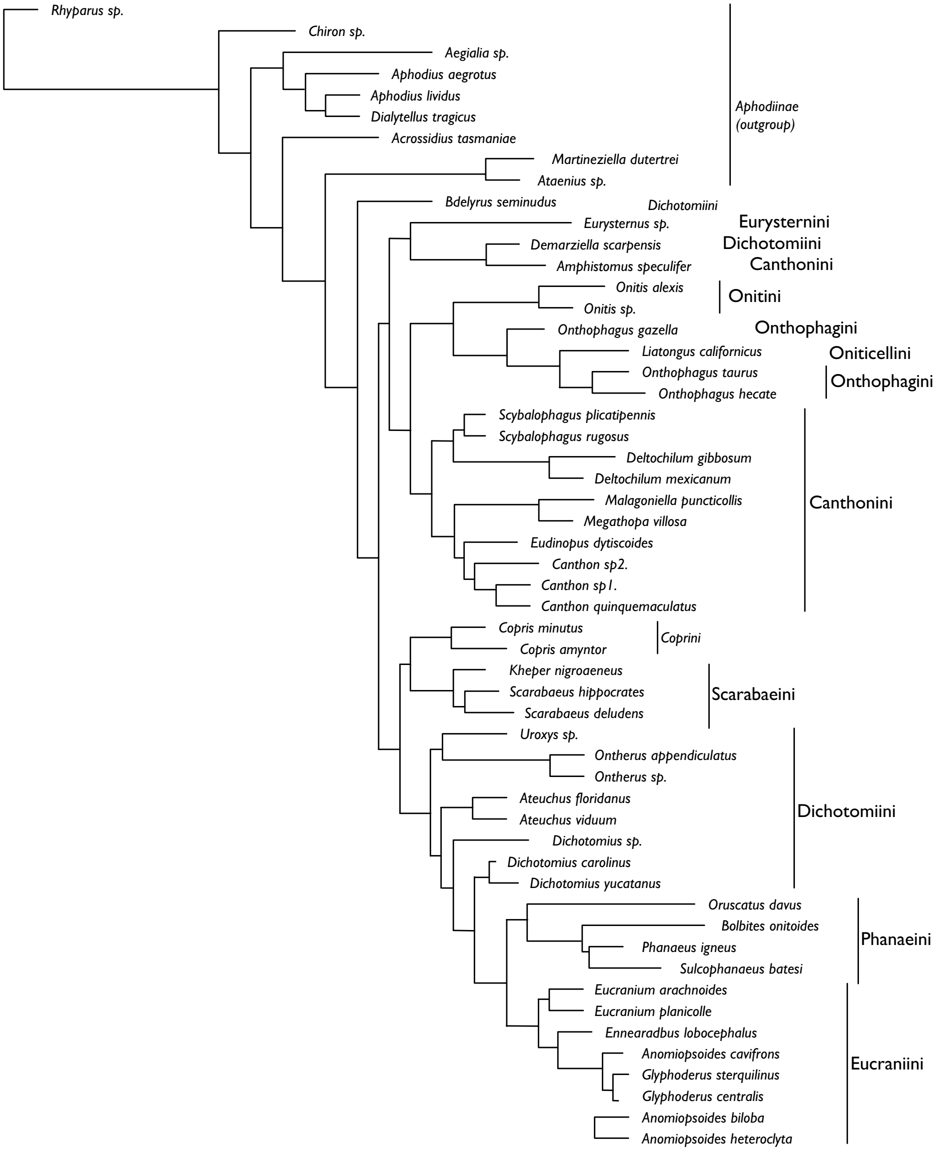


Fig. 12.6. (a) Phylogram of a maximum likelihood tree depicting the phylogenetic relationships of Scarabaeinae beetles included in the analysis (mostly Neotropical groups). (After Ocampo and Hawks 2006).

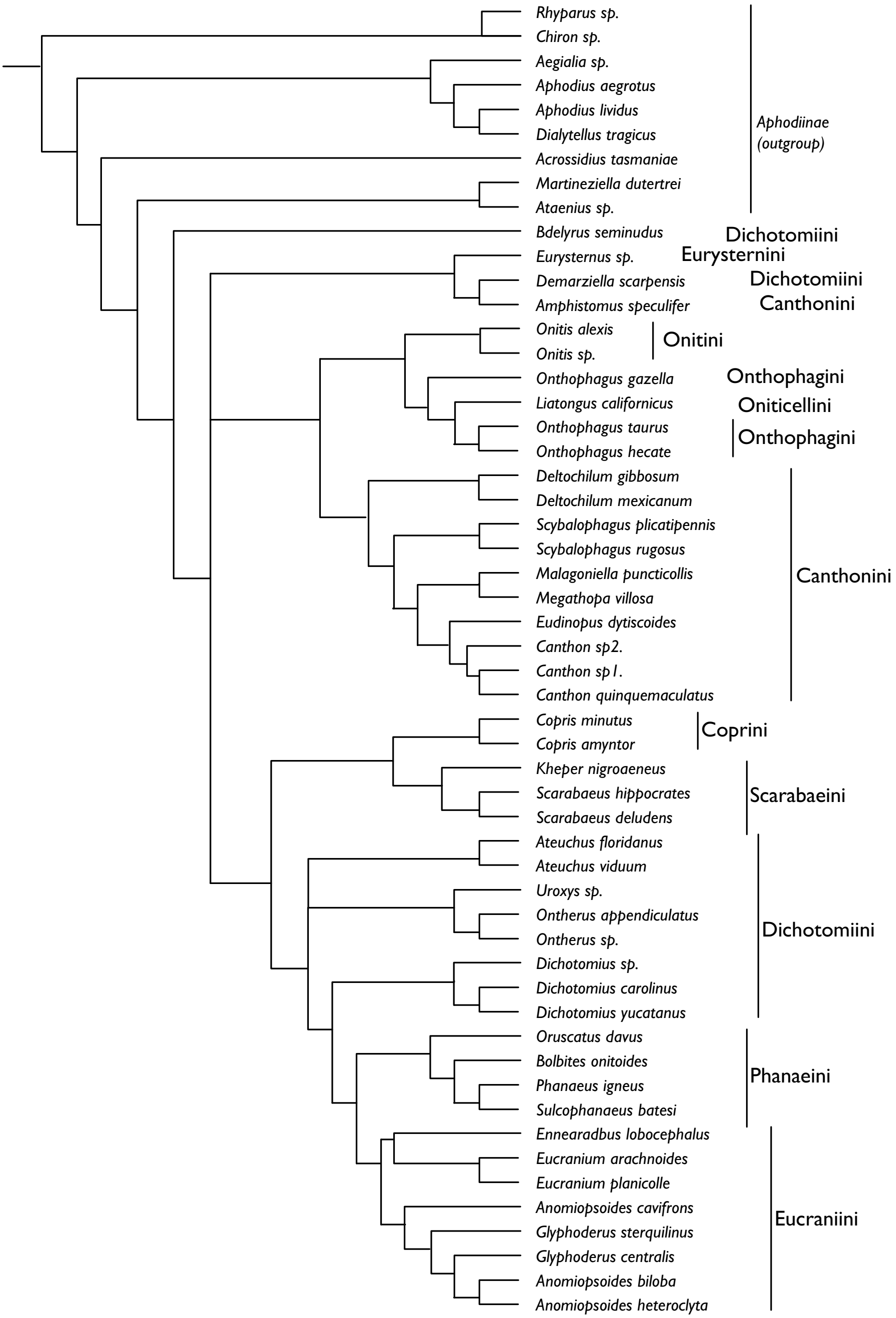


Fig. 12.6. (b) Phylogram of a majority rule consensus tree of the 20 000 trees sampled by the Markov chain (Bayesian analysis) for a selection of, mostly Neotropical, Scarabaeinae. (After Ocampo and Hawks 2006).

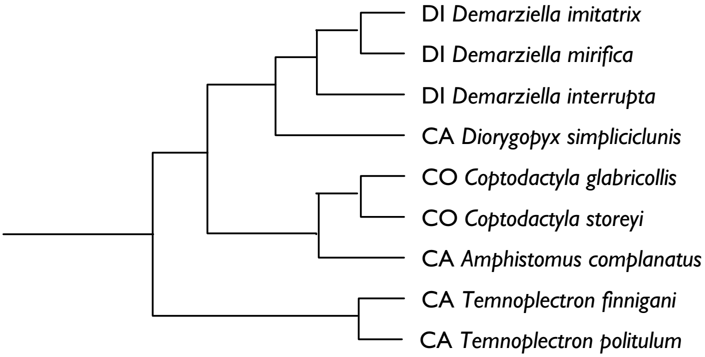


Fig. 12.7. The "Australian" clade extracted from Monaghan *et al.* (2007), illustrates shared ancestry between the Dichotomiini (DI), Canthonini (CA) and Coprini (CO) of the continent.

observed to show necrophagous habits, particularly in *Catharsius* and *Metacatharsius*. The Coprini show predominantly nocturnal flight activity although there are a few diurnal *Copris* species in cooler climates, e.g. the southern African montane species, *Copris caelatus*. The genera are classed as fast-burying tunnellers as dung is first rapidly removed into a tunnel following which it is re-located into one or more deeper tunnels for nest construction. The compound nests of the Coprini comprise brood ovoids or brood balls constructed separately in several chambers in a Type 6 manner (*Catharsius*) or together in a single chamber in a Type 7 manner (*Copris*). There is well developed biparental nesting in *Copris* (Halffter and Edmonds 1982).

12.1.5 Oniticellini

Taxonomy and morphology: The Oniticellini are characterized by antennae with eight articles and by a small but usually visible scutellum. The body shape is elongate, usually quasi-rectangular but occasionally tapering posteriorly, with a slightly flattened, square appearance from an end-on view (Plates12.6-12.8). The mid and hind tibiae are short in all species. The genera show small to moderate body size averaging from 4.5 mm to 18.0 mm long. In general, species separation is based on sculpturing and/or punctuation of the head, pronotal disc and / or elytra (horns, spines, ridges, depressions).

Diversity and distribution: This tribe of about 180 described species comprises 15 genera assigned to three different subtribes, the Helictopleurina, Drepa-

Plate 12.6. Tribe Oniticellini; subtribe Helictopleurina; *Helictopleurus quadrimaculatus*, Madagascar, 12 mm.

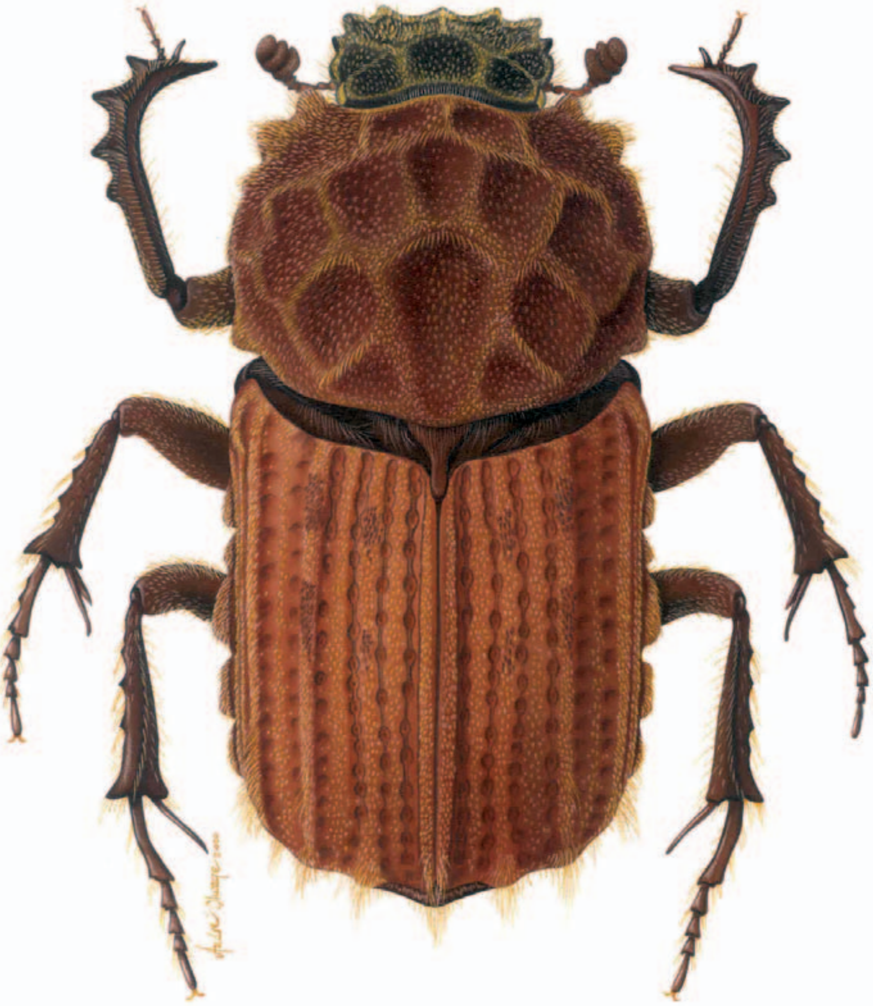


Plate 12.7. Tribe Oniticellini; subtribe Drepanocerina; *Cyptochirus ambiguus*, South Africa, 10 mm.

Plate 12.8. Tribe Oniticellini; subtribe Oniticellina; *Tragiscus dimidiatus*, male, South Africa, 19 mm.

nocerina and Oniticellina. The two genera and about 60 species (the monotypic *Heterosyphus* and *Helictopleurus* (Plate 12.6), with the rest of the species) of the Helictopleurina are restricted to Madagascar whereas the other two subtribes show greatest diversity in Africa but are also represented in the Palaearctic, Oriental, Nearctic and Caribbean regions (Oniticellina), or the Oriental and Caribbean regions (Drepanocerina). Most of the six drepanocerine genera are species-poor (1-6 species) and endemic to particular biogeographical regions, either the Afrotropical (*Drepanoplatynus*, *Cyptochirus* (Plate 12.7), *Scaptocnemis*), the Oriental (*Sinodrepanus*), or the Caribbean (*Anoplodrepanus*), while one genus is more species-rich with an Afrotropical-Oriental distribution (*Drepanocerus*). The seven genera of the Oniticellina are also mostly species-poor with five comprising only 1-8 species. Four monotypic genera are restricted to single biogeographical regions, either the Afrotropical (*Tragiscus* – Plate 12.8), Oriental (*Yvescambefortius*), Nearctic (*Attavicinus*) or the Palaearctic (*Paroniticellus)*. The other genera are more widespread with two species-poor taxa showing an Afrotropical-Oriental distribution (*Tiniocellus*, *Oniticellus*), and two species-rich taxa showing an Afrotropical, Oriental, Palaeartic and Caribbean distribution (*Euoniticellus*), or an Afrotropical, Oriental and Nearctic distribution (*Liatongus*).

Phylogeny and evolutionary history: Oniticellini is the only tribe with three generally-accepted subtribes, the Madagascan endemic Helictopleurina being one of them and although Oniticellini have been considered in fairly recent phylogenetic analyses (Villalba *et al.* 2002 – only European *Euoniticellus*, subtribe Oniticellina; Philips *et al.* 2004b – members of both Oniticellina and Drepanocerina), Helictopleurina have only been included in phylogenetic studies very recently (Monaghan *et al.* 2007; Orsini *et al.* 2007; Wirta *et al.* 2008).

Three recent phylogenetic reconstructions of the Scarabaeinae have yielded some broadly congruent similarities concerning Oniticellini and their position on phylogenetic trees although taxon sampling and characters used have varied considerably. The first [molecular] study of a geographically retricted [Iberian] subset of scarabaeine taxa only included two species of *Euoniticellus* (Oniticellina – Villalba *et al.* 2002). The second was a morphological study with a matrix of 50 taxa and a large suite of morphological characters (Philips *et al.* 2004b) and included eight genera of Oniticellina and Drepanocerina. The third, a molecular study involving three gene regions and 214 dung beetle species (Monaghan *et al.* 2007) also included eight genera but these represented all of the subtribes for the first time. Orsini *et al.*'s (2007) study was aimed specifically at resolving relationships within the genus *Helictopleurus*. Monaghan *et al.*'s (2007) study included five *Helictopleurus* species and Orsini *et al.*'s (2007), 17 species of the genus, also in a molecular phylogenetic study. In a subsequent study to Orsini *et al.*'s (2007), Wirta *et al.* (2008) examined the evolutionary history of the Helictopleurina and its relationship to Oniticellina and Drepanocerina in a molecular study.

Villalba *et al.*'s (2002) results returned a monophyletic Oniticellini, sister to the Onthophagini. According to Philips *et al.*'s (2004b) phylogeny of the Scarabaeinae, the Oniticellini are positioned on a lineage that includes the Sisyphini, together with the Onitini, Onthophagini, and South American Eurysternini (Fig. 12.2) and although the intertribal relationships remained mostly unresolved, the Oniticellini and Onthophagini both show vesicles on the seventh and eighth articles of the antennae, which are likely to be important phylogenetic characters and very likely indicate a shared evolution as sister groups. Monaghan *et al.*'s (2007) study yielded a paraphyletic Oniticellini, with strong support for the inclusion of three onthophagine genera in the clade, and terminal and monophyletic *Helictopleurus* whereas the representatives of the other subtribes showed no phylogenetic pattern, with drepanocerine and oniticelline taxa sorting independently of presumed relationship. The oniticelline clade was sister to, also with strong support, a strictly onthophagine one consisting of a large number of sampled taxa.

Orsini *et al.* (2007) sampled 17 species of *Helictopleurus* and obtained sequence data from two nuclear (18S 28S) and five mitochondrial genes (16S, 12S, COI, CO*b* and COII). They rooted the data with the S-E Asian onthophagine *Onthophagus* (*Parascatonomus*) *penicillatus* and analyzed them using both maximum parsimony and Bayesian analysis. The phylogeny was well resolved and the trees obtained with parsimony and Bayesian analysis were congruent (Fig. 12.8). The analyses returned a monophyletic *Helictopleurus* that apparently underwent rapid radiation close to the origin of the group. Based on the sequence information of the encoding mitochondrial genes, Orsini *et al.* (2007) also estimated the ages of the *Helictopleurus* radiation using the absolute calibration of branch lengths of 2% divergence per million years, a widely used figure for insect mtDNA. On the basis of this they calculated that *Helictopleurus* evolved 8.6 mya. The age of this, Miocene, event is consistent with that of the evolution of other similar taxonomic levels of Scarabaeinae (also see Canthonini section, for Orsini *et al.*'s 2007 ageing of Madagascan genera).

Wirta *et al.* (2008) expanded the Orsini *et al.* (2007) study by examining the position of Helictopleurina relative to members of the other subtribes. Their study included five gene regions (28S, 18S, 16S, COI and Cytb) of about half of the recorded species of *Helictopleurus* known from Madagascar and 24 species of the presumed sister groups of the Helictopleurina. These included African and Oriental Oniticellina, Drepanocerina, Onitini, Onthophagini and Coprini. Their phylogenetic analyses were based on 2 608 aligned base pairs of which

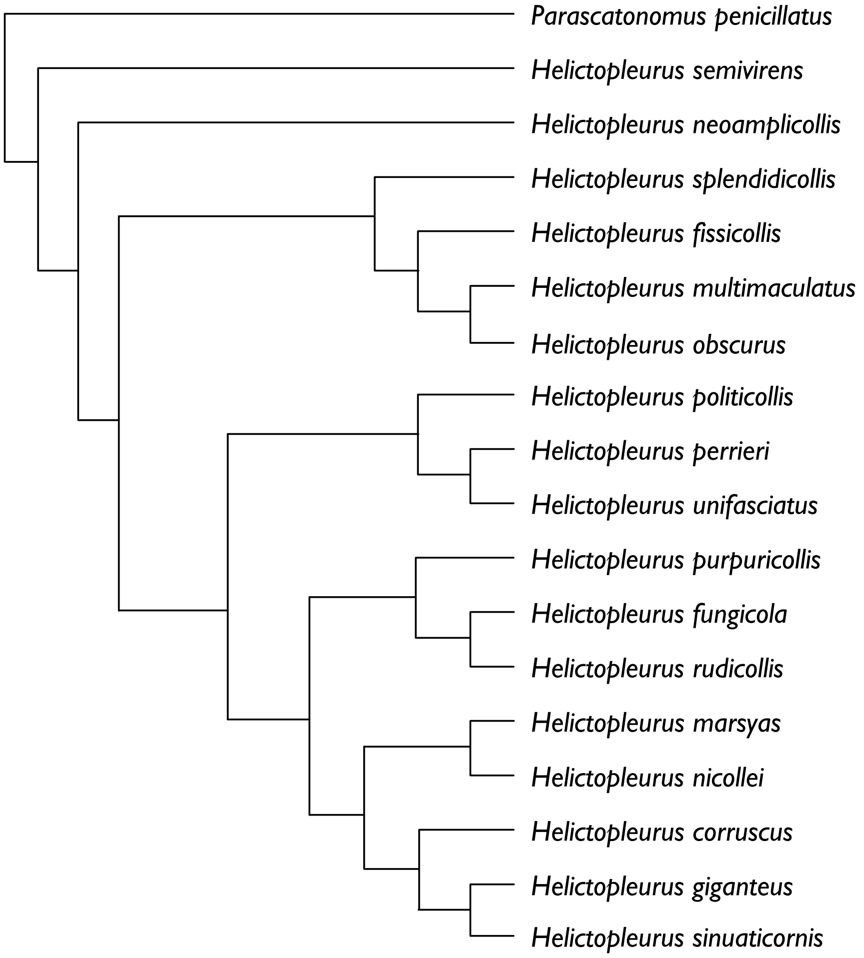


Fig. 12.8. Monophyly of *Helictopleurus* (Oniticellini) of Madagascar. (After Orsini *et al.* 2007).

about half consisted of nuclear sequences. They subjected their data to Bayesian analysis and their majority rule consensus Bayesian tree (Fig. 12.9) supported the following relationships. The outgroup Coprini was strongly supported as separate from the other tribes (posterior probability of 1.00). The next two branches supported clades comprised of eight African Onthophagini species as well as the node separating them from the other Oniticellini and Onitini. Amongst the more derived clades, basal support was weak but the tips were well supported. These latter clades included species from Africa and Asia as well as Onthophagini from Madagascar.

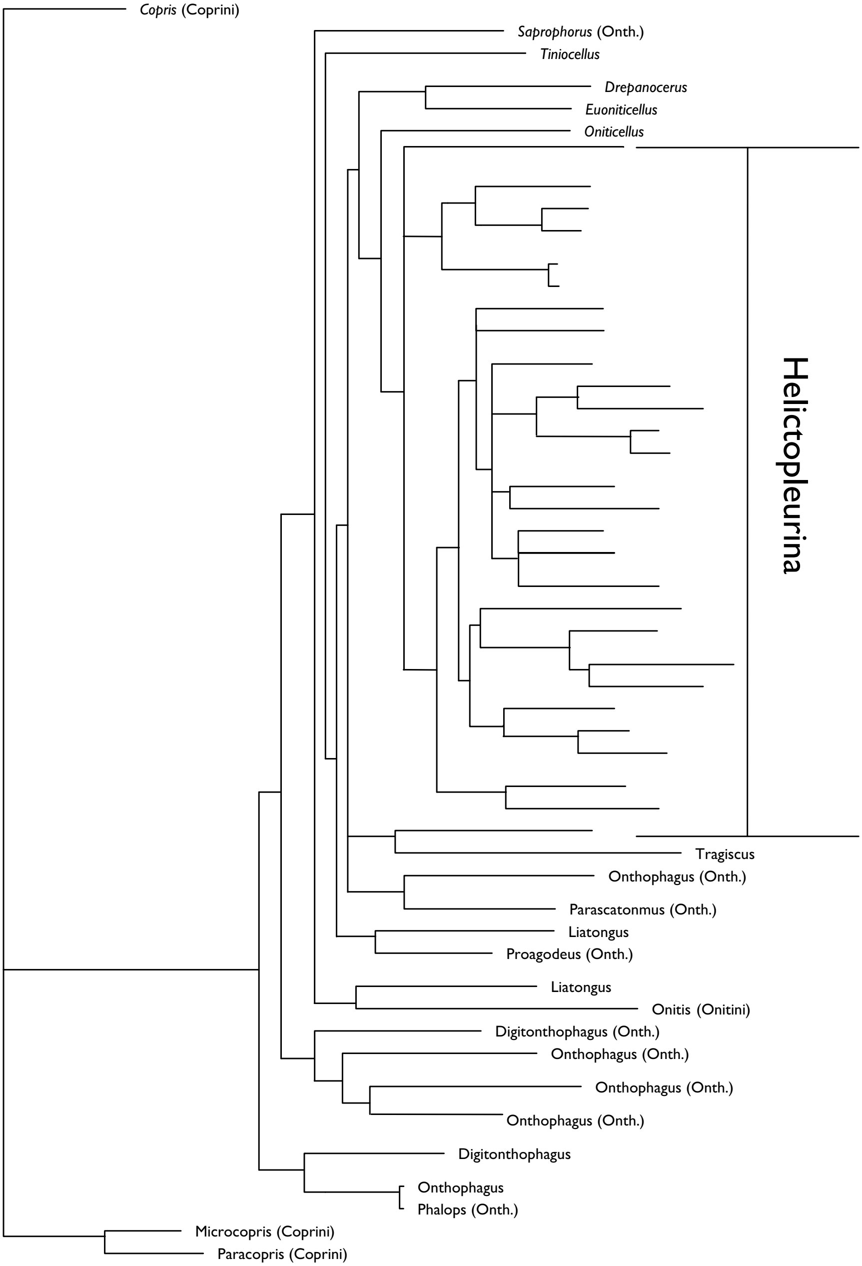


Fig. 12.9. Majority rule consensus Bayesian tree of Madagascan Helictopleurina (Oniticellini) and an assortment of extra-limital Oniticellini (genera on figure without tribal affiliation stated), Onthophagini (Onth.), Onitini and outgroup Coprini. (After Wirta *et al.* 2008).

The Helictopleurini comprised a strongly supported monophyletic clade (posterior probability of 1.00), sister to the African *Oniticellus planatus* (Oniticellini), and they, in turn, were sister to the African *Euoniticellus triangulatus* (Onticellini) and *Drepanocerus laticollis* (Drepanocerina).

Wirta *et al.* (2008) also estimated times of divergence of the groups by pooling two protein-coding mitochondrial regions (COI and Cytb) and assuming rates of evolution of 0.0075 and 0.012 substitutions / site / my to cover the published rates reported. Their timing analysis was done with BEAST 1.4 (Drummond and Rambaut 2002-2006, in Wirta *et al.* 2008) which uses Bayesian MCMC estimation. They used the model GTR+I+G for the concatenated COI and Cytb sequences matrix and assumed the relaxed-clock model and uncorrelated rates for each branch, drawn independently from a lognormal distribution. They used the topology inferred from the Bayesian analysis as the fixed topology, including Helictopleurina and its closest relative, *Oniticellus planatus*. They estimated the time of divergence of the former from the latter and used the TMRCA statistics to estimate the the time of most recent common ancestor for two sets of *Helictopleurus* taxa, one including all the species, the other including two species clusters. They then estimated the the times of branching events using TMRCA statistics and assumed the the rate of 0.012 substitutions / site / my.

Wirta *et al.*'s (2008) estimated time of divergence of Helictopleurina from *O. planatus* was 44 mya (29/64) and 28 (18/39) mya for the rates of 0.0075 and 0.012 substitutions / per site / my (with upper and lower 95% credibility limits given in brackets). The time since the evolution of the most common ancestor of all Helictopleurina was estimated to have occurred 35 (25/44) and 23 (17/29) mya, suggesting that radiation of the Helictopleurina started some 5 my after colonization. Although the 95% credibility intervals are wide, Wirta *et al.* (2008) prefer the more recent time to reflect the more likely evolutionary scenario since it is more in line with other existing ones. Although Orsini *et al.* (2007) put the divergence time of the Helictopleurina at 8.6 mya, Wirta *et al.* (2008) consider their estimates superior to those of Orsini *et al.* (2007). Using lineage-through-time plots (Nee *et al.* 1992 in Wirta *et al.* 2008) they estimated that radiation of the Helictopleurina started 5 my after colonization and that the highest rate of species increase was between 20-10 mya, after which it slowed down.

Geographical origin: The endemism of the Helictopleurina to Madagascar points to an origin on Madagascar and the high numbers of taxa in the Oniticellini/Onthophagini that are centred in Africa imply an origin there. The radiations of the few American representatives of the Oniticellini are thought to have occurred in the Miocene and Pleistocene Epochs which offer the most plausible time frames for the origin of Neotropical Oniticellini, particularly since all land linkages to and within the Northern Hemisphere occurred in the later Cenozoic age (Afrotropical to Palaearctic in the Eocene Epoch, Afrotropical to Palaearctic/Oriental in the Miocene Epoch, Palaearctic to the Nearctic at the Bering Straits in the Miocene and Pleistocene Epochs). It is presently unclear if the radiation of Oniticellina and Drepanocerina was unidirectional across Africa, Eurasia and the Nearctic or bi-directional.

Biological and ecological notes: Although only dung-breeding habits are known for the Afrotropical Oniticellini, Nearctic *Liatongus* are either fungus- (*L. rhinocerulus*) or ant-associated (Halffter and Edmonds 1982). The ant-associated, Nearctic species (previously *L. monstrosus*), *Attavicinus monstrosus*, is so modified in morphology that it recently had a new genus created to accommodate it (Philips and Bell 2008). Nesting by *A. monstrosus* is also distinctive in that it constructs broods in linear series in a single tunnel, and that there are no partitions between larvae in the feeding tunnels. They are simply separated by some distance. This differs to tunnelling genera in Africa (*Liatongus*, *Tiniocellus*, *Euoniticellus*), which show typical compound nests with single brood ovoids in the branched tips of the tunnel. *Attavicinus monstrosus* has a strictly obligatory associaton with the leaf-cutter ant, *Atta mexicana* (Halffter and Edmonds 1982). Adults inhabit and construct their nests beneath the debris piles produced by the ants. The latter is composed of decomposing remains of the ants' fungus gardens, the humus substrate on which it is based, and on dead ants, and is the only known food of adults and larvae.

A trend to surface nesting in some African genera is associated with a diversification of behaviour although there is no apparent phylogenetic signal in this step. This is either towards a simplified Type 1 nest comprising a single brood at the end of a short shallow tunnel or in a pit under the dung as in *Drepanocerus* or *Drepanoplatynus*, or towards greater complexity ranging from a compound brood cake comprising multiple broods in a chamber under the dung, brood ovoids in chambers at the dung earth interface, or spherical broods in chambers in the dropping itself, as exemplified, respectively, by *Cyptochirus*, *Oniticellus*, or *Tragiscus*. As nesting within droppings is shown by the Palaearctic genus *Paroniticellus* and the Afrotropical genera, *Oniticellus* and *Tragiscus*, endocoprid behaviour may have arisen independently more than once within the Oniticellini. All genera of the tribe Oniticellini show diurnal flight activity and most are associated with herbivore dung, although a few *Drepanocerus* are associated with omnivore dung (e.g. *D. caelatus*).

Orsini *et al.* (2007) recorded that many *Helictopleurus* species feed preferentially on lemur dung and speculated that they may have evolved in association with lemurs whose main radiation is thought to have taken place between 10-15 mya (Yoder and Yang 2004, quoted by Orsini *et al*. 2007).

12.1.6 Onthophagini

Taxonomy and morphology: The Onthophagini are characterized by antennae with either nine or eight articles, and by fore tibiae that usually bear four teeth but this number is reduced in some small and very small-bodied, possibly ant-associated genera, e.g. *Amietina*, *Walterantus*, *Alloscelus* (Plate 12.9), with three, and *Haroldius* with two. The mid and hind tibiae are short in all species. In lineages postulated to be basal with nine antennal articles, the body is usually short and convex but parallel-sided, although it tapers posteriorly in *Hyalonthophagus*, most *Phalops* and some *Proagoderus*. In derived lineages that include kleptocoprids but may be dominated by ant or termite association, the number of antennal articles is reduced to eight and the body shape is often either oval, or elongate and narrowed. The scutellum is not usually visible, except in a few taxa with nine antennal articles. Average body size of most genera varies from very small to moderate (1.9 mm to 12.0 mm) but does not usually overlap with that in the morphologically and ecologically similar Onitini, except in some larger-bodied *Diastellopalpus* (Plate 12.10) and *Proagoderus* (up to 22.0 mm). Species separation is based, especially, on horns, ridges and clypeal indentation on the head, sculpturing of the pronotal disc, and on punctuation and/or granulation of the head, thorax and abdomen.

Diversity and distribution: The tribe includes over 2200 species or roughly half of the total number of described scarabaeine species. It has been divided into about 40 genera, some of which are often still cited as subgenera of *Onthophagus*. However, in the strictest sense only slightly more than 1750 species are currently classified within this taxon. Even so, it will remain by far the most species-rich and widespread genus, both within the tribe and the subfamily, as long as the many further constituent subgenera and species groups are not raised to generic status. Native *Onthophagus* species (not introduced by humans) have radiated and speciated throughout the Afrotropical region (790 species), across warmer parts of the Palaearctic (220 species), and Oriental (345 species) regions, and into North (38 species) and South America (95 species). They have also dispersed to, and speciated in, Australia (280 species).

Members of the tribe are represented in all of the warmer ecotypes of the regions where they occur including forests, savannas, highlands, arid areas, and winter rainfall regions, where they show a range of food specializations including,

Plate 12.9. Tribe Onthophagini; *Alloscelus* sp., Kenya, 7 mm.

Plate 12.10. Tribe Onthophagini; *Diastellopalpus monapoides*, Tanzania, 22 mm.

dung, fungi, fruit, carrion and ant-association. Although they comprise primarily tunnelling taxa, some very small-bodied species groups show kleptocoprid habits in that they use dung buried by other dung beetles for breeding purposes. Except for the endemics in the Afrotropical (*Diastellopalpus*) and Oriental regions (*Strandius*), most species-rich genera (15-107 species) other than *Onthophagus*, are shared between Afro-Eurasia (*Caccobius*, *Phalops*), primarily between the Afrotropical and Palaearctic (*Euonthophagus*), or primarily between the Afrotropical and Oriental regions (*Proagoderus*, *Digitonthophagus*, *Cleptocaccobius*, *Haroldius* – the latter is ant-associated and was transferred from the Canthonini). The remaining, mostly species-poor, genera are either endemic to the Afrotropical region (23 genera comprising 1-12 species each) or the Oriental region (four genera comprising 1-7 species each, *Anoctus*, *Cassolus*, *Cyobius*, *Disphysema*, the two former known to be ant-associated). Species-poor, Afrotropical genera with either kleptocoprid or tunnelling habits include: *Hyalonthophagus* in open savanna, *Tomogonus* in more shaded savanna, and *Milichus*, and *Mimonthophagus* in forests and savannas. Most of the remaining 18 genera are relatively poorly represented in collections with limited records on dung, although termite- or ant-association is a recurring, though mostly poorly-studied, theme. The possibly ant- or termite-associated genera mostly show intertropical distributions in lowland forest (e.g. *Amietina*, *Walterantus*, *Alloscelus*) upland forest (e.g. some *Eusaproecius*), or forest savanna mosaic (e.g. *Cambefortius*) with limited radiation into more open, drier savannas (e.g. *Stiptopodius* – Plate 12.11), African *Haroldius*).

The four most basal genera (see below) comprise fairly small to large tunnelling taxa (10.0 to 18.0 mm). *Proagoderus* shows Afrotropical and Oriental distributions and is centred primarily in arid to moist savannas and forest. *Diastellopalpus* occurs primarily in Afrotropical forest (Josso and Prévost 2000) whereas *Phalops* and *Digitonthophagus* are centred in arid to moist savannas of the Afrotropical, western Oriental and the intervening central southern Palaearctic. A number of genera whose phylogenetic relationships have not been assessed have average body size that varies from very small to small (5.5 mm to 11.5 mm). Tunnelling habits probably predominate in *Strandius*, *Onthophagus*, and *Euonthophagus*, but habits of some other genera are unknown (*Milichus*). Several genera also include kleptocoprid species groups (*Onthophagus*) or they may comprise entirely species with kleptocoprid habits (*Caccobius*, *Cleptocaccobius*, *Tomogonus*, *Hyalonthophagus*).

An apparent trend to smaller body size and evolution of kleptocoprid habits may be linked to the radiation of larger-bodied dung beetles (some Scarabaeini, Dichotomiini, Coprini, Onitini) in response to the voiding of increasingly larger droppings by increasingly larger-bodied mammals during the Cenozoic Period. In some more derived, very small-bodied (2.7 mm), putative kleptocoprid taxa

Plate 12.11. Tribe Onthophagini; *Stiptopodius* sp., Mozambique, 6 mm.

(some *Caccobius*, *Cleptocaccobius*) the number of antennal articles is reduced to eight by the fusion of articles three and four. With the exception of *Cambefortius*, this condition is also shown by most of the remaining 18 Afrotropical (and four Oriental) genera of very small to fairly small body size (3.5 mm to 10.5 mm). For these 18 genera, the putative older lineages are very small-bodied with Afrotropical and Oriental (*Haroldius*), Afrotropical (*Megaponerophilus*, *Amietina*), or Oriental distributions (e.g. *Cassolus*) and may represent an earlier radiation that was followed in the Afrotropical region by diversification of the often larger-bodied, probably more terminally-derived 14 genera. However, these 14 genera probably comprise several separate evolutionary groupings: (*Cambefortius*); (*Alloscelus*, *Pseudosaproecius*); (*Pinacotarsus*, *Eusaproecius*, *Heteroclitopus*, *Pinacopodius*, *Sukelus*, *Stiptocnemis*, *Dorbignyolus*, *Krikkenius*); (*Stiptopodius*); (*Stiptotarsus*); (*Neosaproecius*). Limited observations suggest that many, if not all, of these 18 genera may be associated primarily with termites or ants although these are mixed with records from omnivore dung or carrion in some genera, e.g. *Amietina*. Thus, the series of separate radiations represented by the 18 taxa comprise the possibly earlier radiations associated with ants in *Haroldius*, *Megaponerophilus*, and *Amietina*; and the possibly later radiations associated with ants in *Alloscelus*; or termites in *Heteroclitopus*, *Krikkenius*, *Pinacopodius*, *Dorbignyolus*, and *Stiptopodius*. The development of trichomes (distinctive tufts of short or long hairs associated with glandular structures that are thought to produce chemicals that appease ant-hosts) is also considered to be characteristic of ant or termite association and has been observed in several genera, including on the latero-posterior wall of the thorax in *Haroldius* and on the legs in seven of the eight genera of the *Pinacotarsus* grouping (except *Eusaproecius*).

Phylogeny and evolutionary history: Because of the huge numbers of taxa in the Onthophagini any attempts at trying to resolve relationships amongst them have remained a daunting task and it has, understandably, been the advent of molecular analytical techniques and the complementary statistical phylogenetic procedures that have made this prospect appear achievable. Four recent molecular and one morphological study have included some Onthophagini, albeit even in the more "comprehensive" studies, a mere 2-3% of the world's species have been sampled: from representatives of three species of *Onthophagus* (Ocampo and Hawks 2006); two genera *Digitonthophagus* and *Diastellopalpus* – Philips *et al.* 2004b); three genera, including *Onthophagus* with 17 species (Villalba *et al.* 2002); a different three genera and 44 species of *Onthophagus* (Emlen *et al.* 2005b); and 41 species of nine genera (including 29 species of *Onthophagus* – Monaghan *et al.* 2007).

In the Philips *et al.* (2004b) study the Onthophagini were represented by *Digitonthophagus gazella* and *Diastellopalpus thomsoni* and their analyses returned a tree with these two taxa basal and sister to, a clade of oniticellines. The Oniticellini and Onthophagini both show unique vesicles on the seventh and eighth articles of the antennae, which are likely to be important phylogenetic characters that provide strong evidence of shared evolution as sister groups.

In the first molecular phylogenetic study [of Iberian Scarabaeinae] that included onthophagines, Villalba *et al.* (2002) sampled all of the Iberian genera, represented by *Euonthophagus amyntas, Caccobius schreberi* and *Onthophagus* (17 species), and returned a tree with strong support for them sister to *Euoniticellus*, as the only oniticelline sampled.

In a similarly taxonomically limited study but with broader geographic coverage Ocampo and Hawks (2006) sampled three onthophagine species in North America although two of them are introduced species. They were *Digitonthophagus gazella, Onthophagus hecate* and *O. taurus* from three different geographical regions; the first originally from Africa, the second native and the third originally from Europe. *Digitonthophagus gazella* was basal to a clade on their tree that included the oniticelline *Liatongus californicus* and the two *Onthophagus* species, thus rendering the Onthophagini and Oniticellini paraphyletic.

The first comprehensive study of the phylogeny of the Onthophagini was by Emlen *et al.* (2005b) in which they attempted to develop a phylogenetic hypothesis specifically to test for the evolutionary origin and radiation of horns which are a particular characteristic of many species of the tribe. They sampled 48 species of Onthophagini: three of *Proagoderus*; *Digitonthophagus gazella* (although they considered these four species also to be members of *Onthophagus*); 44 belonging to *Onthophagus*; and three outgroup genera (*Ateuchus, Canthidium* and *Phanaeus*). The *Proagoderus* species and *D. gazella* were from South Africa whereas the *Onthophagus* species were representative of all of the major geographical regions. The outgroup taxa were American species; two dichotomiines, and a phanaeine, respectively. They used seven gene regions (four nuclear and three mitochondrial) and recorded strong support for several clades; a basal clade of the *Proagoderus* species, sister to *D. gazella*, which in turn was sister to the *Onthophagus* species which grouped strongly on subclades according to continent of origin. African and Afro-Eurasian groups were basal amongst the *Onthophagus* lineages, and there was strong support for Australian and New World clades. Their data corroborate those of various systematists who have worked on the onthophagines over the years and postulated that *Onthophagus* had an African origin and subsequently colonized Eurasia, Australia and the Americas (Fig. 12.10).

Monaghan *et al.* (2007) studied a comparable number of taxa to Emlen *et al.* (2005b) but the former study included a wider representation of onthophagine genera – nine genera (and 41 species) from all the major biogeographical

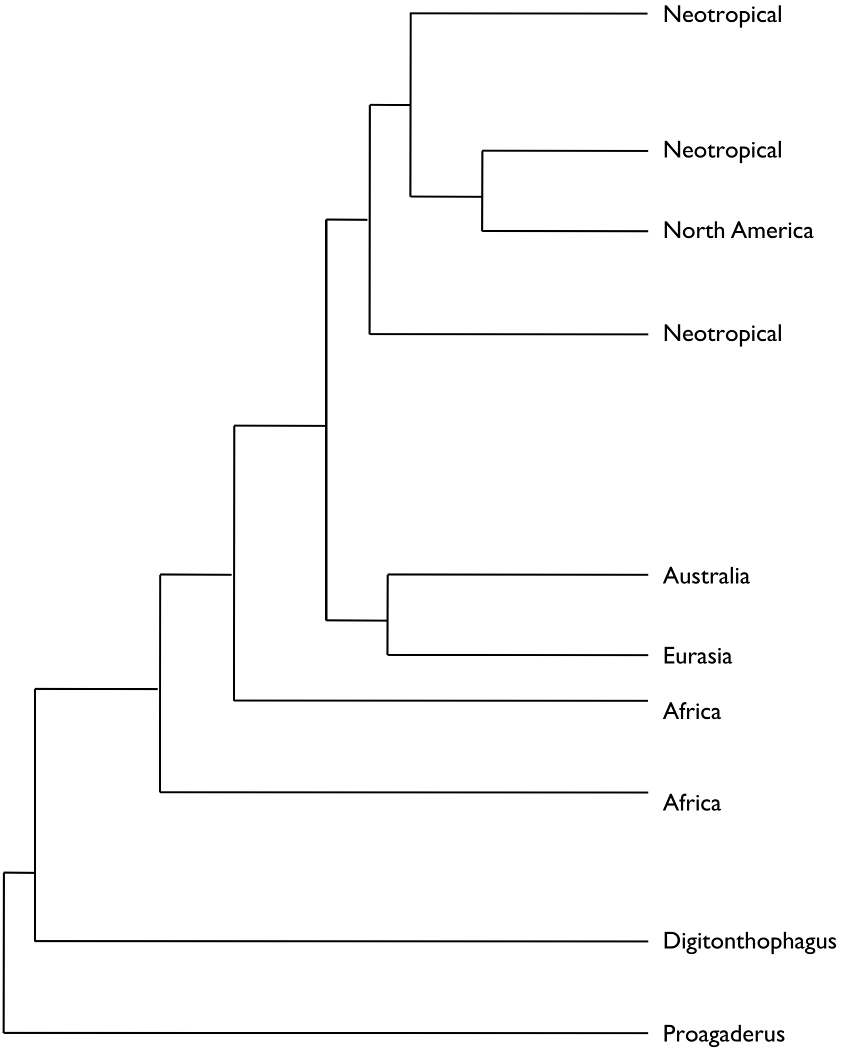


Fig. 12.10. Topology based on fully reserved maximum likelihood tree for 48 Onthophagine species indicates that *Onthophagus* species of different regions are strongly monophyletic. (After Emlen *et al.* 2005b).

regions. Onthophagini lie on four clades of their preferred tree; the most basal, consisting of *Digitonthophagus gazella* and *Phalops ardea* (both from South Africa) is a strongly supported sister to Onitini + Oniticellini, with two onthophagine clades nested within the latter (each with equally strong support – including *Digitonthophagus diabolicus* from Indonesia and *Onthophagus semiareus* from Malaysia in one clade, and two species of *Proagoderus*, *P. bicallossus* from South Africa and *P. schwaneri* from Indonesia on the other, thus rendering Oniticellini without them paraphyletic), and the rest of the onthophagines. The major onthophagine clade consists of several subclades of which an Australian and a mainly Neotropical lineage of *Onthophagus* species are well supported, as is a terminal one comprising *Caccobius, Cleptocaccobius* and *Milichus* species and an unidentified *Onthophagus* species from Turkey.

On the basis of the above analyses there is strong evidence of a common ancestry for the members of the Onthophagini and Oniticellini but that some of the subclades represent monophyletic terminal groups, although not in the traditional tribal configuration. The evidence for the evolution of the basal groups of Onthophagini, and of *Onthophagus* in Africa, is also indicated by the analyses.

Geographical origin: A complex evolutionary history is suggested by the extensive generic and species diversification that resulted from widespread geographical radiation, particularly in *Onthophagus*. Evidence from morphological and molecular phylogenies suggests that the Afrotropical or Afrotropical and Oriental-centred *Proagoderus*, *Diastellopalpus*, *Phalops* and *Digitonthophagus* belong to the most basal lineages. In comparison, Afrotropical *Onthophagus*, and a Western Palaearctic *Onthophagus* (*Palaeonthophagus*), show parallel but probably derived lineages. Furthermore, other Palaearctic or Oriental *Onthophagus* (*Onthophagus*) and *Onthophagus* (*Serrophorus*), as well as those of the Americas and Australia, are separate lineages derived variously from Afrotropical, Palaearctic or Oriental ancestors. Fossil evidence from the southwestern Palaearctic indicates that the history of *Onthophagus* stretches back at least as far as the Oligocene (Krell 2006).

Although three of the basal genera show greatest diversification in Africa with limited or no representation in the Oriental region, this in itself does not qualify as evidence of origin as the fourth basal genus, *Digitonthophagus*, is more diverse in the Oriental region than in Africa. A partial study of relationships within *Proagoderus* (Palestrini 1992) suggests that it has a comparatively recent history in the Oriental region as the few Oriental species occur in only three of the nine clearly dissimilar species groups, each of which also includes Afrotropical species. A phylogeny of another of the basal genera *Phalops* (Barbero *et al.* 2003) also suggests a comparatively recent history of limited radiation outside of Africa. These radiations have occurred in only three of the six clades. Each of the three comprises both Afrotropical and non-Afrotropical species although the Oriental species are basal in two of the clades. In conclusion, consideration of the evidence suggests that the Afrotropical region is the most likely origin of the tribe although it is likely that at least some onthophagine taxa have radiated into Africa from the Palaearctic and, possibly, from the Oriental region.

We might ask what characteristics predisposed the onthophagines, and especially *Onthophagus*, to have radiated and speciated so spectacularly compared to other groups with essentially the same life-styles? It is already a huge group with 2000-odd described species as well as, quite probably, numerous undescribed ones from different, poorly-studied regions (e.g. Hanski and Krikken 1991 predicted that the numbers in S-E Asia might increase up to six-fold, from about 320 to about 2000 species). From an apparently African origin and not much earlier than the Miocene, they have invaded every major geographical region and occur in virtually every conceivable suitable habitat while still numerically dominating dung beetle communities in Africa. They have apparently also invaded habitats that were already occupied by other dung beetle species with similar requirements but continue to co-exist with them. Furthermore, any dung pile in an area where they occur may have from a few to many species of *Onthophagus* present which are mostly also numerically dominant, and apparently co-existing successfully with each other and other, unrelated, species. What gives them this competitive edge? From the discussion of the virtually worldwide radiation of *Onthophagus* species over a relatively short space of evolutionary time, it might be useful to examine the dispersal ability of onthophagine species using the African species *Digitonthophagus gazella* as a model. From Emlen *et al.* (2005b) and Monaghan *et al*'s (2007) studies it would appear that there have been one to at most a few founder events in the terminal extensions of *Onthophagus* distribution, i.e. Australia in the east and South America in the west. This is contrary to, for example, Matthews (1972) who postulated at least 34 independent invasions of Australia by *Onthophagus* founders but this seems unlikely in view of the more recent molecular studies. If we are to accept that the *Onthophagus* radiations were precipitated by a wave of dispersal and speciation by isolates of this wave, then it is possible that a particularly aggressive invading species or group of species led the dispersal event.

In Africa most *Onthophagus* species are dung-feeders where they form a "guild" of small tunnellers that is mostly separated by size from behaviourally similar but larger Onitini. In regions where these similar but larger tunnellers are absent, such as on the island of New Guinea, large *Onthophagus* species (up to 20 mm long) have evolved (Hanski and Krikken 1991), apparently taking the place of the large tunnellers. However, most of the geographical regions that *Onthophagus* has invaded had no or few small tunnellers present so vacant niche space was available for colonization. This may partially explain their spectacular success in Australia, S-E Asia, continental parts of the Oriental region, as well as the Palaearctic and Nearctic regions. Their relatively lower numbers in the Neotropics, and their apparent slow spread southwards in South America (although *O. hirculus* has reached Nequen and Rio Negro Provinces in Argentina, at about 40ºS latitude, possibly following the spread of cattle ranching – Federico Ocampo, personal communication), could be accounted for by time (they have just not radiated further because of their relatively recent radiation into South America), or equally, by the fact that there are many dichotomiines already established in the small tunneller niche there.

Whatever the species, it/they would have required a suite of generalised characteristics that pre-adapted them to be able to cope with a host of variable environmental conditions. What would some of those attributes be? Clearly the ancestral species would need to have been small, simply to escape from the competitive pressure of the larger and phylogenetically older Onitini which have similar ecological requirements and feeding and breeding behaviour. Small species usually have relatively shorter life-cycles and simple nests leading to rapid generation turnover and multiple breeding episodes per favourable breeding season, i.e. they are typically r-selected. An added advantage would be the propensity to utilize many different food sources in various ways in a host of diverse habitats, in other words, the ability to quickly fill vacant niche space. The extremely successful and aggressive "pioneer" extant species, *Digitonthophagus gazella*, may serve as a model for this putative ancestral pioneer. This is a tropical African species which, in view of its r-selected attributes, was considered a suitable candidate for introduction into regions where cattle had been introduced and their dung represented a whole new habitat for dung feeding insects other than dung beetles (Australia), or where livestock numbers were maintained at unnaturally high levels in intensive farming enterprises (USA, Brazil), and where their dung accumulated to levels where native dung beetles were unable to cope. The dung, consequently, accumulated and caused physical and chemical fouling of pastures, and provided an ideal medium for flies to breed in. To try to alleviate these undesirable environmental consequences, *D. gazella* was introduced into Australia, USA and Brazil in the late 1960's and 1970's for the biological control of cattle dung. Its subsequent spread from points of release are discussed in Chapter 1.2.

Biological and ecological notes: The range of food associations, distribution patterns, and diel activity patterns shown by the Onthophagini is nearly as a wide as that shown by the entire subfamily, but some generalizations follow.

All studied genera show simple or compound Type 2 nests. In the simple nests of some *Onthophagus*, an elongate brood is constructed at the tip of a subterranean tunnel under the dropping. The larva feeds from one end to the other and then turns to repeat this feeding cycle in the opposite direction. In the compound nests of other *Onthophagus*, typical brood ovoids are constructed in linear series along a tunnel, each separated by soil. In a further variant of compound nests, brood ovoids are constructed at the tips of branches in a tunnel as in *Digitonthophagus*. Most larger-bodied species bury their own dung supply but kleptocoprid species use dung buried by other dung beetles, either ball-rollers or tunnellers. In the Onthophagini, kleptocoprid species groups occur in *Onthophagus* and in several other genera that may be exclusively kleptocoprid (*Caccobius*, *Cleptocaccobius*, *Hyalonthophagus*). Most, though not all, putative kleptocorid taxa are characterized by very small body size. Several diurnal species of various genera, including *Onthophagus* and *Cleptocaccobius*, have been recovered from balls of dung rolled away by large Scarabaeini of the *Scarabaeus* subgenus *Kheper*. These are often actively colonized at or close to the dung pat, or at the site of burial whilst the ball-roller is excavating the tunnel. Although kleptocoprid habits appear to be widespread in the Afrotropical region, few species have been confirmed to show such behaviour and details on their nesting habits are poorly known, particularly for species that may colonize dung buried by tunnellers.

Some of the more unusual and specialised food preferences and biological attributes of the Onthophagini are [inadvertently] pollinating specialised carrion-scented flowers, feeding on fruit or millipedes, hanging from wallaby anuses in Australia, and living in termite and ant nests, often of very aggressive insect predatory species. And then, some *Onthophagus* species have the dubious distinction of being the cause of scarabiasis in humans.

Halffter and Matthews (1966) quote at length an eloquent report by Arrow (1931) of an early Indian record of two carrion-feeding onthophagines (*Caccobius diminutivus* and *Onthophagus tarandus*) that are attracted to carrion-scented flowers and which are captured and imprisoned by the flowers for 24 hours while the pollen matures after which an escape tunnel leading past the stigmas, which are now covered in sticky pollen, opens and the beetles, covered in pollen escape, only to be attracted to another flower. Although this was reported to imply that the beetles fly from one flower to another performing their pollination duties, this is possibly a bit simplistic since the beetles would need to find carrion regularly to feed and breed and could, at best, only irregularly survive the entrapment.

Feeding on fallen and rotting fruit is a common accurrence in many, particularly tropical, *Onthophagus* species (Halffter and Matthews 1966), but most of the records imply that this is simply opportunistic behaviour of generalist feeders that also feed on dung or carrion, or of more specialised fruit feeders, but once again, in a fairly loose association. There is, however, at least one record of a true fruit specialist – the fig-feeding *Onthophagus rouyeri* from the rain forests of Borneo (Davis and Sutton 1997). This species was found to be common in fallen figs but in no other fruits (although a relative, *O. deflexicollis*, was often found in other, larger fruits) and was never trapped with dung or carrion, even when baited traps were placed amongst the fallen figs. The authors implied, but did not record, that the beetles buried and bred in the fig tissue.

Millipede-feeding is a fairly widespread but highly specialised behaviour amongst various disparate groups of dung beetles (Canthonini, genus *Canthon* – Bedoussac *et al.* 2007; Scarabaeini, *Scarabaeus* subgenus *Sceliages* – Forgie *et al.* 2002) but is most common amongst *Onthophagus* species where it has been recorded for some generalist necrophages (Brühl and Krell 2003) but also for feeding specialists (see Chapter 2.1.1.2 and Schmitt *et al.* 2004 for further references to the subject).

One of the most remarkable specializations yet recorded for dung beetles is that of the six Australian *Onthophagus* species of the *Macropocopris*-group which are phoretic on wallabies, clinging to the fur around the anal region with specially modified tarsal claws (Halffter and Matthews 1966) and attaching to dung pellets as these are extruded by the wallaby and dropping with them to the ground where they are immediately buried. This is possibly a strategy evolved in the arid areas where the beetles occur to access moist dung and to be able to utilize it before it dries out.

There are numerous records of onthophagines (and other species) associated with various ant species' nests. Some are commonly found in various forms of rotting humus, but others, such as the New World species, *O. rufescens*, appears to be more or less dependent on the moist and partially decomposed debris ejected from nests of a species of leaf-cutter ant (*Atta mexicana*). The beetles are ignored by the ants (Halffter and Matthews 1966). All the species of the small Oriental onthophagine genus, *Anoctus*, appear to be myrmecophilous, and have been recorded from nests of different ant species (Halffter and Matthews 1966). The tropical African *Megaponerophilus megaponerae* has been recorded in association with the very aggressive termite-predator ponerine ants *Megaponera foetens* (now *Pachycondyla analis*) which have been seen in the columns of marching ants but by which they are apparently tolerated (C.H. Scholtz, personal observation). Three of the four tropical African *Alloscelus* species have been recorded with the notoriously viscious driver ants of the genus *Dorylus*, and these are also apparently tolerated by the ants.

Various African onthophagine genera have been found associated with termites (*Dorbignyolus, Heteroclitopus*, *Krikkenius*, *Pinacopodius* and *Stiptopodius*) but the nature of the association is unknown (Davis *et al.* 2008b).

Finally, scarabiasis was first recorded in the 1920's in India (Halffter and Matthews 1966). This is an affliction of small children living in unsanitary conditions and in which adult dung beetles enter the anus of children soiled with faeces at night and then enter the intestine. The beetles apparently damage the intestinal wall causing bloody diarrhoea, and no doubt, if untreated, would lead to peritonitis and other complications. *Caccobius vulcanus* and two species of *Onthophagus*, *O. bifasciatus* and *O. unifasciatus*, are the pathogenic species recorded, with the latter two most frequently.

A recent incident of scarabiasis, also in India (Karthikeyan *et al.* 2008), reported no clinical symptoms in a 4-year old child from whom eight individuals of an *Onthophagus* species (not identified by the authors, but easily diagnosable as such from photographs in the paper) were passed during three episodes over three months. The medical staff who wrote the paper then rather fancifully described the route of infection as that of the female dung beetle entering and ovipositing in the rectum, the larvae then maturing there and the next generation adult eventually emerging from the rectum!

12.2 ROLLERS

12.2.1 Canthonini

Taxonomy and morphology: The Canthonini include both flying and flightless taxa of variable body shape. Although some species are elongate and somewhat rectangular, most are oval (Plate 12.12). The genera vary from distinctly convex, to fairly flattened. The average body size ranges from very small to very large (1.9 mm – 32.5 mm long) depending on the genus. The antennae are nine-segmented in all species. The external edges of the fore tibiae do not bear more than three teeth, sometimes fewer, and the fore tarsi are usually, but not always, present. The mesocoxae are usually parallel or slightly oblique. They are separated by a distance of approximately one mesocoxal length in most genera but not, for example, in the African genera *Peckolus* and *Circellium* (Plate 12.12), where they are closer together. Also in many genera the posterior lateral edges of the body are formed by the sublateral edges of the elytra, which are acutely angular and carinate beyond the seventh or eighth interstriae. In these genera, the true lateral edges of the elytra are downwardly inflexed as pseudepipleurae and conceal the upper lateral edges of the abdomen. The species are often black or dull purple with a muted metallic sheen although some genera have bright metallic colouration (Favila *et al.* 2000). The Scarabaeini are similar to the Canthonini in some respects but differ in having four teeth on the fore tibia (one sometimes much reduced) and oblique mesocoxae that are much closer together than one coxal length. The fore tarsi are absent in all Scarabaeini.

Plate 12.12. Tribe Canthonini; *Circellium bacchus*, South Africa, 40 mm.

It is doubtful that the genera placed in the Canthonini are derived from a single common ancestor which is why it is difficult to provide a set of universal characters that define the tribe. Although, in the past, various characters and associated nomenclature have been proposed for further subdivision of the genera, none has proved universally acceptable. Therefore, we have thought it best to retain the traditional tribal membership until a comprehensive phylogenetic study has been undertaken. Even so, it should be noted that some African genera (particularly *Circellium*, *Hammondantus*, *Pycnopanelus*, *Odontoloma*) are only very tentatively placed in the Canthonini. *Circellium* has a suite of morphological and molecular characters that distance it from other canthonines, whereas the other three genera share several characters with the Onthophagini, including the moderately expanded middle and hind tibiae. It is primarily because they have three teeth on the fore tibia that these genera have been considered to be canthonines, even though the traditional Dichotomiini, Coprini, and several genera now accepted into the Onthophagini, also have three or fewer.

Diversity and distribution: Like the genera of other basal lineages (see Dichotomiini, Coprini), those classified as Canthonini show an overall ancient Gondwana distribution centred on southern land masses (South America, Africa, Madagascar, Australia, plus nearby islands). The tribe comprises a global total of about 120 genera, which represents about 44% of the valid genera in the subfamily. Although, as constituted, it is the most genus-rich of all the tribes, it is represented by only about 800 species, or about 15% of the global total.

The tribe is still prominent in some world dung beetle faunas, whereas it is in the minority in others. In the Americas, similar proportions occur in the faunas of both continents at 36 % (four genera) and 27 % (24 species) in the North, and at 41 % (28 genera) and 26 % (299 species) in the South. In other southern regions the proportions are often greater at 87 % (26 genera) and 30 % (130 species) in Australia and at 65 % (13 genera) and 72 % (142 species) in Madagascar. Canthonines are also prominent in outlying islands or island groups that harbour endemic genera. This stands at 40 % (four genera) and 67 % (28 species) in the partly endemic Caribbean fauna. In entirely endemic island faunas, this stands at 50 % (one genus) and 20 % (one species) in Mauritius, at 100% (eight genera, 13 species) in New Caledonia, and at 100% (two genera, 14 species) in New Zealand.

In Afro-Eurasia, the Canthonini comprise smaller proportions of the native dung beetle faunas. Furthermore, most genera and species show restricted distributions irrespective of whether they are relicts or recently radiated. In the Oriental region, the proportions stand at 17 % (eight genera) and 6 % (44 species). In the Palaearctic region, representation is miniscule at 6 % (one genus) and 1 % (three species). In Africa, proportional representation is similar to that in the Oriental region at 20 % (20 genera) and 4 % (80 species) with 17 genera endemic and all but two, species-poor. However, new genera and species await description from isolated eastern forests in South Africa.

Canthonini overwhelmingly dominate the roller groups in the New World which has (mostly the neotropics) about 30 genera and 330 species. Eight of the genera are monotypic and another eight have between two and five species while two are very speciose (*Canthon*, with about 175 species; and *Deltochilum* with about 80). *Canthon* has been divided into numerous diverse subgenera and species groups and it is very likely that the genus is para- or polyphyletic as presently constituted and will be further divided into smaller groups in future (Medina *et al*. 2003). The genus is also very widespread in the New World, occurring from Argentina northwards to Canada (Padilla-Gil and Halffter 2007). Only one genus is endemic to the Nearctic region (*Melanocanthon*), which clearly indicates that high endemicity among scarabaeines in South America and very low endemicity in North and Meso-America supports the hypothesis of northward radiation of the fauna from South America after the advent of the Great American Interchange during the Pliocene (Davis *et al*. 2002a).

The Australasian roller fauna consists exclusively of canthonines. There are about 30 genera and 160 species described. One-third of the genera are monotypic and another one-third has between two and five species. The final third consists of larger genera, although only two of these have more than 20 species (*Amphistomus, Lepanus*).

Madagascar is inhabited by a few species of Scarabaeini, but as with the Neotropics and Australasia, the roller fauna is dominated by canthonines which consist of about 13 genera and 170 species (Orsini *et al*. 2007). Five of the genera are monotypic and three have more than 20 species (*Aleiantus, Arachnodes, Sphaerocanthon*).

Most genera classified as Canthonini in Africa show relict distribution patterns. In the absence of an acceptable phylogeny, they are grouped according to their climatic, geographical, or vegetation associations. The largest group of 10, not necessarily related, genera is restricted to small montane or coastal forest patches in southeastern Africa from Kenya to the Western Cape of South Africa. *Gyronotus* shows a patchy occurrence across this entire range whereas the other genera are more regional, occurring in Tanzania (*Janssensantus*, *Tanzanolus*, with *Madaphacosoma* purportedly shared with Madagascar), in Mozambique (*Canthodimorpha*), in Malawi and Zimbabwe (*Panelus* shared with the Oriental and Palaearctic regions), and in South Africa (*Peckolus*, *Endroedyolus*, *Outenikwanus*, *Bohepilissus*). A further five genera are centred on arid regions from the Northern Cape, South Africa, to southwest Namibia (*Pycnopanelus* shared with Sudan and the Oriental region, *Byrrhidium*, *Dicranocara*), or in southwest Namibia (*Hammondantus*, *Namakwanus*). Two genera occur in shrubland on sandy soils in the Eastern Cape (*Circellium*) or the southwest of the Western Cape (*Aphengoecus*) of South Africa. Two other species-rich genera have apparently radiated from cool southwestern centres. One of these is a small-bodied genus that has radiated across forest, winter rainfall shrubland, arid Karoo shrubland, and highveld grassland of South Africa (*Epirinus*). The other very small-bodied genus is apparently widespread in Africa but has been patchily collected outside of southern Africa (*Odontoloma*). The final single widespread, large-bodied genus (*Anachalcos*) is the only African canthonine taxon (besides *Odontoloma*) that has radiated across the moist savanna of tropical regions to the west of the eastern highlands. Unlike, in Australia, Madagascar and South America, African canthonines are hardly represented in tropical lowland rainforest or adjacent vegetation types.

Phylogeny and evolutionary history: Some Canthonini have been included in four recent phylogenetic analyses (Philips *et al.* 2004b: Ocampo and Hawks 2006; Monaghan *et al.* 2007; Orsini *et al.* 2007) but in view of the large number of genera in the tribe that occur on all of the southern continents and major island groups, the proportional representation was necessarily small. In Philips *et al.*'s (2004b) study, genera were sampled from Africa (*Analchalcos, Circellium*), Australia (*Amphistomus, Cephalodesmius, Lepanus*), Madagascar (*Arachnodes*) and the New World (*Canthon*). Ocampo and Hawks (2006) included five Neotropical genera (*Deltochilum, Eudinopus, Malagoniella, Megathopa, Scybalophagus*) and one Australian (*Amphistomus*). Monaghan *et al.* (2007) sampled a total of 36 Canthonini genera from all of the major land masses and islands where they occur (Africa – five genera; Australia – 11 genera; Madagascar – five genera; New Caledonia – five genera; New Zealand – one genus; the New World – seven genera; and S-E Asia – two genera).

Philips *et al.* (2004b) recovered the genera on four major clades and one subclade, most of which were sister to different tribal representatives, in other words they were completely polyphyletic.

The Neotropical genera Ocampo and Hawks (2006) sampled formed a monophyletic clade with strongly-supported sistergroup relationship to Onthophagini + Oniticellini + Onitini. The Australian *Amphistomus* was recovered sister to the Australian dichotomiine, *Demarziella* and they, in turn were sister to the Neotropical Eurysternini, also with strong support.

Although Monaghan *et al.*'s (2007) preferred phylogenetic analysis returned 11 clades in which Canthonini were represented, a large majority of the genera they sampled actually only lies in four clades, albeit widely spread on their tree, and each of which has a strong geographical bias. These are: (i) a mostly-Madagascan clade consisting of five Madagascan genera and two extra-limital ones (one South-East Asian and one Australian) (Fig. 12.11); the African *Epirinus* clade (Fig. 12.12); the Australasian clade (Fig. 12.7 – these three discussed below; and their Clade I, consisting almost entirely of Neotropical genera (Fig. 12.13). Molecular analyses of a larger representation of genera from each of these regions, and the inclusion of more gene regions will undoubtedly return at least four strongly monophyletic clades of geographically widely separated and distantly related "canthonines".

Of all the Canthonini, the African taxa appear to have the most diverse ancestries on the Monaghan *et al.* (2007) tree since all of the ones sampled lie on different, albeit sometimes poorly-resolved clades – *Odontoloma* + *Dicranocara* are strongly supported, and lie in a basal position; *Epirinus* is a well-supported sister to Sisyphini + Onitini + Oniticellini + Onthophagini; *Circellium* is in a poorly-resolved clade with the Neotropical dichotomiine genus *Ateuchus* and together they are sister to the tribe Scarabaeini, albeit, not convincingly so; and *Anachalcos* is sister to a likewise weakly-supported Neotropical clade of dichotomiines and eurysternines. Philips *et al.* (2004b) demonstrated a similar pattern of lack of evidence of shared ancestry amongst these groups (*Odontoloma* and

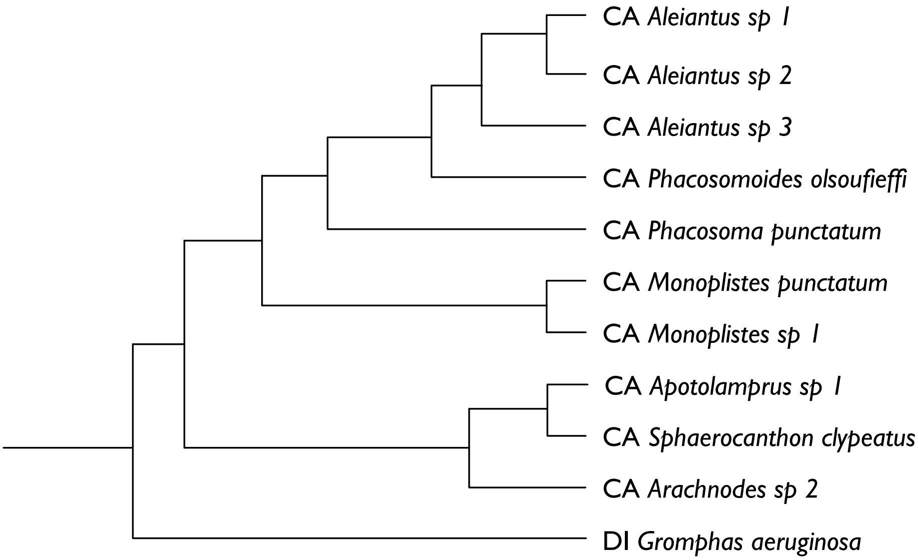


Fig. 12.11. A "mostly-Madagascan" lineage of Canthonini extracted from Monaghan *et al.* 2007.

Dicranocara were not included in their study) which may demonstrate that these are all very ancient, probably, relictual groups, with no close extant ancestors.

Orsini *et al*. (2007) analyzed sequence data from two nuclear (18S, 28S) and five mitochondrial (16S, 12S, COI, COII and CO*b*) genes for 27 Madagascan species of Canthonini from five genera (*Aleiantus*, *Apotolamprus*, *Arachnodes*, *Pseudoarachnodes* and *Sphaerocanthon*). Since appropriate outgroups representing putative African or Australian relatives of Madagascan canthonines were not available to Orsini *et al*. (2007) they used one of their sequences of *Aleiantus* as an outgroup, since this genus was thought to be basal based on morphology (Montreuil, in Orsini *et al*. 2007). The trees Orsini *et al*. (2007) obtained with

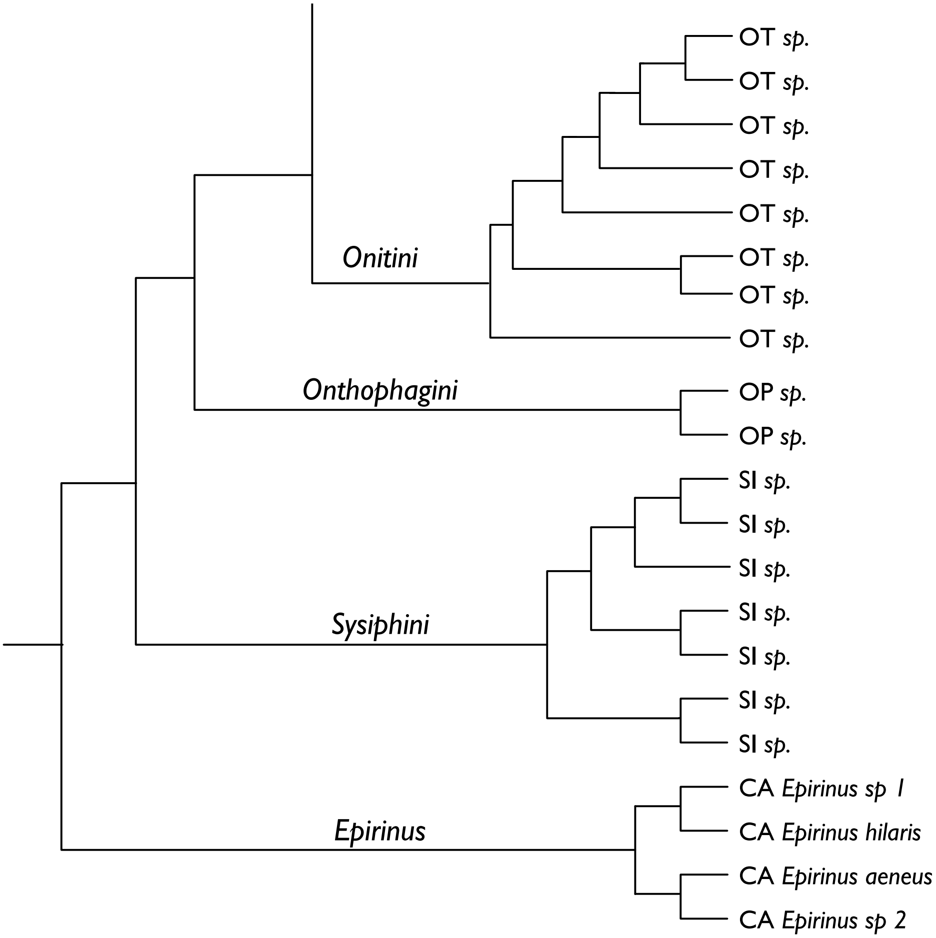


Fig. 12.12. Clades sister to the basal "true" roller, *Epirinus*, an African member of the Canthonini. Extracted from Monaghan *et al*. 2007.

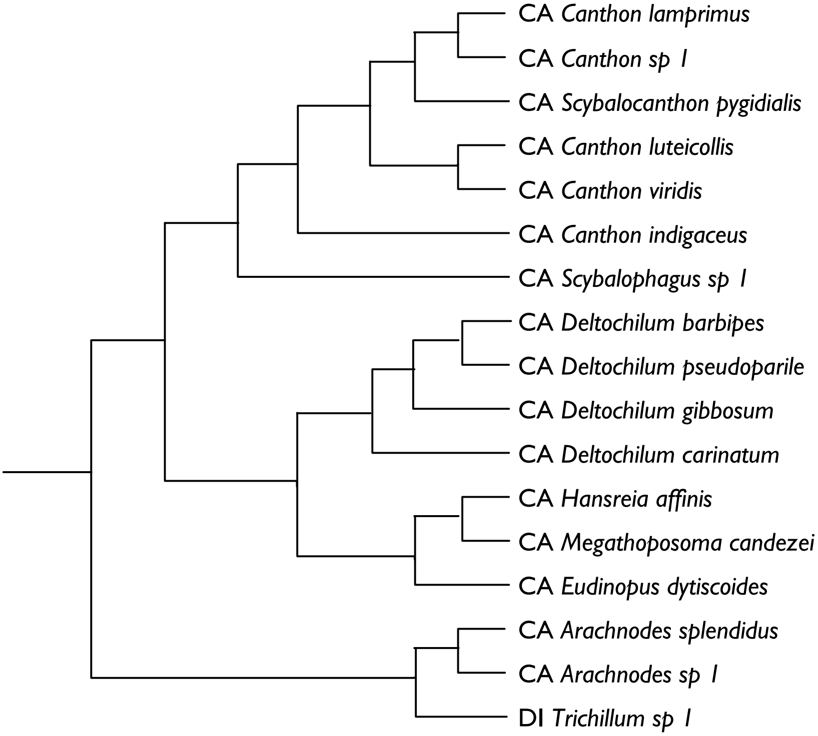


Fig. 12.13. A "Neotropical" clade of Canthonini sister to *Trichillum*, a genus of Neotropical Dichotomiini. (After Monaghan *et al.* 2007).

different genes produced inconsistent clustering of species and, in some cases, conflicting results. *Aleiantus* and *Sphaerocanthon* clustered, as expected based on morphology and current taxonomy, but the latter did not form a monophyletic group in all gene trees. *Arachnodes* was never monophyletic and was paraphyletic with *Apotolamprus* in all gene trees. Their results from parsimony and Bayesian analysis were highly comparable although the Bayesian analysis yielded a larger number of supported nodes than the parsimony tree.

Based on the sequence information of the encoding mitochondrial genes, Orsini *et al.* (2007), estimated the ages of the Canthonini clades using the absolute calibration of branch lengths of 2% divergence per million years, a widely accepted figure for insect mtDNA. They estimated the ages of the individual clades in the Canthonini to be 5.6, 9.3 and 12.3 myr for *Sphaerocanthon*, *Apotolamprus* and *Arachnodes*, respectively. The sister clades *Sphaerocanthon* and *Apotolamprus* diverged 10.4 mya while the split between *Arachnodes* and the *Sphaerocanthon* / *Apotolamprus* group happened 14 mya. Although Orsini *et al.* (2007) appeared uncomfortable with the apparent young ages of their Madagascan Canthonini lineages and tried to justify them in terms of the prevailing hypothesis (Paulian 1987, quoted by Orsini *et al.* 2007) that the canthonine fauna on the island must have colonized there during the Cretaceous (144-65 mya), their evidence of multiple colonization events since the Miocene is much more plausible in view of their own and other recent phylogenetic studies of the Scarabaeinae.

The traditional membership of the Canthonini probably includes both older and more recent lineages. One early attempt (Matthews 1972) to formalize divisions within the tribe works well with the Australasian fauna in which the New Zealand, New Caledonian and most of the Australian fauna comprises so-called mentophiline genera, characterized, especially, by very well-developed pseudepipleurae and non-ball-rolling habits, leading to claims of old ancestry. By contrast, a few Australian and most South American genera are non-mentophiline taxa in which pseudepipleurae are considered absent and ball-rolling habits are often prominent. Some support is provided by a few mentophiline genera identified in the South American fauna, which belong to older, relatively basal lineages. However, in the African fauna, at least one mentophiline genus (*Anachalcos*) has been observed to roll balls and this genus is in a more derived position on Monaghan *et al.*'s (2007) tree than the Australian non-mentophiline (*Lepanus*). Furthermore, limited glandular structures in some mentophiline canthonines appear to result from regression rather than representing the plesiomorphic condition. Thus, unraveling the complexities of canthonine ancestry and evolution will require much further phylogenetic analysis.

Geographical origin: Although the oldest Canthonini occur only on sub-basal lineages, they are centred primarily on southern continents that result from the fragmentation of Gondwana. Like the traditional Dichotomiini, they are represented on each of the three major southern land mass fragments of West (South America, Africa) and East Gondwana (Australia) but, unlike the Dichotomiini, they also occur on other fragments (west: Madagascar, Mauritius; east: New Caledonia, New Zealand). The greater diversification may result from the perceived prominence of ball-rolling habits in the Canthonini which are, perhaps, better suited to the small dung types available on islands (Caribbean, Madagascar, New Zealand, New Caledonia, Mauritius) or large regions (Australia, South America) where smaller dung types dominate in the native mammal faunas. However, there is relatively poor documentation of the incidence, evolution and importance in the Canthonini of other habits, particularly forest leaf litter associations accompanied by very small-bodied size, or tunnelling habits in often specialized non-ball-rolling taxa.

Despite polyphyly in the Canthonini, apparent close relationships between some older genera on some larger land masses suggest that at least some lineages pre-date the fragmentation of Gondwana. However, as phylogenetic studies on the different genera are incomplete, it is not yet possible to identify the pre-fragmentation and post-fragmentaion ancestral lineages that have given rise to the different canthonine faunas of each region. Therefore, it is not, presently, possible to determine any particular geographical origin, or set of origins, for the disparate traditional membership of the canthonine fauna.

The African canthonine fauna is less prominent than that in other southern land masses. Many African genera are monotypic or have relict distribution patterns lying between southern and East Africa where they are restricted to the cooler conditions of temperate climate, coastline, or highlands. It seems likely that many of the monotypic genera are relicts of otherwise extinct lineages. Some other genera may represent polyphyletic lineages resulting in artificial assemblages of non-related species. Convergence of characters complicates the question of affinities. For example, there are often parallel adaptations to similar environmental factors such as habitat and food type, or similar morphological changes that accompany the loss of wings. A total of 55 % (11) of traditional canthonine genera in Africa are flightless whereas two further genera include flightless species.

The origin of the relictual status of African canthonines is unclear. It has been suggested that it is a response to environmental change, or to competition and replacement by modern African ball-rolling tribes (Scarabaeini, Gymnopleurini, Sisyphini), or to both. Most African canthonine genera now occur in cooler southern regions or show cooler southeastern forest distributions. There is some overlap with other ball-rolling groups but the ball-rolling faunas of West and Central African rainforests comprise primarily Sisyphini with few Gymnopleurini and even fewer Canthonini. The historical origins of the present status quo may result from the cumulative effects of post-Miocene Epoch geological and climatic events. These would include: (1) the uplift of the eastern highland barrier between east and west; (2) oscillations between cool dry and warm wet climate during the Plio-Pleistocene Epochs; (3) much greater cooling in the Atlantic Ocean compared to the Indian Ocean during the last glacial maximum, and its different effects on western versus eastern rainfall patterns, which are associated with forest contractions, forest persistence or forest expansions; and (4) regional differences in post-Miocene Epoch survival, range contractions, range expansions, or adaptive evolution in the different ball-rolling tribes.

Biological and ecological notes: Traditionally, the Canthonini have been considered to represent an ancient lineage of ball-rolling dung beetles. Some of the larger species certainly show such behaviour and it appears that the absence of fore tarsi in some groups is associated with ball-rolling. However, it is doubtful that the many smaller species in forest leaf litter are capable of such habits. Furthermore, some of these species appear to prefer carrion over dung which, in view of its lack of malleability, would seem to rule out rolling behaviour. It is not clear whether these species have either lost the ability to roll balls or have arisen from lineages that never could roll balls.

The Canthonini are now known to show a wide range of food exploitation behaviours. Although only some of these habits have, so far, been recorded in the African fauna, those of 10 genera remain unknown. Only three African genera have been observed rolling balls (*Epirinus*, *Anachalcos*, *Circellium*) and one other very convex, short-legged genus may tunnel (*Aphengoecus*). Whereas four very small-bodied genera have been sifted from forest leaf litter (*Bohepilissus*, *Peckolus*, *Endroedyolus*, *Outenikwanus*), two genera from arid regions have been recovered only in association with hyrax (Hyracoidea: *Procavia capensis* (Pallas)) dung middens (*Dicranocara*, *Namakwanus*). None of the other specializations recorded for the tribe has been noted in African genera, including ant associations (several Oriental genera), saprophagy or mycetophagy (some Australian genera). Observations on African canthonines suggest that they are attracted to various dung types although some also come to carrion. Most appear to fly (e.g. *Epirinus*), or be active (e.g. *Gyronotus*) by day, although *Anachalcos* is a night-flying genus.

As nesting behaviour differs between the few large South American, Australian, and African taxa that have been studied, it is not possible even to speculate on the behaviour of the many unstudied taxa particularly that of small-bodied forest litter species. However, the large-bodied genera show several variations of ball-rolling and other nesting behaviours (see Chapter 4.1.5.2).

The Neotropical genus *Zonocopris*, with two species (Vaz-de-Mello 2007) has one of the most unusual feeding associations yet recorded for a dung beetle. Both species appear to have an obligatory association with giant land snails (*Strophoceilus* and *Megalobulimus* – Vaz-de-Mello 2007; also see Chapter 2.1.1.4)

12.2.2 Scarabaeini

Taxonomy and morphology: The Scarabaeini comprise three genera, *Scarabaeus*, with 136 species, *Pachylomera* with two, and *Pachysoma* (Plate 12.13) with 13 species (Forgie *et al.* 2005; Forgie *et al.* 2006). The tribe is characterized by members with the anterior margin of the head, which is sexdentate, comprising the quadridentate anterior margin of the clypeus and two lateral teeth formed by the anterior angles of the genae. The beetles have long legs for ball- rolling and/or fast running. The tibiae of the forelegs are quadridentate, although the

Plate 12.13. Tribe Scarabaeini; *Pachysoma gariepinum*, Namibia, 20 mm.

proximal tooth may be represented by only a vestige. There are no fore tarsi. The species are mainly black although some show either red elytra or red patches on the elytra (some *Scarabaeus*, *Pachysoma*). A few are metallic-coloured (some *Kheper*). They vary in size from quite small (7.0 mm) to very large (48.5 mm). Most of the spcies fly strongly but a number of desert taxa are flightless (including all the *Pachysoma* species) and, because of morphological changes associated with flightlessness, such as increased convexity and decreased hind body size relative to pronotum size (see Scholtz 2000 and Chapter 5.5.1), have historically been assigned to different genera.

Scarabaeus comprises four subgenera, the nominate subgenus, *Kheper*, *Scarabaeolus* and *Sceliages*. *Kheper* and *Sceliages* had been considered to be distinct genera until recently (Forgie *et al.* 2005). *Pachysoma*'s taxonomic status has changed several times over the past 20 years, from being considered a valid genus, to a synonym of *Scarabaeus*, a subgenus of the latter, and back to full generic status, as currently recognised. All of the recent changes have come about as a result of a morphological (Forgie *et al.* 2005) phylogenetic analysis and of a study combining morphology and molecules (Forgie *et al.* 2006). The genus *Drepanopodus* was synonymised with *Scarabaeus* by Forgie *et al.* (2005) and older synonymies confirmed. These names are provided here since some are still used in spite of evidence that they cannot be justified on morphological, molecular or behavioural grounds: *Madateuchus, Mnematidium, Mnematium, Neateuchus, Neomnematium* and *Neopachysoma*.

Diversity and distribution: The Scarabaeini comprises about 150 species. Species distributions are centred in the Afrotropical (about 130 species), Palaearctic (22 species), and Oriental regions (three species in India and Sri Lanka), as well as in southwest Madagascar (three species). Another two species are shared between the Palaearctic and Oriental regions (India), and a further two between the Afrotropical and Palaearctic.

The dominant distribution pattern within the Scarabaeini is defined, especially, by the most species-rich subgenus (*Scarabaeus*). It is centred on drier areas at higher latitudes. Specifically, the pattern is centred primarily on drier regions in southern and northeast Africa (connected by a dry corridor in the Pleistocene Epoch) and on the band of drier climate that extends from the circum-Mediterranean region across the Middle East to southern, central and eastern Asia. Whereas the subgenus *Scarabaeus* is represented across this entire range, with limited representation also in West and northern Central Africa, the other genera and subgenera occupy only parts of the range. *Scarabaeus* (*Kheper*) is an exception as it shows a divergent pattern centred primarily on dry to moist savanna that is largely continuous throughout Africa with a disjunction from India and Sri Lanka. All other genera and subgenera are centred primarily on winter rainfall shrubland, dry savanna, and adjoining

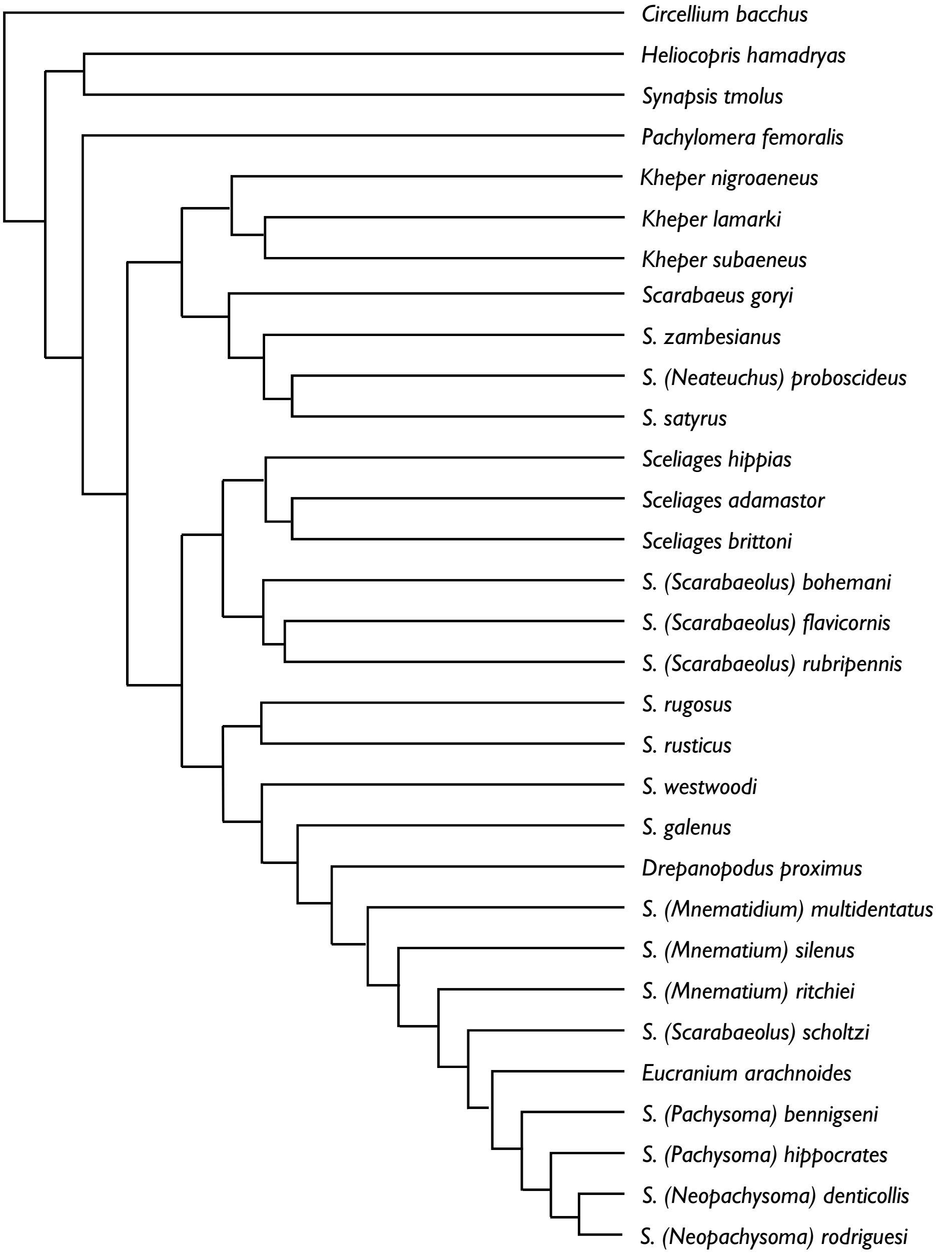


Fig. 12.14. Phylogeny of the Scarabaeini based on morphological characters. (After Forgie *et al.* 2005).

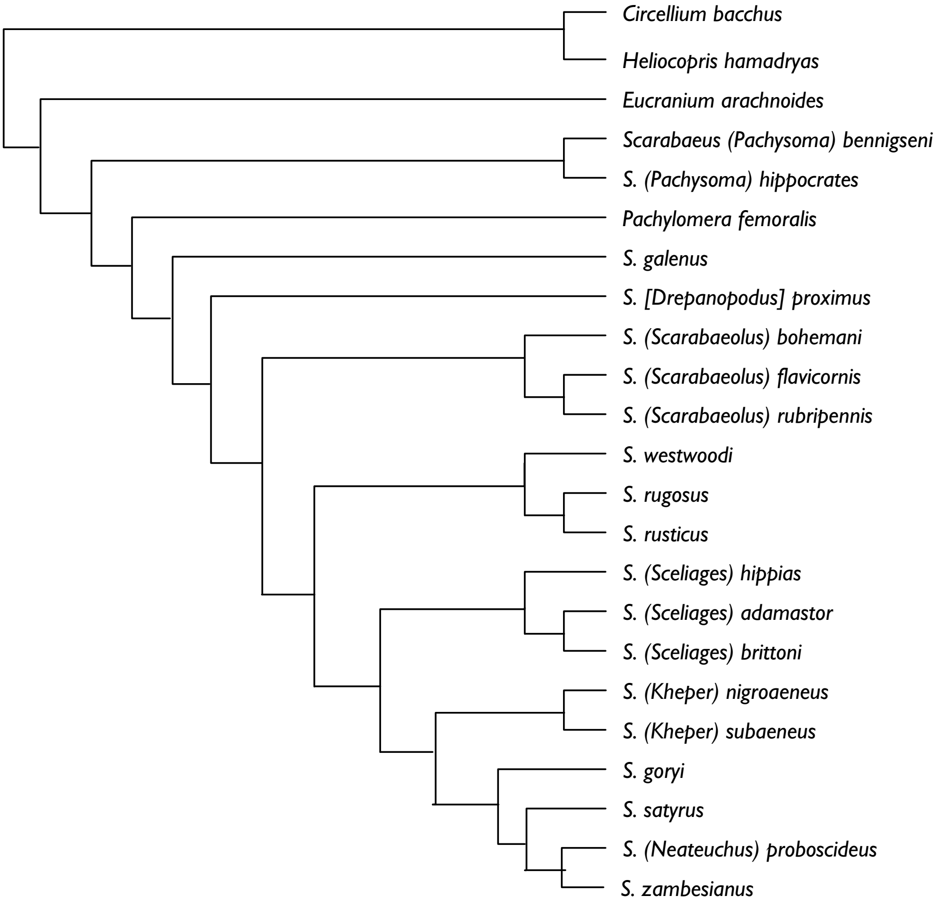


Fig. 12.15. Phylogeny of the Scarabaeini based on morphological and molecular data sets. (After Forgie *et al.* 2006).

upland grasslands, with some moist savanna species on deep sands in west southern Central Africa and east southern Africa. *Pachylomera* and *Scarabaeus* (*Sceliages*) are restricted to southern and south-western Central Africa. *Scarabaeus* (*Scarabaeolus*) is also found primarily in southern and west-southern Central Africa, although there are a few representatives in North East Africa, one in West Africa, and flightless species in Somalia and the Middle East. The other flightless taxa are classified in the subgenus *Scarabaeus* and are found in parts of the southern Palaearctic (North Africa and the Middle East), southwestern Africa (*S. cancer*), and southwest Madagascar. *Pachysoma* and most other flightless taxa are found in arid coastal regions subject to coastal mists and/or receiving rainfall during the coolest season.

Phylogeny and evolutionary history: Although the monophyly of the Scarabaeini has never seriously been questioned there have been only three attempts to place them relative to the other tribes in the subfamily (Villalba *et al.* 2002; Philips *et al*. 2004b; Monaghan *et al*. 2007). In the first study, Scarabaeini were sister to Gymnopleurini on the tree, albeit with weak support. In the second, the scarabaeines (two genera *Scarabaeus* and *Kheper*) yielded a monophyletic clade sister to one containing the canthonine *Circellium*. The last also returned a monophyletic clade [but which included two, obviously misplaced, Neotropical dichotomiines] and sister to one consisting of the New World Phanaeini, Eucraniini and some Dichotomiini, albeit with poor support. Consequently, none of these studies has provided overwhelming evidence of a convincing sistergroup relationship for the tribe.

The first comprehensive study of the tribe Scarabaeini which took into account taxonomy, morphology, biology and phylogeny was by Mostert and Scholtz (1986). In that paper many of the taxonomic inconsistencies that had arisen as a result of the pre-eminence that the group has enjoyed in beetle and dung beetle taxonomy and classification over the past 200 years, were clarified and a number of older generic names were placed in synonymy with the geographically widespread genus *Scarabaeus*. These were *Madateuchus, Mnematium, Mnematidium* and *Neateuchus*, none of which had been re-assessed in a revisionary taxonomic context since their description and followed on the synonymy of *Neomnematium*, also with *Scarabaeus* (Ferreira 1961) and *Neopachysoma* with *Pachysoma* (Mostert and Holm 1982).

Mostert and Scholtz (1986) presented the first tribal phylogeny in a strictly Hennigian sense of a scarabaeine tribe using a data matrix of 26 morphological characters and five genera. Their results confirmed the monophyly of the tribe (considered a subtribe of Scarabaeini in the sense of Janssens (1949) and as followed by workers of the period e.g. Halffter and Matthews (1966) and Halffter and Edmonds (1982)). The South American Eucraniini were used as outgroup and their analysis confirmed the monophyly of *Sceliages, Scarabaeus, Drepanopodus, Pachylomera* and *Kheper*, with *Sceliages* basal and *Kheper* terminal. These results stood for 18 years until a modern phylogentic analysis by Forgie *et al*. (2005) using a data matrix of 247 characters, 27 ingroup and four outgroup (*Circellium* – Canthonini; *Eucranium* – Eucraniini; *Heliocopris* – Dichotomiini; *Synapsis* – Coprini) taxa presented a different hypothesis of relationship. Their ingroup taxa included representatives of all of the recognized scarabaeine genera and subgenera as well as members of synonymised genera. They subjected their data to various analyses and their preferred tree (Fig. 12.14) had a length of 1673 steps a CI = 0.24 and RI = 0.49. Their analyses supported a monophyletic origin for the tribe, and the outgroups *Circellium, Heliocopris* and *Synapsis* fell

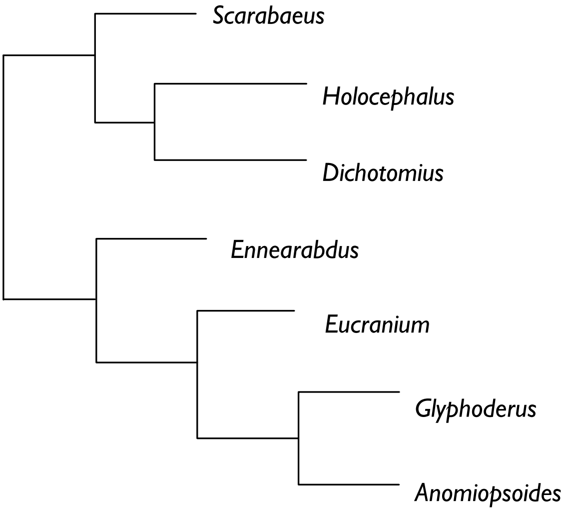


Fig. 12.16. Cladogram of the Eucraniini. (After Philips *et al.* 2002).

outside of the ingroup but *Eucranium* was nested with the flightless scarabaeines. *Pachylomera* was basal and *Pachysoma*, terminal. Although the morphological character matrix that Forgie *et al.* (2005) subjected to various analyses always returned trees with *Eucranium* nested with flightless scarabaeine species, they concluded that this was as a result of morphological convergent similarity between the taxa, and could be disregarded. They also referred to unpublished molecular evidence that contradicted this hypothesis of relationship. In a subsequent study, Forgie *et al.* (2006) combined the morphological data set used by Forgie *et al.* (2005) with a molecular one and analysis of the combined data set yielded similar trees to that of Forgie *et al.* (2005) except that the eucraniines (they used two species), fell outside of the ingroup (see discussion below).

On the basis of their analysis Forgie *et al.* (2005) proposed several changes to the taxonomy of the Scarabaeini. These included that only *Scarabaeus* and *Pachylomera* be retained as genera, that *Drepanopodus* be synonymised with *Scarabaeus*, that the status of *Kheper* and *Sceliages* be changed from genera to subgenera of *Scarabaeus*, and that the subgeneric status of *Pachysoma* be maintained.

In the subsequent study by Forgie *et al.* (2006) that led on from the Forgie *et al.* (2005) study, a combined morphological and molecular approach to test relationship amongst scarabaeine taxa was followed. It included essentially the same morphological data set except for a suite of 28 characters associated with flight or flightlessness since it was thought that these may have resulted in the apparent relationship portrayed between the eucraniines and scarabaeines, and a molecular data set consisting of 1197 bp of the mitochondrial COI gene and 461 bp of 16S rRNA.

Although the two gene regions used in the study differ markedly in rates of evolutionary change and pooling of such heterogeneous data are known to yield weakly congruent topologies, combining them with the morphological data set recovered a single most parsimonious tree of 3413 steps, CI = 0.30 and RI = 0.39 (Fig. 12.15). This "total evidence" tree contained more highly supported groupings than weighted or unweighted morphological trees produced by Forgie *et al.* (2005). In spite of reasonable congruence between the two data sets when analyzed separately, the addition of a molecular data set to the morphological one produced more clarity on the position of *Pachysoma*. Although it was on a monophyletic clade in the morphological analyses, this was a subclade of a larger clade that contained most of the flightless taxa, and *Eucranium*, which were obviously pulled together by the characters associated by loss of flight capabilities. Analysis of the combined data set, however, separated *Pachysoma*, with high bootstrap support, from all others. This prompted Forgie *et al.* (2006) to re-validate the genus.

The generic status of *Pachysoma* has been questioned and considered in several studies over the past 20 years (see Forgie *et al.* 2005; Forgie *et al.* 2006; Sole *et al.* 2005). There are currently 13 species in the genus, all with very similar general morphology and foraging behaviour. The morphological similarity can be attributed to their characteristic body shape that resulted from loss of flight,

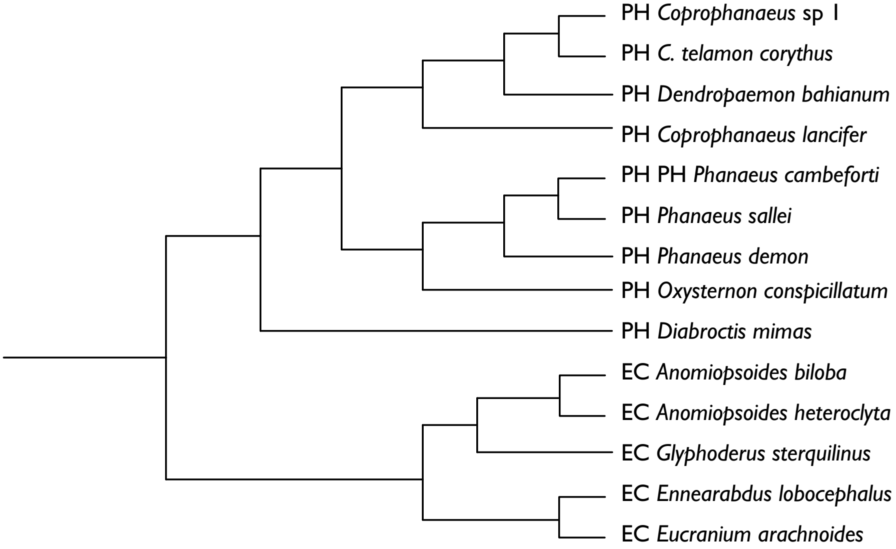


Fig. 12.17. Strongly-supported monophyletic clade of Phanaeini and Eucraniini extracted from Monaghan *et al.* 2007.

and their highly unusual foraging involves collecting and feeding on dry dung pellets and detritus which they hold in their hind legs and drag forwards. They occur in deep sand habitats in south-west African coastal deserts where the species are hypothesised to have evolved about 3 mya, when coastal fog precipitation became regular and provided free water in this otherwise hyperarid area (Sole *et al.* 2005).

Geographical origin: It is likely that the Scarabaeini originated in southern Africa, given that the basal genus, and by far the greatest diversification into genera, subgenera and species, is centred in that region. However, phylogenetic support is limited as the studied taxa are primarily Afrotropical and the derivation of most Palaearctic and Madagascar taxa remains unknown. Molecular clock calibration for the mtDNA studied by Forgie *et al.* (2006) indicates that the Scarabaeini evolved during the Miocene, between 23-9.8 mya, and, although this is considerably more recent than speculated in the past (see Forgie *et al.* 2006), it is well supported by the pattern currently emerging from recent studies that extant groups of dung beetles are no older than the Miocene (see Table 1.1 and Chapter 1.1 on the evolution of dung beetles).

Biological and ecological notes: The Scarabaeini comprise primarily coprophagous species. They may be readily attracted to many dung types, or more specialized, with some also strongly attracted to carrion. However, supporting data are limited. Although quantitative studies suggest that *S.* (*Kheper*) *lamarcki, Scarabaeus goryi*, *S. palemo*, and *Pachylomera femoralis* are attracted preferentially to omnivore dung, both *S. lamarcki* and *P. femoralis* have been observed to visit elephant and cattle dung in large numbers, given that these droppings are both more numerous and comprise much greater quantities of dung than those of omnivores. Some species may visit dung pellets, particularly in areas where pellet-dropping herbivores dominate the mammalian fauna in terms of numbers. For instance, many burrows of *Scarabaeus galenus* were found adjacent to piles of impala pellets in the Kruger National Park, South Africa (also see Ybarrondo and Heinrich 1996). Furthermore, species of the flightless, arid-adapted genus *Pachysoma* collect dry pellets or even detritus, which, it has been speculated, is re-moistened in their burrows at the edge of the water table, perhaps for dung feeding or even feeding on fungi that grow on the food store (Scholtz 1989; Holter *et al.* 2009 – but see Chapter 6.4). However, other food associations also occur, as the subgenus *Sceliages* is specialized to feeding and breeding using the body contents of dead millipedes (Forgie *et al.* 2002 – see Chapter 2.1.1.2).

The majority of the Scarabaeini comprises flying taxa, although 20 out of 150 species are flightless. Most species are active by day but some *Scarabaeus*, *Scarabaeolus* and *Kheper* are night-active. Whereas flightless species drag pellets and detritus, most flying species engage in ball-making and ball-rolling, although *Pachylomera* usually roll relatively unfashioned portions of dung and *Sceliages* use their heads and forelegs to relocate millipede carcasses. If ball-making and ball-rolling species form pairs at the dung, the males roll the ball with the female clinging to the side (*Kheper*, *Scarabaeus* (*Scarabaeus*)) or following behind (*Scarabaeolus*). At least one night-flying *Scarabaeus* uses polarised moonlight to navigate whilst rolling balls (*S. zambesianus* – Dacke *et al.* 2003a,b – see Chapter 8.2). When large numbers of Scarabaeini are active there is frequently combat between early arrivals at a dropping that have completed a ball and late arrivals that attempt to take possession of this ball. During such encounters, the object is to dislodge the incumbent from its defensive position on top of the ball or to deter the attacker by using the front legs to lift and flip the opponent away. The ball may be rolled some distance before being buried in a burrow where it is used either for feeding or breeding. The dung balls rolled by Scarabaeini are colonized by a spectrum of small-bodied kleptocoprid species, particularly Onthophagini from the genera *Cleptocaccobius*, *Caccobius*, and *Onthophagus*. These species may be buried with the ball into the burrow of the ball-roller. Subsequent behaviour has not been observed in Scarabaeini, but in Gymnopleurini, kleptocoprids have been observed to destroy the brood after the departure of the parent in order to use the dung to construct their own nests. Nests of most Scarabaeini (*Kheper*, *Scarabaeus* (*Scarabaeus*)) comprise a chamber at the end of the burrow in which one or more brood pears are constructed and tended by the parent female. The derived desert genus, *Pachysoma*, is exceptional in having a free-living larva that develops in a mass of shredded organic material that probably indicates a loss of brood construction behaviour (Scholtz *et al.* 2004).

Flight activity patterns may be related to the cooler conditions under which most species have been observed to fly, i.e. in the middle of the day under cooler conditions, but in the early morning, late afternoon, or at night under warmer conditions and, especially, after rainfall with its cooling effect on daily temperatures. At least some species are able to raise their body temperatures, enabling them to fly and exploit dung under cooler conditions (*S.* (*Kheper*) *nigroaeneus*, *S.* (*Kheper*) *laevistriatus*, *Scarabaeus catenatus* – see Chapter 8.1 on "Endothermy"). They are also able to regulate their body temperatures to a lesser or greater extent. This may be by passive diffusion, which may bar a species from flying under warmer conditions, or by active heat transfer, which extends the range of warmer temperatures under which a species may remain active. Temperature limits on activity may account for the low species richness of Scarabaeini in the hot lowlands of West Africa and the apparent emphasis on night-active species.

12.2.3 Gymnopleurini

Taxonomy and morphology: Members of this ball-rolling tribe are characterized especially by an emargination of the lateral edge of each elytron that exposes the underlying pleural sclerites (Plate 12.14). The middle and hind tibiae are mostly long and thin for manipulating the dung balls whereas the fore tibiae bear a terminal spur, four tibial teeth, and tarsi. Most species have moderate body size, ranging on average from 10.5 mm to 17.5 mm long. Separation of the genera is based on clypeal dentition, tibial spurs and features exposed by the elytral emargination. However, owing to many close relationships within the genera, species separation is based largely on differing punctation, granulation, body size, and colour, which leads to a degree of taxonomic confusion within at least two species complexes of African *Gymnopleurus* and some possible duplication of names for the same African species in *Allogymnoplerus* and *Garreta*. There is little sexual dimorphism in Gymnopleurini. In the three genera represented in Africa, the fore tibia is more elongate in males with a broadening at the tip of the terminal spur whereas the fore tibia is somewhat broader in females with an acute terminal spur. In males of some *Allogymnopleurus*, there is also a spine on the internal tip of the fore tibia, or a bulbous swelling as in *Garreta* males.

Many of the species show metallic colouration, particularly copper, green, or blue, even violet or non-metallic shiny black. One or more of these metallic, or non-metallic, shades may be shown by the same species. Brink *et al.* (2007) reported on the reflection of circularly polarised light in *Gymnopleurus virens*. This species is sometimes bright green or sometimes red and that the two colour morphs show characteristic differences in the modulation of their respective reflectance spectra. However, there may be some genetic coding for colour similar to that which has been demonstrated for colour variation in some Canthonini (Favila *et al.* 2000). In the Gymnopleurini, such colour variation is also linked to geographical variation in climate from warmer to cooler, or drier to moister regions. Thus, depending on their climatic range or the seasonal range of their breeding, species may show limited or wide colour variation (Davis *et al.* 2008a). In many species, the colour morphs have been separated as subspecies or varieties, each with its own scientific name. In *Allogymnopleurus* and *Garreta*, it is possible that several African species, currently considered valid, are merely colour varieties of a single species.

Diversity and distribution: The Gymnopleurini comprise about 110 ball-rolling species in four relatively species-rich genera (all greater than 10 species each). Whereas the genus *Paragymnopleurus* shows a primarily Oriental forest distribution, the other three genera show Afro-Eurasian (*Gymnopleurus*) or Afro-Oriental distributions (*Allogymnopleurus*, *Garreta*), with distributions centred, variously,

Plate 12.14. Tribe Gymnopleurini; *Gymnopleurus leei*, South Africa, 12 mm.

from forest to more open, drier vegetation types. This trend in vegetation associations extends in a sequence from *Garreta* through *Allogymnopleurus* to *Gymnopleurus* and parallels a trend in morphological characters. *Garreta* shows the largest average body size and mostly comprises species centred in forests or moist savannas and upland grassland. *Allogymnopleurus* shows intermediate, average body size and comprises species centred primarily in upland grassland and moist or dry savannas. *Gymnopleurus* has the smallest average body size and comprises species centred especially in drier savannas or arid regions. Each of the genera is represented throughout the climatically suitable regions of Africa but all are absent from the winter rainfall region of the Western Cape, South Africa, in contrast to the winter rainfall distribution shown by four species of *Gymnopleurus* in the circum-Mediterranean region. In Africa, gymnopleurine species are apparently more prominent where, or when, other ball-rolling taxa of similar body size are less abundant. Thus, they are less prominent on deep sands, particularly in the southwest, where species of the *Scarabaeus* subgenus *Scarabaeolus* (tribe Scarabaeini) are centred along the coastline, or in the central Mega-Kalahari basin (15+ species). The latter are active primarily in cool conditions immediately after rainfall. In contrast to *Scarabaeolus*, more species of *Allogymnopleurus* and *Gymnopleurus* show northerly compared to southerly centres of distribution. Where their ranges overlap with *Scarabaeolus*, particularly in the arid regions to the south, they are more active under hotter rather than cooler conditions.

Phylogeny and evolutionary history: In the study of Iberian scarabaeine taxa by Villalba *et al.* (2002), Gymnopleurini were sister to Scarabaeini, and the two, in turn, were sister to *Copris* which was sister to *Sisyphus* (Fig. 12.5). In a phylogeny constructed from a study on 20% of the scarabaeine genera and 200-odd morphological characters (Philips *et al*. 2004b), the Gymnopleurini were basal on an evolutionary branch comprising predominantly ball-rolling genera (Fig. 12.2). The sister genera comprised Canthonini from South America and Australia with African Scarabaeini and South American Eucraniini in a derived position. Subsequent analysis of the relationships of the Eucraniini (Ocampo and Hawks 2006) has indicated that their relationships are, in fact, closer to South American Phanaeini and Dichotomiini. They did not include Gymnopleurini in their study. Monaghan *et al*. (2007) included representatives of all four of the gymnopleurine genera and returned a strongly supported monophyletic clade for the group, with strong support for a sistergroup relationship to the coprines *Catharsius* and *Metacatharsius*. Close relationships and many varieties within the genera suggest that there has also been much recent radiation, isolation and taxonomic diversification, particularly in Africa from whence the majority of the *Garreta*, *Allogymnopleurus* and *Gymnopleurus* species have been described.

Geographical origin: In view of the limited information on the phylogenetic relationships of the Gymnopleurini, only speculation is possible on the geographical origin of the tribe. This could be from a simple unidirectional radiation or, more likely, from a complex history in which radiation and vicariance events have occurred on more than one occasion to, or from, any of the three regions in which Gymnopleurini are represented. Although the Oriental *Paragymnopleurus* is the only genus endemic to a single region, this does not necessarily indicate an Oriental origin for the tribe. One or more vicariant event may equally have separated forest taxa that persist in the Oriental and Afrotropical regions (*Paragymnopleurus*, *Garreta*), followed by their divergence. Diversification of drier adapted taxa may stem from later events followed by radiation to, and isolation in, drier parts of other regions in the western Orient, western Palaearctic or Africa. However, generic and species level phylogenies are required to determine the lineages, elucidate the geographical routes, provide support for these suggestions, or generate alternative hypotheses.

Biological and ecological notes: Nesting behaviour in at least three genera of the ball-rolling Gymnopleurini is of a typical Type 4 pattern in which a ball intended for brood construction is rolled away from the dung, possibly by a single beetle, possibly by male/female pairs (Prasse 1957). In *Allogymnopleurus* (*A. thalassinus*), the two sexes may co-operate in ball construction and ball rolling with the male pushing the ball with the hind legs and the female pulling it with the fore legs. There is similar co-operation in *Garreta,* (*G. nitens*, *G. unicolor*), with the difference that the female rolls and the male pulls. The ball is buried at the end of a short tunnel in the soil where it is re-worked by the female within a chamber. Once the ball has been re-constructed, a depression is excavated in the ball, an egg is laid at its base, and dung is pulled over the egg to enclose it within an egg chamber, thus forming a brood. This brood is then coated with a mixture of soil and dung before it is abandoned. The soil coat may be an adaptation to prevent fungal attack of the larval dung supply as the brood ovoids of *Allogymnopleurus* show high survivorship in drier soils. By contrast, there is poor survivorship in wet soils, either sand, as in *A. thalassinus*, or clay as in *A. consocius* (Osberg *et al*. 1994). The shape of the brood varies between genera, being oval in *Garreta* and *Allogymnopleurus* but pear-shaped in *Gymnopleurus*. All species of Gymnopleurini show diurnal flight activity.

12.2.4 Eucraniini

Taxonomy and morphology: The tribe comprises four genera: *Anomiopsoides* (with five species – Plate 12.15); *Ennearabdus* (one species – Plate 12.16);

Eucranium (seven species); and *Glyphoderus* (three species) (Philips *et al.* 2002; Ocampo and Hawks 2006). The species are black and range in average size from about 11.0 – 28.0 mm. All of the species except *Ennearabdus lobocephalus* are flightless and, consequently, have the typical convex facies of flightless beetles in which the hind body is small relative to the pronotum because of flight muscle reduction and decrease in meso-thoracic size (Scholtz 2000; Chapter 5.5.1). Some of the species have elongated clypeal prongs. The flightless species have long legs relative to body length but they are much shorter in *E. lobocephalus*. Each of the genera is characterised by a set of distinctive characters and is composed of several externally similar species (except the monotypic *Ennearabdus*). *Anomiopsoides* is characterised by the presence of four clypeal processes; *Glyphoderus* pronotum has horns and tubercles; *Eucranium* has a narrow mesosternum and contiguous mesocoxae. *Ennearabdus lobocephalus* is the smallest of the eucraniine species and although generally similar to various dichotomiines it shares several characteristics with the other eucraniines (see "Phylogeny" below).

Diversity and distribution: As presently constituted the Eucraniini consist of four genera and 16 species, making it the least speciose scarabaeine tribe. All species are restricted to desert thorn scrub habitat in Argentina (Ocampo and Hawks 2006).

Phylogeny and evolutionary history: Although the genera are well defined and there has traditionally been little disagreement amongst researchers about their confines, the definition of the tribe has been less clear. This was mainly because of the very different facies of the flightless species compared with *Ennearabdus lobocephalus* which resulted in it being placed in its own tribe (Martinez 1959, in Halffter and Matthews 1966 who followed this placement) or it was treated as a phanaeine (see Philips *et al.* 2004a). Mostert and Scholtz (1986) considered the similarity between the flightless eucraniines and the superficially similar flightless south-western African genus *Pachysoma* to be as a result of possible relationship. Zunino *et al.* (1993) pointed out that this similarity was probably as a result of convergence selected by similar ecological conditions, and were the first researchers to place the four currently-recognised genera together in a tribe, and suggested an ancient relationship with the Afro-Eurasian Onitini. Cambefort (1991b) followed this tribal arrangement.

Philips *et al.* (2002) undertook a phylogenetic study of representative species of each of the flightless genera and *Ennearabdus lobocephalus*, using 64 morphological characters. Their outgroups were selected based on their own hypothesis that the Eucraniini are derived from a dichotomiine-like ancestor, or that they

Plate 12.15. Tribe Eucraniini; *Anomiopsoides heteroclyta*, Argentina, 30 mm.

Plate 12.16. Tribe Eucraniini; *Ennearabdus lobocephalus*, Argentina, 12 mm.

are sister to the Scarabaeini as proposed by Mostert and Scholtz (1986). Two New World dichotomiine genera and an African *Scarabaeus* species were used. Their results yielded a single tree with a length of 91 steps and consistency and retension indices of 0.80 and 0.81, respectively. None of the outgroup taxa was found within the ingroup, and there was strong support for monophyly of the tribe and for inclusion of the four genera (Fig. 12.16). This was followed by a molecular phylogenetic study by Ocampo and Hawks (2006) in which they undertook an analysis of a broad range of scarabaeine taxa in an attempt to place the Eucraniini relative to members of the other dung beetle tribes. They used a roughly 1080 bp fragment of the D2 and D3 expansion regions of 28S rDNA and a fragment of about 900 bp of the 18S rDNA gene region and 45 taxa comprising 29 genera of all the Scarabaeine tribes except Gymnopleurini and Sisyphini. Their tree was rooted with the Aphodiinae. Their results provided strong evidence for monophyly of the Scarabaeinae as well as that of the Eucraniini including *Ennearabdus lobocephalus*, and that they are sister to the Phanaeini (Fig. 12.16). Monaghan *et al.* (2007) provided support for monophyly of a eucraniine clade sister to a monophyletic phanaeine clade but as subclades of a strongly supported clade incorporating only these two groups (Fig. 12.17). Sister to this clade was one consisting of several species of the dichotomiine genera *Dichotomius* and *Canthidium*.

Geographical origin: Ocampo and Hawks (2006) provided a biogeographical scenario of the evolution and radiation of the Eucraniini. They hypothesised that the tribe evolved in the Monte biogeographic province of Argentina to which they are endemic. This is a warm desert between Salta (24°35'S) and Chubut (43°26'S). Monte province has high insect endemicity – 11% of genera and 35% of species, based on several orders and families of insects (Roig-Juñent *et al.* 2001, in Ocampo and Hawks 2006). The Monte dung beetle fauna consists of 17 genera and 36 species of which 35% and 42% respectively are endemic. Rollers [and lifters] in the form of Canthonini and Eucraniini predominate while Dichotomiini and Phanaeini are relatively poorly represented. This supports Davis *et al.*'s (2002a) contention that rollers predominate in areas with low dung diversity – dung in the Monte Province is mainly in the form of rodent pellets and other small mammal droppings. Ocampo and Hawks (2006) hypothesised that the Eucraniini probably evolved in the region, after isolation from a phanaeine-like ancestor, when the uplift of the Andes occurred during the middle Miocene (16 – 12 mya). This event produced large plains with lowered rainfall on which developed an arid-adapted flora and fauna. These would have been the conditions that selected for the food preference and food relocation behaviour of modern eucraniines.

Biological and ecological notes: The Eucraniini have traditionally been treated as "rollers" for want of a better term although it has been known since the earliest natural history observations of the species that they lift their food and run forwards, carrying it in the fore legs to a pre-constructed burrow. This behaviour is amongst the most unusual amongst the Scarabaeinae although only the flightless species consistently use it – to lift and carry dry dung pellets. The winged *Ennearabdus lobocephalus*, on the other hand, behave typically as a tunneller and feed on the wet dung of large mammals (albeit mainly of "recently" introduced species to the area – humans, cattle and canids) when available, but behave as do the others when only dry pellets are available (Ocampo and Hawks 2006). Breeding biology has not been recorded.

12.2.5 Eurysternini

Taxonomy and morphology: The tribe is monobasic, with only the genus *Eurysternus* (Plate 12.17), and 20 species. The species, which vary in size, from about 6.0 – 24.0 mm, are sub-rectangular beetles characterised by the elytra being flattened dorsally and sharply downflexed laterally. The scutellum is clearly visible. Labial palpi are 2-segmented. Their colour varies from light- to chocolate brown, and the elytra are sometimes mottled with orange. The cuticle surface is matte, finely sculpted with ridges and pits, densely covered with short hairs. The metatibiae are elongate and slender, not expanded apically. The mesocoxae are widely spaced and the metasternum is broad. Metafemora in many species are characterised by a species-specific spur on the hind margin, or spines on the inner margin. Males can be distinguished from females by: a protibia with a patch of setae present ventrally at the apex, and weakly-developed teeth, or these absent – females do not have the patch of setae, and the lateral teeth on the protibia are well developed; the tip of the metatibia in males is acutely angled, with a spur that may articulate – the tip is transverse in females, and the spur articulates (Jessop 1985).

Diversity and distribution: All the species have tropical distribution in the New World occurring from about central Mexico to southern Brazil.

Phylogeny and evolutionary history: The tribe Eurysternini was erected by Vulcano *et al*. (1960) mainly on morphological grounds, specifically to accommodate the genus *Eurysternus*. Zunino (1983), based on male and female genitalic characters, confirmed that *Eurysternus* is unique amongst Scarabaeinae. The tribal status has been accepted by most dung beetle researchers since the tribe was established (Halffter and Matthews 1966; Halffter and Edmonds

Plate 12.17. Tribe Eurysternini; *Eurysternus caribeus*, Costa Rica, 15 mm.

1982; Jessop 1985; Cambefort 1991b). Curiously, though, the Eurysternini, because of their unusual breeding biology, have been considered "rollers" that have reverted to a form of tunnelling although they are active, [and roll balls] beneath the dung pat, at the soil interface (Cambefort 1991b) but there has been some agreement that they should rather be considered "dwellers" and that their behaviour is more like that found in some African oniticellines (Halffter and Edmonds 1982; Cambefort 1991b).

All of the phylogenetic studies of the Scarabaeinae undertaken so far that have included Eurysternini (Philips *et al.* 2004b; Ocampo and Hawks 2006; Monaghan *et al.* 2007) agreed that the group is essentially monophyletic, although their data do not convincingly show it. Philips *et al.*'s (2004b) morphological study indicated a sister group relationship between Eurysternini and a higher clade consisting of Onitini, Onthophagini and Oniticellini (Fig. 12.2). Ocampo and Hawks' (2006) phylogenetic reconstruction renders the Eurysternini distinctly paraphyletic (Fig. 12.6) as did Monaghan *et al.*'s (2007) because on the latter's preferred tree the Eurysternini clade also included two dichotomiine genera, *Canthidium* and *Ontherus*.

Geographical origin: There have been no specific studies to trace the geographical origin of the eurysternines but it is probable, based on their current distribution that they evolved in humid tropical South America from a dichotomiine-like tunnelling ancestor, and then entered North America after the Panamanian land bridge opened in the Pliocene, as did many other insect groups, including other scarabaeines. They are mainly restricted to moist tropical areas, and as will be seen below, their breeding biology depends on the dung source being suitable for feeding and breeding for long periods, something that would not be possible if the dung dried out quickly.

Biological and ecological notes: Eurysternines have some of the most extraordinary breeding biology amongst scarabaeines. They depend on large sources of wet dung under humid conditions for breeding since their specialised behaviour would not have been possible if small dung sources were used or if the resource dried out rapidly.

As mentioned above, they have traditionally been considered "rollers" because [most species] form perfect balls just beneath the dung source, but their behaviour is actually superficially most similar to some of the African Oniticellini which are considered to be "dwellers" (Halffter and Matthews 1982; Cambefort 1991b; Huerta *et al.* 2003; Huerta *et al.* 2005). The unusual aspects stem from the fact that some of the species produce large numbers of balls which are then either not bred in or fed on; others, or under some conditions, produce balls, the female oviposits and then after a few days the adults consume the brood balls with eggs in. Alternatively, some atypical species do not form balls at all but the female oviposits directly into a dung mass collected from the source and placed into a shallow burrow directly beneath the source.

The highly unusual general breeding pattern in eurysternines is discussed in Chapter 4.1.5.2.

The *Eurysternus* species have not been subjected to phylogenetic analysis so it is not possible to discuss evolutionary trends but several studies (see above) have indicated that the genus is closely related to several dichotomiine genera which implies that the specialised breeding recorded in most species is derived from a more typical form of tunnelling. And then, it could be expected that a species such as *E. foedus*, with the most typical tunnelling behaviour might be basal, and that the species with more specialised behaviour might be more derived.

12.2.6 Sisyphini

Taxonomy and morphology: The Sisyphini are characterized by eight antennal articles, relatively short bodies that are laterally compressed and flattened, especially at the sides of the pronotum, elytra that are broad proximally but attenuate posteriorly, and the exceptionally long middle and hind legs (Plate 12.18). The tribe comprises species of small to moderate body size averaging 7.0-10.0 mm. The elongate, middle and hind legs give the beetles a superficial resemblance to spiders. Indeed, one of the species is named *Neosisyphus tarantula*.

Separation of the species is notoriously difficult because many of them are very similar in appearance with the result that the taxonomy of the group is very confused. In *Neosisyphus*, identification is based primarily on the presence or absence of spines and protuberances on the legs. In *Sisyphus*, it is based, especially, on the shape of clypeal indentations and dentition, and on the shape and distribution of hairs and setae. These may be absent, forming bare patches on the pronotal disc, or they may be distributed individually or as tufts on the pronotal disc and / or elytra. They may or may not also form distinct pleural tufts visible from above at the sides of the elytra.

Diversity and distribution: This tribe is currently considered to comprise 60 species in only three genera. *Nesosisyphus* is endemic to the Indian Ocean island of Mauritius and comprises only four species while the other two genera are more species-rich with wider distributions. *Neosisyphus* is centred in Africa with representatives in the Oriental region. *Sisyphus* is centred in the Afrotropical and Oriental regions with representatives in the southwestern Palaearctic and in Cen-

Plate 12.18. Tribe Sisyphini; *Neosisyphus mirabilis*, South Africa, 12 mm.

tral America. These two genera are found primarily in forest, savanna, and upland grassland regions where there are, undoubtedly, a number of undescribed species.

Phylogeny and evolutionary history: In the Philips *et al.* (2004b) phylogeny, the Sisyphini are basal, and the only ball-rolling tribe on a lineage that includes the tunnelling Onitini and Onthophagini, and the tunnelling or endocoprid Oniticellini (Fig. 12.2). The lineage also includes the South and Central American Eurysternini, a tribe comprising 22 species in a single genus that constructs nests containing brood balls immediately under dung in an endocoprid manner, which both differs to that of the Oniticellini, and undoubtedly has a separate evolutionary origin. Villalba *et al.* (2002) returned a phylogenetic hypothesis indicating that *Sisyphus* is sister to *Copris*, although the supposed relationship is weakly supported. Monaghan *et al.* (2007) included species of *Sisyphus* and *Neosisyphus*, all from South Africa, in their study and their analyses yielded a monophyletic group of species, sister to a large clade consisting of Onitini, Oniticellini and Onthophagini which shows somewhat surprising congruence with Philips *et al.*'s (2004b) tree. The species level separation between Eurasian and Central American *Sisyphus* suggests that this biogeographical pattern originated in a relatively recent range expansion and vicariance event.

Geographical origin: Owing to the somewhat confused taxonomy and the contradictory signals that result from the phylogenetic analyses, the geographical origin of the Sisyphini is uncertain. However, the greatest diversification and the strongest links are with Africa and adjacent territories. The American *Sisyphus* probably originate in fairly recent range expansion from Afro-Eurasia and subsequent vicariance in Central America due to range contraction driven by geological uplift and climatic change, which would probably be coeval with historical trends in the American Oniticellini and Coprini. The endemism of *Nesosisyphus* on Mauritius is remarkable since this island is considered to be of volcanic origin with an age of only 8 my. It is unclear how the ancestor could have reached this isolated oceanic island.

Biological and ecological notes: The Sisyphini comprise entirely ball-rolling species. Pairs co-operate in ball rolling with the male pushing using the back legs, and the female pulling using the front legs. The female constructs a single uncoated brood ovoid or brood pear in a typical Type 4 manner. These broods are mostly buried at the end of a short tunnel preferably in moist soil under the edge of a stone or, perhaps, under other features that offer surface shade such as grass clumps. In a departure from the general trend, a few *Neosisyphus* species abandon their broods at the surface. The Sisyphini are entirely composed of species showing diurnal flight activity.

CHAPTER 13
PHYLOGENETIC STUDIES OF THE SCARABAEINAE

Even though the Scarabaeinae have been the focus of a large number of studies, particularly over the past 50 years, that implied or stated that certain aspects of dung beetle taxonomy, morphology and ecology contain phylogenetic information, it was not until the end of the 20th century that the first modern phylogenetic studies on the group were undertaken. Furthermore, the increasing use of molecular techniques to test hypotheses of relationship over the past 10 years has added a level of refinement that was impossible when only morphology was considered because of the very high degree of homoplasy amongst different groups that result from similar habits and adaptations. However, a lot still has to be done but we have, without doubt, entered one of the most exciting phases of our understanding of relationships amongst the various dung beetle groups, and the evolution of numerous intriguing behavioural patterns that appear to, or actually do, unite them.

Below is a historical overview of phylogenetic studies of dung beetles undertaken over the past 25 years.

13.1 ZUNINO (1983)

The first study of the evolutionary lineages of the major groups of the Scarabaeinae in a Hennigian sense was by Zunino (1983). However, only a few characters of the external morphology of male and female genitalia of a small number of genera, albeit representing most of the major taxa, were used in the "analysis" which was essentially intuitive since there was no empirical step-wise comparison of character states with those of an outgroup, and no statistical values of support for any of the nodes were provided. In spite of these perceived inadequacies, some of the broad general patterns found (Fig. 13.1) have largely been vindicated by recent, more empirical studies. Some of these were that: *Coptorhina*, the mushroom-feeding African genus, is basal; Onthophagini and Oniticellini share phylogenetically significant characters; [some] Coprini and

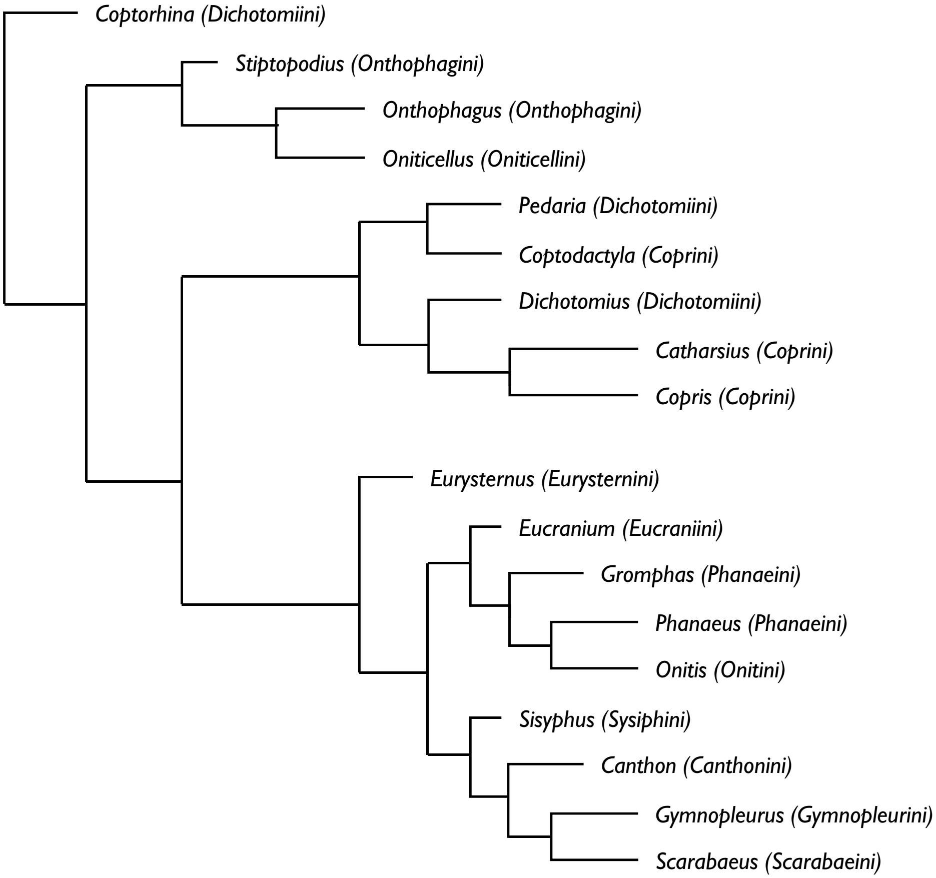


Fig. 13.1. The first phylogenetic tree produced on a [limited] suite of morphological characters of the Scarabaeinae. (After Zunino 1983).

Dichotomiini together form a monophyletic group; Eucraniini is sister to a clade that includes Phanaeini. The first of these, the basal nature of *Coptorhina*, is particularly intriguing since it has subsequently been supported by an analysis of a large suite of morphological characters of 50 scarabaeine genera (Philips *et al.* 2004b) as well as a molecular phylogenetic analysis using three gene regions of about 200 taxa (Monaghan *et al.* 2007) and by a 5-gene region study of the basal African dung beetle groups (Sole and Scholtz 2009). The relationship indicated between Eucraniini and Phanaeini was also novel since the traditional assumption was that the eucraniines are "rollers" and so would be expected to group with those rather than with the tunnelling Phanaeini.

13.2 MONTREUIL (1998)

The Dichotomiini, as the biggest and most widespread tribe of tunnelling dung beetles has long been suspected to be comprised of taxa with doubtful affiliations as indicated by the array of morphologically and behaviourally diverse groups it represents. Compounded by this, some taxa traditionally placed in the Coprini appear to be more similar to ones placed in the Dichotomiini than to some other putative relatives. This situation led Montreuil (1998) to question the monophyly of the Dichotomiini and Coprini in a cladistic morphological study of 26 [he claimed to have analyzed 27 but omitted one from the analysis – see below] of the 40 genera purported to represent the two tribes. Montreuil's study considered taxa from all geographic regions and included most of the genera of doubtful affinity. He selected 39 characters of sclerotized external morphological structures and three of male genitalia and coded these as present or absent. He used characters of *Onitis* and *Onthophagus* as outgroups for the analysis. His cladistic analysis of the 26 taxa and 42 character matrix yielded five trees with a minimum length of 115 steps, CI = 0.383 and RI = 0.733. His consensus tree is illustrated in Fig. 12.1. Philips *et al.* (2004b) re-analyzed his data because he discussed, but omitted, the genus *Aphengium* from his analysis, which resulted in a slightly different tree topology but the main conclusion of Montreuil's study remained unchanged; that the Dichotomiini and Coprini are not monophyletic and that changes to the current classification of the tribes were necessary (these are discussed below). Philips *et al.* (2004b) considered Montreuil's choice of the near-terminal genera *Onitis* and *Onthophagus* as outgroups for the phylogenetic analysis as inappropriate for an analysis of basal groups, and claimed that the omission of other basal groups such as the Canthonini in the analysis compounded the lack of clade resolution. In view of these reservations, they suggested that the changes Montreuil proposed are unjustified.

On the basis of the two principal lineages indicated by his study, Montreuil (1998) suggested some fairly profound changes to the classification of the Scarabaeinae. One lineage expanded the former membership of the Coprini by adding Coprini-like genera from the Dichotomiini. The other lineage comprised the depleted membership of the Dichotomiini and had to be renamed the tribe Ateuchini according to the international rules of nomenclature because the type-genus of the Dichotomiini, *Dichotomius*, now resides in the reconstituted Coprini. In this system, the Ateuchini are hypothesised to be basal but that both tribes are represented on all major land masses except Madagascar.

13.3 VILLALBA, LOBO, MARTÍN-PIERA AND ZARDOYA (2002)

The first phylogenetic analysis of the Scarabaeinae using molecular characters, albeit of a geographically localised and taxonomically restricted [Iberian] fauna, was that of Villalba *et al.* (2002) but because of the geographic restrictions of the data-set, representatives of the extra-limital Canthonini, Dichotomiini, Eucraniini, Eurysternini and Phanaeini were omitted. They analyzed partial nucleotide sequences (about 1221 base pairs) of the mitochondrial oxidase I and II genes of 33 taxa which represent all the Iberian tribes and genera. They used four species each of the Aphodiinae and Geotrupidae as outgroups.

Maximum-parsimony analysis of their mitochondrial sequence data yielded one most-parsimonious tree (see Fig. 12.5) of 5330 steps when a 2:1 Tv:Ts (transversions: transitions) weighting was assumed and Geotrupidae species were used as outgroup. This yielded a consistency index (CI) of 0.27 and a retention index (RI) of 0.49. Alternative weighting schemes (1:1, 3:1) recovered similar tree topologies (Villalba *et al.* 2002).

Villalba *et al.*'s (2002) results supported, with high bootstrap values, the monophyly of the tribes they included in their study, and provided tentative evidence of the monophyletic origin of rolling and tunnelling behaviour. One unexpected result from their analysis was that the genus *Copris*, as a representative of the tribe Coprini, which had always been considered to be closely related to some other tunnellers, was suggested to be more closely related to the rollers Scarabaeini, Gymnopleurini and Sisyphini, and Villalba *et al.* (2002) tentatively suggest that Coprini may have reverted to tunnelling from a rolling ancestor.

13.4 PHILIPS, PRETORIUS AND SCHOLTZ (2004)

In the first comprehensive phylogenetic study of representatives of roughly 20% of all scarabaeine genera and a suite of 200 external and internal morphological characters, Philips *et al.* (2004b) hypothesised a very different picture to that traditionally accepted of the evolution of the major dung beetle groups and the different patterns of dung-feeding and -breeding behaviours so typical of each group. They rooted their tree with members of the Aphodiinae. Their results indicated that the two basal tribes, Dichotomiini and Canthonini, from which all others are thought to have evolved, are poly- or -paraphyletic, and that rolling evolved several times, each time from a tunnelling ancestor.

Their three most parsimonious trees based on unweighted data had a length of 1633 steps, a CI of 0.21 and an RI = 0.48 (see Fig. 12.2 for their consensus tree). All of the topologies supported the paraphyletic dichotomiines as the ancestral tribe which includes the African mushroom-feeder *Coptorhina*, as most basal lineage with two dung-feeding New World genera, *Anomiopus* and *Canthidium* as the second and third oldest lineages, respectively. These were followed by clades composed of coprines and canthonines, both of which were polyphyletic. Their results indicated that all other tribes were monophyletic, including the: Phanaeini (sister to two dichotomiines, *Dichotomius* [New World] and *Heliocopris* [Afro-Asian], and a coprine *Synapsis* [Asian]; Scarabaeini (sister to the southern African canthonine *Circellium*) and; Eucraniini, Eurysternini, Oniticellini, Onitini, Onthophagini and Sisyphini, although the precise relationship among the latter tribes varied slightly. Philips *et al*. (2004b) only included one genus from the tribe Gymnopleurini, the African *Garreta*, (of four Afro-Asian genera) in their analysis but they justified this because of the overall similarity of the genera. It appeared as sister to the New World canthonine genus, *Canthon*.

13.5 OCAMPO AND HAWKS (2006)

Ocampo and Hawks (2006) studied a wide selection of scarabaeine genera from different tribes, albeit with representatives mostly from the New World, in order to assess the phylogenetic position of the Eucraniini. They sampled 45 species of Scarabaeinae of 29 genera which represented all the tribes except Sisyphini and Gymnopleurini. They rooted their characters with the Aphodiinae. They amplified and sequenced a 1080 bp fragment of the D2 and D3 expansion regions of 28S rDNA and a 900 bp fragment of 18S rDNA of their taxa which yielded 1950 bp of nuclear ribosomal DNA sequences (801 bp from 28S D2, 378 bp 28S D3 and 769 bp from 18S). They analyzed this as a single data set using parsimony, maximum-likelihood and Bayesian methods.

Maximum parsimony yielded 117 equally parsimonious trees (length 1707 steps, CI = 0.412, RI = 0.582) and all topologies supported the monophyly of the Scarabaeinae. Basal lineages were not supported and there was low resolution at the base of the consensus tree, with weak support for Dichotomiini, Coprini and Eurysternini. Three clades were recovered: Eucraniini + Phanaeini; Canthonini; and Onthophagini + Onitini + Oniticellini. The monophyly of the Eucraniini was well supported, with bootstrap value of 99%.

Maximum likelihood and Bayesian analyses using the GTR+I+G model yielded highly congruent topologies (see Figs. 12.6a and 12.6b). Again, the monophyly of the Scarabaeinae was well supported with a posterior probability value of 1.0. *Bdelyrus*, a New World dichotomiine, was recovered as the basal taxon. Both analyses recovered the monophyly of the Canthonini, Phanaeini and Eucraniini. The other major lineages were: Scarabaeini + *Copris*; Onitini + Oniticellini. The Australian taxa *Demarziella* (Dichotomiini) and *Amphistomus* (Canthonini) were sister to the Eurysternini.

An interesting result of Ocampo and Hawks' phylogenetic analysis was monophyly of the Canthonini and the congruence of their hypothesis of the close relationship between *Copris* and the Scarabaeini with that of Villalba *et al*. (2002), and of the congruence with Monaghan *et al.*'s (2007) hypothesis of close relationship between Australian canthonines and dichotomiines (see below for further discussion). Less surprising was their agreement with Villalba *et al*. (2002) and Philips *et al*. (2004b) on polyphyly in the Dichotomiini and close relationship between Onthophagini + Onitini + Oniticellini. Their finding of a [largely] monophyletic Canthonini is in contrast to Philips *et al*. (2004b) and Monaghan *et al*. (2007) and is clearly as a result of the selection of only a few taxa from the New World. The one other non-New World genus they studied, *Amphistomus*, from Australia, fell well outside of the New World clade of canthonines, so in spite of their claims of monophyly, their data actually indicate a polyphyletic origin of the Canthonini.

13.6 MONAGHAN, INWARD, HUNT AND VOGLER (2007)

In the most comprehensive phylogenetic analysis of the Scarabaeinae to date, Monaghan *et al*. (2007) undertook an analysis of 214 species in 98 genera (about 40% of the world total) representing all of the tribes from all of the major biogeographical regions using partial sequences from one nuclear (28S) and two mitochondrial (*cox1, rrnL*) genes. They conducted seven phylogenetic analyses, using three "model-based" and four "parsimony" methods, and Aphodiinae as outgroup. They also investigated distribution patterns by the study of character transformations on phylogenetic trees of different biogeographical regions defined as character states.

The trees from model-based, parsimony, and direct optimization analysis were assessed in the light of the existing taxonomy, recent phylogenetic reconstructions and biogeographical distributions and it was found that the 7-partition Bayesian tree exhibited the highest degree of taxonomic and geographic monophyly for the nodes assessed. The seven partitions were obtained by partitioned Bayesian analysis separating the combined data matrix; one for each codon position of *cox1*, and a length-invariable and a length-variable partition for each of *rrnL* and 28S. This tree returned eight of the 12 tribes as monophyletic: Eucraniini, Eurysternini, Gymnopleurini, Onitini, Oniticellini, Phanaeini, Scarabaeini and Sisyphini. The Coprini and Onthophagini were widely dispersed into several independent lineages, and the Canthonini and Dichotomiini were highly polyphyletic, separating into 11 and nine clades, respectively, most of which consisted of small monophyletic groups of a genus or several genera.

The basal node of the Scarabaeinae was occupied by a lineage of African dichotomiine genera *Coptorhina* + *Sarophorus* which was a well supported sister to all other Scarabaeinae (posterior probability 0.94). The clade of African canthonines *Odontoloma* + *Dicranocara* was also near the base, as was the southern African dichotomiine *Macroderes* [but not the Neotropical dichotomiine *Gromphas*, as mentioned by Monaghan *et al.* (2007), whose position was apparently mistakenly read from the phylogram]. All remaining taxa were divided into two large clades of approximately equal size. The first was comprised of a large well-supported group of Onthophagini + Oniticellini + Onitini + Sisyphini + *Epirinus* (a southern African canthonine), along with several other groups from the polyphyletic clades (se Fig. 12.12). The second major clade consisted of several smaller lineages, including a clade of Neotropical canthonine genera (see Fig. 12.13) dichotomiines, coprines, and the monophyletic groups Eucraniini + Phanaeini (see Fig. 12.17) + Eurysternini, Gymnopleurini + *Catharsius* + *Metacatharsius* (both Afro-Asian coprine genera), and Scarabaeini. This major clade also included the majority of non-*Onthophagus* Australasian taxa (canthonines, coprines and dichotomiines), and some Neotropical and African dichotomiines.

When the six biogeographical regions were optimised as character states under parsimony between 38 – 48 character transformations were inferred (Monaghan *et al.* 2007). These involved multiple changes for all the biogeographical regions, but the majority (29 – 35 transitions) affected Africa. In their preferred 7-partition Bayesian reconstruction (29 changes) the African taxa *Coptorhina* + *Sarophorus* (Dichotomiini) and *Odontoloma* + *Dicranocara* (Canthonini) constituted the inferred ancestral state when mapped on trees. On deep nodes, only forward changes were recorded and on higher nodes only two widespread groups, Coprini and Onthopagini, showed reversals and generally high rate of change between biogeographical regions. A number of major clades were confined to a single biogeographical region: (i) the Australasian clade see (see Fig. 12.7) with subclades for New Caledonian and New Zealand taxa nested within the Australian clades; (ii) a South American clade of seven canthonine genera (see Fig. 12.13) (iii) New World Phanaeini + Eucraniini + *Dichotomius* + *Canthidium* (both dichotomiines); and (iv) a large composed largely of African, Afro-Eurasian and Madagascan groups: *Epirinus* (Canthonini - Africa) + Sisyphini (only southern African taxa included in the analyses) + Onitini (Afro-Eurasian) + Oniticellini (representatives of all three subtribes, Depanocerina - Afro-Asian, but only South African taxa studied; Helictopleurina – Madagascan endemic; Oniticellina – Afro-Eurasian) + Onthophagini (cosmopolitan).

In spite of the very rigorous use of multiple phylogenetic analytic approaches that Monaghan *et al.* (2007) used, their different analyses produced largely similar tree topologies and their results are in broad general agreement with patterns already identified by Philips *et al.* (2004b), and to a lesser extent by Villalba *et al.* (2002) and Ocampo and Hawks (2006). That is of the non-recovery of the Canthonini, Coprini, Dichotomiini and Onthophagini, and monophyly of the other eight recognised tribes at some hierarchical level. The monophyletic tribes are consistently recovered, albeit at different hierarchical levels in the various phylogenies, but their monophyly, the morphological similarity of their components, and the generally similar ecological attributes of their members, seemingly support the assumption of naturalness of the groups.

A number of the Monaghan *et al.* (2007) clades deserve further discussion since much of the detail of these was not discussed in their paper. Some terminal ones are unresolved, which is to be expected in a study of this nature, or appear to be made up of unlikely groupings of taxa and these are quite probably an artefact of the analytical procedures used; others, though, obviously contain a wealth of phylogenetically important information that will be discussed below.

Perhaps the most interesting of the clades identified by Monaghan *et al.* (2007) are the basal ones with the *Coptorhina* + *Sarophorus*, *Odontoloma* + *Dicranocara* and *Macroderes* clades being most basal. All of these taxa are centred in southern Africa. *Coptorhina*, the obligate mushroom-feeding genus, has been placed as basal and sister to all other Scarabaeinae in two other phylogenetic studies (Zunino 1983; Philips *et al.* 2004b – but see Sole and Scholtz 2009, discussed below) with very different data matrices and approaches to that of Monaghan *et al.* (2007). *Coptorhina*, *Sarophorus*, *Macroderes* and a few other southern African endemic genera, which have traditionally been treated as dichotomiines, were considered to be closely related in a study by Frolov and Scholtz (unpublished). *Odontoloma* and *Dicranocara* have traditionally been considered as canthonines but with reservation (see Scholtz and Howden 1987a; Davis *et al.* 2008b). The reservations about the tribal position of *Odontoloma* (*Dicranocara* was only recently described) were based on weak morphological support for the "canthonine" characters of the groups and the somewhat circular reasoning that because they are [possibly] canthonines they must be rollers although a simple glance at the very small beetles (average 2.5 mm long) with the squat, short-legged features typical of an *Odontoloma* species immediately confirms the suspicion that they are unlikely to be able to roll balls. Because of these features some species currently placed in the genus *Odontoloma* were originally described as members of the onthophagine genus *Caccobius* (Davis *et al.* 2008b). Recently Deschodt *et al.* (2007) recorded that *Dicranocara* and obviously related genera, are, in fact tunnellers, not rollers.

One of the Monaghan *et al.* (2007) clades that they did not discuss, (apparently weakly supported) but which appears worthy of further consideration is another fairly basal lineage, sister to the *Copris* + *Microcopris* + *Panelus* + *Heliocopris* and *Epirinus* + Sisyphini + Onitini + Oniticellini + Onthophagini clades, which consists of 10 canthonine and one unsupported and obviously misplaced, dichotomiine species. The canthonines belong to seven genera, five of which are Madagascan (*Aleiantus*, with three species, *Phacosomoides olsoufieffi*, *Apotolamprus* sp. *Sphaerocanthon clypeatus* and *Arachnodes* sp. 2). The other two genera are the Australian *Monoplistes* (two species studied) and the Oriental *Phacosoma* (the Indonesian *P. punctatum* studied). A subclade with all the *Aleiantus* species, *Phacosomoides*, *Phacosoma* and both *Monoplistes* was strongly supported, as was a subclade of the remaining genera. Interestingly though, another two species of *Arachnodes*, *A. splendidus* and sp. 1, were placed in a distant clade of Neotropical canthonines. This might, of course, only imply an artefact of the analytical procedure but Orsini *et al.* (2007), in a phylogenetic analysis of some Madagascan canthonines, studied 13 species of *Arachnodes* and found the genus to be polyphyletic, but the groups are apparently closely related to other Madagascan species. So, clearly, with the implied close association between Madagascan, Oriental, Australian and Neotropical (but no African) fauna, more study is obviously necessary to resolve these hints of ancient related ancestry.

One of the Monaghan *et al.* (2007) clades, although strongly supported by their analyses, about which there must surely be doubt is their *Copris* + *Microcopris* + *Panelus* + *Heliocopris* clade. They included *Copris* species from South Africa, Indonesia, Costa Rica and China and a *Microcopris* species from Indonesia in their analyses which yielded a strongly-supported monophyletic group but with *Microcopris* nested in *Copris* (which adds support to the validity of the former being treated as a synonym of the latter by some authorities, or at most, a subgenus of *Copris*). However, the strong support indicated by the sister relationship of the *Copris* clade to *Panelus* and *Heliocopris* appears suspect. *Panelus* is a genus of tiny beetles (average about 2.5 mm long) thought to belong to the Canthonini, which in view of the obviously polyphyletic nature of the “tribe” is not in itself strong support for its actual relationship, but based on its size and general morphology, is likely to be a tunneller. *Copris* and *Heliocopris* species have highly evolved breeding behaviour, bi-parental co-operation and strong selection by females for large-horned males as mates. Although *Panelus* biology is unstudied, it is very unlikely that they have anything but the simplest breeding behaviour so to have them nested in a clade with groups such as *Copris* and *Heliocopris* appears suspect.

Another intriguing relationship indicated by the Monaghan *et al.* (2007) analyses is the strong support of *Epirinus* as sister to Sisyphini + Onitini +

Oniticellini + Onthophagini. *Epirinus* is a monophyletic South African canthonine genus consisting of 29 described species (Medina and Scholtz 2006) and several undescribed ones. The species vary in size between 3.0 – 13.5 mm (average length 8.3 mm) and winged and wingless species are widespread through the distribution range of the genus. The smaller species tend to be wingless (and have been accorded generic status in the past) and the larger species, winged. All of the species so far studied have been seen to roll balls of dung or carrion. Monaghan *et al.* (2007) analyzed four species of the genus, *E. aeneus* and *E. hilaris* and two unidentified species and indicated strong support for the monophyly of the genus. The former species is a large (12.0 mm), winged dung feeder and the latter is a small (4.5 mm), wingless species with undocumented biology.

The placement by Monaghan *et al.* (2007) of *Epirinus* as basal to the four tribes indicated above is especially interesting as this is the most basal [African] true roller recorded and lends tentative support to the first independent evolution of rolling in the Scarabaeinae. [This was recently supported by Sole and Scholtz's (2009) study]. It is sister to a clade that includes another group of true rollers, the Sisyphini, and a large group of tunnellers that appear terminal on all recent phylogenetic studies of the Scarabaeinae (Villalba *et al.* 2002; Philips *et al.* 2004b; Ocampo and Hawks 2006). All other groups in which rolling has actually been recorded lie on the other major clade that Monaghan *et al.*'s (2007) analyses identified. In the Philips *et al.* (2004b) phylogeny, *Epirinus* is sister to the mainly Afro-Eurasian coprine genera, *Copris* and *Metacatharsius*.

The Oniticellini in Monaghan *et al.*'s (2007) preferred tree topology are made paraphyletic by the inclusion of four onthophagine species, two of *Proagoderus* (one from South Africa, the other from Indonesia), *Onthophagus semiareus* (Malaysia) and *Digitonthophagus diabolicus* (Indonesia). Interestingly, another species of *Digitonthophagus*, the very widespread Afro-Eurasian species *D. gazella* (Monaghan *et al.* 2007 studied South African individuals of the species) was sister to *Phalops* and they, in turn were sister to, albeit with weak statistical support, the rest of the Onitini + Oniticellini + Onthophagini. *Phalops* and *Digitonthophagus* (with *Proagoderus* and *Diastellopalus*, which was not studied by Monaghan *et al.* 2007) have been considered the basal onthophagines (see Davis *et al.* 2008b). Monaghan *et al.*'s (2007) analyses strongly support the monophyly of the Madagascan genus *Helictopleurus*, with about 60 species, the numerically dominant one of two genera in the subtribe Helictopleurina, but members of the other two geographically widely distributed subtribes, Drepanocerina and Oniticellina, were paraphyletic, thus questioning the validity or desirability of subtribal differentiation. *Helictopleuris* was also considered to be monophyletic by Orsini *et al.* (2007).

The Australian Scarabaeinae consist of 29 genera of Canthonini, one of Dichotomini (*Demarziella*), two of Coprini (*Coptodactyla* and *Thyregis*), all of which are endemic, and the cosmopolitan genus *Onthophagus*, with 280 species. The dung beetles of New Caledonia and New Zealand are all endemic canthonines.

The strongly-supported monophyletic Australasian clade identified by Monaghan *et al*. 2007 is sister to another, nearly as strongly supported, consisting of the Neotropical dichotomiine genera *Uroxys* and *Bdelyropsis*, and the Australian canthonine genus *Boletoscapter*. The former clade contains representatives of many (all those sampled except *Boletoscapter*) of the Australian rolling genera (exclusively canthonines), the only dichotomiine, *Demarziella*, and one of the two coprine genera (*Coptodactyla*), as well as all the representative [monophyletic] New Caledonian and New Zealand genera. All the sampled taxa including the representatives of the Coprini and Dichotomiini were embedded in the clade and were nested amongst the Canthonini, thus rendering the former two tribes paraphyletic, and the Canthonini polyphyletic in the Australasian clade, or paraphyletic if the position of *Boletoscapter* in the sister clade is considered. One curious, though strongly supported, inclusion in the Australasian clade, was *Pedaria*, an African dichotomiine genus consisting of about 56 species of which many are kleptocoprid parasites of nests of large tunnellers such as *Heliocopris*. This could simply be explained as an artefact of the analysis but there is some congruence with the Philips *et al*. (2004b) phylogeny, in which *Pedaria* is sister to the Australian dichotomiine *Demarziella* and they, in turn, are sister to the Australian canthonine, *Lepanus* and the Madagascan canthonine, *Arachnodes*, so the close ancestry between these geographically widely-separated groups in two very different data sets may actually indicate an ancient link.

Of all the Canthonini, the African taxa appear to have the most diverse ancestries since all of the ones sampled lie on different, albeit sometimes poorly-resolved, clades of the Monaghan *et al*. (2007) tree – *Odontoloma* + *Dicranocara* are strongly supported, and lie in a basal position; *Epirinus* is a well-supported sister to Sisyphini + Onitini + Oniticellini + Onthophagini; *Circellium* is in a poorly-resolved clade with the Neotropical dichotomiine genus *Ateuchus* and together they are sister to the tribe Scarabaeini, albeit, not convincingly so; and *Anachalcos* is sister to a likewise weakly-supported Netropical clade of dichotomiines and eurysternines. Philips *et al*. (2004b) demonstrated a similar pattern of lack of evidence of shared ancestry amongst these groups (*Odontoloma* and *Dicranocara* were not included in their study) which may demonstrate that these are all very ancient, probably, relictual groups, with no close extant ancestors. See comments below on Sole and Scholtz's (2009) findings in this regard.

Although Monaghan *et al.*'s (2007) preferred phylogenetic analysis returned 11 clades in which Canthonini were represented, a large majority of the genera they sampled actually only lies in four clades, albeit widely spread on their tree, and each of which has a strong geographical bias. These are: (i) a mostly-Madagascan clade consisting of five Madagascan genera and two extra-limital ones (one South-East Asian and one Australian) (Fig. 12.11); the *Epirinus* clade (Fig. 12.12); the Australasian clade (Fig. 12.13 - these three discussed above; and their Clade I, consisting almost entirely of Neotropical genera (Fig. 12.14). Molecular analyses of a larger representation of genera from each of these regions, and the inclusion of more gene regions will undoubtedly return at least four strongly monophyletic clades of geographically widely separated and distantly related "canthonines" The tribe that suffers the poorest resolution in any of the clades is the Dichotomiini – there is virtually no coherent pattern in their associations. Monaghan *et al.*'s (2007) analyses returned 9 clades in which dichotomiines were nested but most of these were little more than representatives of a single genus and whose inclusion was generally poorly-supported. The strongest support for a group of dichotomiines lay with the basal African group of *Coptorhina* + *Sarophorus* [+ *Macroderes*]. The only other one was the small group of Neotropical genera [and the Australian canthonine, *Boletoscapter*] sister to the Australasian clade. Virtually every other major clade had at least one, often poorly-supported, dichotomiine nested in it, often at the root.

13.7 SOLE AND SCHOLTZ (2009)

Sole and Scholtz (2009, unpublished) recently convincingly demonstrated that the basal African Canthonini and Dichotomiini fall in three clades, all with very high bootstrap support (Fig. 13.2). The genera *Odontoloma, Frankenbergerius, Sarophorus, Delopleurus* and *Coptorhina* consistently formed a basal lineage in all the data analyses. The genera *Delopleurus*, *Coptorhina* and *Frankenbergerius* are classified as Dichotomiini, whereas *Odontoloma* is considered an atypical Canthonini. A second lineage contained the genera *Endroedyolus, Peckolus, Outenikwanus, Byrrhidium, Dicranocara* and *Namakwanus*, all from the tribe Canthonini. The third lineage contained genera from both tribes: *Anachalcos, Aphengoecus, Bohepilissus, Canthodimorpha, Circellium, Dwesasilvasedis, Epirinus, Gyronotus, Hammondantus* and *Pycnopanelus* (all Canthonini) and *Heliocopris, Macroderes, Pedaria, and Xinidium* (Dichotomiini). Sole and Scholtz also aged the split of the Scarabaeinae from their purported ancestor the Aphodiinae at about 56 mya and the three major lineages of the dung beetles mentioned above to be about 40, 36 and 34 mya respectively.

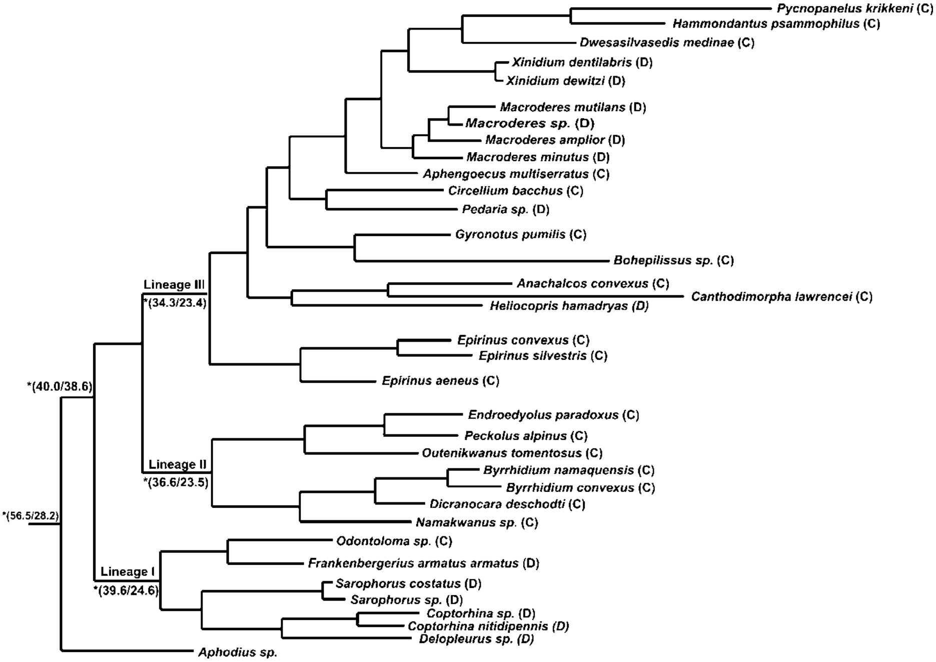


Fig. 13.2. Molecular phylogeny (Sole and Scholtz 2009) of the basal African Canthonini and Dichotomiini, with ages of major radiation events.

Final comments

It appears obvious from the above that no natural group representing a circumscribed taxon that can justifiably be called Dichotomiini actually exists. Virtually every major clade has some member of the current tribe nested in it, often at the root. This implies that the "Dichotomiini" is nothing more than a large and highly artificial group of basal taxa whose "members" lie in all the large clades of the geographical region in which they occur. What does this tell us about the ancestral tunneller and roller? Undoubtedly, every major clade or tribe evolved from a tunnelling ancestor and a closer look at the majority of "rollers" will reveal that most of them are actually tunnellers, as long suspected, which besides the constraints of ancestry, are too small to roll effectively anyway. If this view were adopted there would be no reason to try to explain reversals to tunnelling or other non-rolling behaviours in groups that we have been conditioned by tradition to believe are "rollers". Rolling, on the other hand, has evolved multiple times in different lineages on different continents when ecological conditions have necessitated or favoured it. From the examples quoted in Chapter 4, it is apparent that even tunnellers sometimes resort to rolling chunks or carrying pieces of dung at times, or using pre-formed dung pellets, or that rollers switch between a rolling and a tunnelling tactic even within a breeding episode, so the evolutionary step from tunnelling to rolling is apparently quite simple and this is clearly reflected in how the different groups of dung beetles studied are constituted.

From the recent comprehensive phylogenetic studies (Philips *et al.* 2004b; Monaghan *et al.* (2007); Sole and Scholtz 2009), it is clear that the basal Dichotomiini and Canthonini are polyphyletic, and that most of the terminal "tribes" are monophyletic, albeit at different hierarchical levels, so the question of whether they should retain their current tribal status needs further consideration.

Some of the clear trends to emerge from these studies, however, are that the ancestral fauna on each of the older continents and continental fragments is probably monophyletic across tribes but that detailed phylogenetic study of each of the faunas is required to untangle the history. In other words, the African, South American and Australian "Canthonini" will prove to be monophyletic within each continent. The same probably applies to the African and South American "Dichotomiini", with the Australian representatives of the group being unrelated to those of other of the former two continents, but quite probably closely related to their continental "Canthonini" counterparts. There is unequivocal evidence that the "intermediate" and "modern" tribes *sensu* Cambefort (1991b) are African or have an African origin. Furthermore, there is a strong suggestion that Oniticellini are nested in Onthophagini. Finally, there is now very strong evidence to suggest that the most basal dung beetles yet studied fall in two discrete African groups, one comprised of the genera *Odontoloma, Frankenbergerius, Sarophorus, Delopleurus* and appear basal in data analyses. The genera *Delopleurus*, *Coptorhina* and *Frankenbergerius* are currently classified as Dichotomiini, whereas *Odontoloma* is considered an atypical Canthonini [it has been considered a possible onthophagine, and never thought of as possibly related to "dichotomiines"]. The other basal group, which is sister to this one, contains the genera *Endroedyolus, Peckolus, Outenikwanus, Byrrhidium, Dicranocara* and *Namakwanus* all southern African members of the tribe Canthonini. However, no members of these groups are "rollers", one of the supposed traits of all Canthonini.

There is also very strong support, now, for the radiation of dung beetles during the Tertiary, probably in concert with the radiation of the major mammalian dung producers, particularly from the Miocene onwards. This implies dispersal after fragmentation of Gondwana as the most parsimonious model to explain the current distribution of major dung beetle groups on their respective continents, but in view of the unequivocal evidence that *Onthophagus* has dispersed quickly and widely across the Holarctic and Asia into Australia from a probable African origin, in now not as far-fetched a scenario as previously thought.

Finally, these studies imply that all groups of rollers evolved from a tunnelling ancestor and that this happened several times. However, the most basal group of true rollers yet recorded is the southern African canthonine genus *Epirinus* which is basal in lineages that comprise several others such as *Sisyphus* (Sisyphini) and *Circellium* (Canthonini, albeit doubtfully so).

Suggested changes to dung beetle classification

Possibly the most significant changes needed to the currently accepted dung beetle classification should reflect the identification of two monophyletic groups of basal African taxa that most approximately represent the ancestral dung beetles in DNA, [some] morphology and behaviour. All are tunnellers, feed on dry dung accumulations [or fungus] and have mouthparts adapted for eating hard particles. Their larvae are not enclosed in a ball. This raises the intriguing, though improbable, possibility that these groups have remained unchanged since the origin of dung beetles. However, to have a suite of basal molecular and morphological characters [although a number of these basal taxa are flightless, an obviously derived condition] and an almost complete reversal to what was very likely the primitive condition of feeding and breeding, appears highly coincidental.

As a consequence of the phylogenetic results of the above studies we believe it is desirable to morphologically re-assess at least the genera of these basal groups with a view to considering them to be members of basal "tribes". However, in view of their apparent lack of superficial shared morphological characters, this might be more difficult than it apprears. Loss of wings in some groups will undoubtedly compound the problems by introducing convergent similarities caused by this phenomenon. Furthermore, the tiny size of members of the genera *Endroedyolus, Peckolus,* and *Outenikwanus* (< 3 mm long) will complicate the assignment of synapomorhic characters between them.

Section D

HISTORICAL BIOGEOGRAPHY OF THE SCARABAEINAE AND ITS PHYSICAL AND BIOTIC DRIVERS

Adrian L.V. Davis

A fundamental requirement of biogeography is a classification system that divides the world biota into defined taxonomic units for which spatial distribution patterns may be described. These studies may be extended by phylogenies that analyze relationships among the taxa and provide a framework for analyzing the historical origins and evolution of their spatial patterns. Fitting an absolute time scale to such phylogenies permits the points of divergence between taxa to be matched to dated factors that have driven their historical biogeography, either physical events or coeval biotic evolutionary influences. In the case of the scarabaeine dung beetles, previous global biogeographical studies have relied primarily on distribution data collated and interpreted according to the traditional classification system (Cambefort 1991b; Davis and Scholtz 2001) and, recently, also on a partial phylogeny derived from morphological data (Philips in Davis *et al.* 2002a; Philips *et al.* 2004b), which provided a rank order of derivation although not a relative nor an absolute time scale for divergence events in the subfamily.

Two recent global studies have considered the effect of historical and ecological processes on both the diversity (Davis and Scholtz 2001) and biogeography of the Scarabaeinae (Davis *et al.* 2002a). On this global scale, primary responsibility was ascribed to two parallel sets of historical processes with additional current ecological influence. These were: (1) evolutionary ecological specialization leading to co-evolution with other groups; (2) taxon divergence in geographical isolation followed by unidirectional movement or interchange of taxa between regions; and (3) constraints on taxon richness by current ecoclimatic factors. Thus, due consideration was given to the importance of trophic specialization and trophic diversification, which have driven the co-evolution of the subfamily with the vertebrate taxa that provide their food and breeding resource. Due consideration was also given to the possible importance of plate tectonics to taxon divergence. This may have driven the history of hypothesized Mesozoic origin in Gondwana followed by vicariance on Gondwana fragments. This, in turn, was hypothesized to have been followed by Cenozoic range expansions, dispersal or faunal interchange across narrow barriers or re-established land links, the results of which may be preserved in the current levels of taxonomic separation between regions. Finally, due consideration was given to the degree of historical versus ecological influence on current attributes of the subfamily in different biogeographical regions.

Tectonic events were hypothesized to account for the major global separation into Americas, Afro-Eurasian, and East Gondwana centres of taxon divergence. Centring and dominance on southern continents in basal tribes was hypothesized to result from Mesozoic vicariance on Gondwana fragments. However, the subsequent regional histories of orogenics, climate-driven vegetation change, and co-evolution with vertebrates would be largely responsible for characterizing the divergent dung beetle faunas of those southern regions. This was hypothesized to have been overlain in the Cenozoic by range expansions (Africa and, possibly, India to Eurasia to Americas), dispersal (Oriental to Australia) or faunal interchange (North and South America) that populated the northern Laurasian fragments of North America and Eurasia, and modified the faunas of some southern Gondwana fragments. These historical events were supported by between-region differences in generic and species level patterns and by other geographical trends. Thus, the tribal to generic level separations that dominate east to west taxon relationships in southern continents were hypothesized to be related mainly to Mesozoic Gondwana fragmentation, vicariance, and subsequent taxon evolution. The species level separations that dominate north to south taxon relationships, and east to west relationships in the northern hemisphere, were hypothesized to be related mainly to speciation that followed Cenozoic generic range expansions across land links established by the reconnection of southern Gondwana and northern Laurasian fragments. Dispersal across sea barriers was thought to have played a limited role.

Coevally, against this background of isolation followed by faunal intermingling, the evolutionary history of the Scarabaeinae has been especially shaped by derivation from soil-living, mycetophagous ancestors (Scholtz and Chown 1995) overlain by more recent trophic specialization, primarily to coprophagy. Therefore, due consideration was given to the possible importance of dinosaurs, with which early dung beetles may have overlapped in time during the late Mesozoic, and to the Cenozoic diversification of mammals with whose dung types the majority of the modern fauna has certainly co-evolved. Regional character of the modern fauna was thought to relate, especially, to the degree of change in the local mammal faunas over time. These either remained dominated by small bodied mammals and their small dung types or they became modified by the addition of increasingly larger bodied mammals with their larger dung types of differing physico-chemical characteristics. Change was mostly limited in east Gondwana fragments with dominance by dung beetle genera of basal tribes despite a brief Pleistocene trend to gigantism in mammals of larger fragments. Greater change is observed in South America where larger body size was more diverse in the past leading to greater evenness in representation between genera of basal tribes and those resulting from limited diversification to higher taxonomic level. However, it was highly changed in Africa where past trends to larger body size have persisted to the present, leading to high evenness in diversity between genera resulting from extensive diversification to higher taxonomic level. However, species level patterns were held to be partly modified by Cenozoic additions to the faunas of East Gondwana fragments and the Americas from those of Afro-Eurasia made possible by tectonic and climatic events.

As regards differences in functional attributes of the global dung beetle fauna between biogeographical regions, significant correlations were interpreted as suggesting that historical influences were important where taxon identity was involved (originating by evolutionary process) but that current ecological factors were important where taxon number was involved (constrained by the current ecological status quo). Thus, historical influence may account for the strong correlation of lower dung type diversity (small droppings only) with lower tribal diversity (high dominance of generic numbers within basal tribes) and dominance by ball-rolling as opposed to tunnelling taxa (East Gondwana fragments, especially). Conversely, historical influence may equally account for the strong correlation of greater dung type diversity (high diversity of both small and large dung types) with higher evenness in tribal diversity (greater sharing of generic numbers between tribes) and greater dominance of tunnelling taxa (Afro-Eurasia and Nearctic, especially). However, the strong correlation of generic and species richness with area of suitable climate (combined areas of tropical, subtropical to warm temperate summer rainfall, and Mediterranean-type winter rainfall climate) would be primarily attributable to species area relationships imposed by current ecological factors.

Having developed these hypotheses for the evolution and current geographical occurrence of the subfamily, the most recent study concluded with recommendations for the necessity of further ecological, taxonomic, and phylogenetic research to support or disprove the hypotheses. A few years hence, advances have been made although they seem to mostly deconstruct rather than augment these earlier studies. Taxonomic revisions and new descriptions have changed the numbers and affiliations of taxa in all major biogeographical regions with continuing, sometimes, radical revisions in preparation. Molecular phylogenetics research, especially, has further questioned the current classification system by providing additional support for marked polyphyly in basal Gondwana tribes whose distributions are centred in southern continents (Canthonini, Dichotomiini, Coprini). Such polyphyly in basal tribes had already been postulated by a morphological phylogeny (in Davis *et al.* 2002a; Philips *et al.* 2004b). However, molecular studies (Monaghan *et al.* 2007) also suggested limited polyphyly in a further derived Afro-Eurasian centred tribe (Onthophagini) although monophyly in the other derived tribes or subtribes remained well supported with their

Americas (Eucraniini, Phanaeiini, Eurysternini), Madagascar (Helictopleurina), or Afro-Eurasian centres of diversity (Scarabaeini, Gymnopleurini, Sisyphini, Onitini, other Oniticellini but with the subtribal division into Drepanocerina and Oniticellina lacking support).

Using dispersal / vicariance analysis (Ronquist 1997) of molecular data, a relative timescale has now been proposed for the subfamily (Monaghan *et al.* 2007) that supports the relative old age of tribal elements although there is still no overall absolute timescale. However, such timescales have been calculated for a few genera (*Pachysoma*: Sole *et al.* 2005; some Madagascar canthonine genera: Orsini *et al.* 2007; *Helictopleurus*: Wirta *et al.* 2008). In the case of the Madagascar *Helictopleurus*, matching molecular results to historical events supports an origin in Cenozoic dispersal (Wirta *et al.* 2008), which is not consistent with the hypothesized origin of the Madagascar dung beetle fauna in Mesozoic Gondwana vicariance (Davis *et al.* 2002a). Furthermore, Monaghan *et al.* (2007) have suggested that the basal position of endemic African genera in their phylogenies indicate "Out of Africa" origins that were unexpected given the hypothesis for basal derivation of regional faunas in Gondwana vicariance (Davis *et al.* 2002a). However, molecular phylogeny (Emlen *et al.* 2005b) does provide support for the tracking of the genus *Onthophagus* from Afro-Eurasian ancestors to the rest of the warmer parts of the globe (Davis *et al.* 2002a) although no timescale was calculated.

Thus, to recap, the tribal level classification of basal genera is currently in disarray, including that of genera derived from basal lineages that retain plesiomorphic characters. Furthermore, the evolutionary timescale and origins in dispersal hypothesized by Monaghan *et al.* (2007) are at odds with the vicariance hypotheses developed by Davis *et al.* (2002a). These were largely derived from the literature for global tectonic history. Therefore, the present discussion of the historical biogeography of the Scarabaeinae is intended as an update on previous overviews. It considers: (1) how perceptions of the relative importance of different historical biogeographical processes have shifted from vicariance towards dispersal since 2002; (2) discusses how this resurgence of dispersal hypotheses results from the growth of molecular systematics in which the recent ages generated by molecular clock analyses are often incompatible with the older ages cited for tectonic events previously hypothesized to drive the phylogenies, even though the accuracy of molecular aging techniques remains controversial (Brochu 2004; Graur and Martin 2004); and (3) integrates the compatible findings of older and more recent work, discusses the implications of incompatible findings, and generates a series of questions that need to be answered.

CHAPTER 14
HISTORICAL ORIGIN, EVOLUTIONARY TIMESCALE, AND ITS DRIVERS

There are two pertinent questions concerning the evolution of the Scarabaeinae. What drove the dietary specialization to coprophagy and, when did the subfamily diverge as a distinct taxon? Current hypotheses and evidence suggest possible ancestral pre-adaptation to a soft fungal diet followed by a transfer to coprophagy, possibly in response to the increasing density of droppings or, possibly, via attraction to the fungi growing on this resource (see Chapter 1.3). This may have occurred in either the Mesozoic or the Cenozoic. However, it is difficult to provide convincing answers owing to the contradictory findings of morphological and molecular phylogeny, the weakness of support for some of the nodes, the failure to fit an acceptable absolute timescale to the clades, and conflicting evidence in the literature for phylogeny, tectonic and fossil history, evolutionary ecology, and biogeography.

14.1. ANCESTRAL DERIVATION AND EVOLUTIONARY SPECIALIZATION TO DUNG

Are there any clues to the history of the Scarabaeinae according to how it fits within the superfamily Scarabaeoidea? This superfamily is taxon-rich comprising a diversity of families, subfamilies and tribes. These higher taxa show an array of diets, which include living or dead plant matter, dung, or carrion. As phylogenetic analyses suggest that the ancestral habit was soil tunnelling with a mycetophagous diet (Scholtz and Chown 1995), coprophagy would be derived behaviour within the superfamily. However, this finding is based on a phylogeny derived from morphological characters whose topology is not consistent with that of a more recent molecular phylogeny (Smith *et al.* 2006). Furthermore, the ancestral diet is questioned by Krell (2006) in favour of testing hypotheses for mycetophagy in adults with humus-eating larvae.

In the morphological phylogenies, there were three major lineages. One comprised a single family (Glaresidae) whereas the other two were highly diversified into many taxonomic groups (Browne and Scholtz 1995; 1998; 1999) that appear to represent similar radiations across an equally diverse array of different diets. These were claimed to represent older (separated at family level – Mesozoic) and more recent diversifications (separated at subfamily level within the family Scarabaeidae – Cenozoic). These putative older and younger lineages were each subdivided into two major clades. Dung feeders in the family level lineage (Geotrupidae) were included in a clade together with fungus and carrion feeding families whereas dung feeders in the subfamily level lineage comprised sister taxa (Aphodiinae, Scarabaeinae) in a clade that includes mycetophages, necrophages, saprophages and xylophages. However, a recent molecular phylogeny radically rearranges the topology of the two family level lineages and moves some carrion and fungus-eating families into the Scarabaeidae clade where weak support is provided for their close relationships to the subfamilies Aphodiinae and Scarabaeinae (Smith *et al.* 2006).

Despite these contradictory results for the systematics of higher taxa, the sister relationship between the Aphodiinae and Scarabaeinae endures in both morphological and molecular phylogenies (Browne and Scholtz 1998; Smith *et al.* 2006; Monaghan *et al.* 2007) although the support is weak. Therefore, strengthening the statistical support for their sisterhood is a most important consideration for instilling confidence in future analyses of the Scarabaeinae that are rooted using aphodiine taxa. Furthermore, assuming that the Scarabaeinae is a monophyletic assemblage (Philips *et al.* 2004b; Monaghan *et al.* 2007), it is imperative to determine an acceptable absolute timescale for subfamily divergence and within subfamily evolution. Only a relative timescale has been calculated to date. This may be because calculation of an absolute time scale is dependent on using rates of sequence divergence published for other insect groups and these show great variation (Farrell 2001; Juan *et al.* 1995). In addition, the existing scarabaeine sequence data seems not to be sufficiently comprehensive to generate useful results. Nevertheless, until an acceptable timescale is calculated, the juxtaposition between divergence events in the Scarabaeinae and events in physical and evolutionary history will remain speculative and make it impossible to determine the veracity of historical biogeographical hypotheses.

14.2 MESOZOIC VERSUS CENOZOIC ORIGIN

Does the existing literature provide strong evidence for the early origin of the Scarabaeinae in the age of the dinosaurs followed by radiation on mammal dung in the Cenozoic, or does it suggest a later origin coeval with increase in density, size, and diversity of mammalian dung types in the early Cenozoic? Past estimates for the age of the subfamily range from the mid-Mesozoic (Jeannel 1942; Halffter 1972) to the late Mesozoic (fossil evidence: Krell 2000; 2006; biogeographical evidence: Davis *et al.* 2002a), end of the Mesozoic (Cambefort 1991b), to the early Cenozoic (phylogenetic evidence: Scholtz and Chown 1995).

CHAPTER 15
EVIDENCE FOR VARIOUS EVOLUTIONARY HYPOTHESES

15.1 PHYLOGENETIC EVIDENCE

As discussed above, the existing literature fails to provide a consensus phylogeny for the Scarabaeinae or an exact timescale for Scarabaeine evolution. In view of the conflicting hypotheses for relationships from superfamily down to subfamily level and the degree of variation in published rates of sequence divergence, what is the best approach to calculate an acceptable timescale for the evolution of the subfamily Scarabaeinae? Owing to variable support for the sister status of the Aphodiinae and Scarabaeinae and variability in within-subfamily topologies, it is not currently easy to evolve a believable timescale by a broad-based approach. However, timescales have been calculated from molecular data for species of single well-supported genera some of which occupy terminal branches of subfamily level phylogenies (e.g. *Helictopleurus*). Such results may be used to calibrate absolute values from a relative time scale, such as that produced for the subfamily Scarabaeinae by Monaghan *et al* (2007). This approach would be independent of the different topologies for subfamily level phylogenies yielded by different data sets or different analytical methods. The use of several species level timescales for different terminal genera would permit a cross check for consistency as regards possibly different taxon and regional rates. However, although such an analytical approach circumvents mutability in topology of subfamily level phylogenies, the calculations remain severely weakened by reliance on the variable rates of sequence divergence reported for other insect taxa in the absence of specific known rates for any scarabaeine taxa.

Despite the great differences in absolute ages yielded when using the wide range of published rates for cytochrome oxidase subunit one (CO1) sequence divergence, it is tempting to use these ages to calibrate the relative time scale for scarabaeine evolution provided by Monaghan *et al*. (2007). As *Pachysoma* was not studied by Monaghan *et al*. (2007) and there is conflict between molecular

Madagascar canthonine results (Orsini *et al.* 2007) and traditional classification, the only currently acceptable findings for use in calibration are those for the well-supported monophyletic genus *Helictopleurus*, that are derived from 25 out of 65 valid species in the Helictopleurina (Wirta *et al.* 2008). Monaghan *et al.* (2007) use three named *Helictopleurus* species, two from clade II and one from clade III (Wirta *et al.* 2008). Therefore, the basal node between *Helictopleurus* species in Monaghan *et al.* (2007) would be roughly equivalent to that between clades II and III, which Wirta *et al.* (2008) date at 34 (25 / 44 – confidence limits) or 21 (16 / 27) my, using the extremes of sequence divergence rates reported for other insect groups. If these numbers are used to calibrate an exact age for the basal *Helictopleurus* node on the 0-1 relative scale provided for the subfamily phylogeny (Monaghan *et al.* 2007), then dates of 71 (estimated confidence limits: 52 / 92), or 44 (33 / 56) my, are yielded for the subfamily point of origin (Tables 1.1, 15.1). The latter estimate equates to an Eocene origin close to the estimated Oligocene age of the earliest reliably identified fossils (Cambefort 1991b; Krell 2000) belonging to terminal genera (Monaghan *et al.* 2007). The former estimate yields a mean origin close to the Mesozoic / Cenozoic boundary at 65 MY, with estimated confidence limits as late as the early Cenozoic (early Eocene) or as early as the late Mesozoic, but at a time when Gondwana was already well fragmented according to Sanmartin and Ronquist (2004) (110 my), and Scotese (1993) (93 my). Thus, in order to support vicariant origins of the Scarabaeine lineages through Gondwana fragmentation, one would have to hypothesize average CO1 molecular substitution and sequence divergence rates that are about twice as slow as the slowest so far cited for any insect group.

Thus, it may be concluded from gross phylogenetic manipulations that the initial question remains unanswered since the origin of the subfamily could equally be either late Mesozoic or early Cenozoic. Furthermore, the current timescale places even the earliest estimate for evolution of the subfamily at a point that post-dates the fragmentation of Gondwana. If this were accurate, then there would be little support for origin of the basal scarabaeine genera in Gondwana vicariance. However, the great range in published rates of sequence divergence does not instil confidence in these results. These rates may vary between different taxa (Brower 1994; Farrell 2001; Brochu 2004) and different genetic material, and could also show different rates of change in different geological ages or geographical regions. Thus, their use might over or underestimate the long term duration of the subfamily history. As the applicability to Scarabaeinae of results from other insect groups is unclear, more work on rates of molecular substitution is required to improve understanding of how the process varies between taxa and across space and time. This might facilitate the development of stronger, more acceptable predictions of age for the Scarabaeinae.

Table 15.1. Relative and absolute ages for the subfamily Scarabaeinae, for nine validated tribal lineages, and for the most basal internal nodes in those tribal lineages, as derived from a relative age scale (Monaghan *et al.* 2007), which was calibrated using the fastest and slowest published DNA molecular sequence divergence rates for insects as applied to the phylogeny of the genus *Helictopleurus* by Wirta *et al.* (2008).

Taxa	**Relative age (0-1 scale)**	**Absolute age (my)***		**Tribe age minus basal node age****	
		Slowest rate	**Fastest rate**		
Subfamily Scarabaeinae	1.00	71.1 (late Cretaceous)	43.9 (Eocene)	-	
Basal lineage	0.93	66.1 (late Cretaceous)	40.8 (late Eocene)	-	
Two major lineages	0.83	59.1 (Palaeocene)	36.5 (late Eocene)	-	
Lineage 1 – tribal lineages					
Phanaeini***	0.50	35.7 (late Eocene)	22.1 (early Miocene)	-	
Eucraniini***	0.50	35.7 (late Eocene)	22.1 (early Miocene)	-	
Eurysternini	0.55	38.8 (late Eocene)	23.9 (late Oligocene)	-	
Gymnopleurini	0.61	43.5 (Eocene)	26.9 (Oligocene)	-	
Scarabaeini	0.64	45.5 (Eocene)	28.1 (Oligocene)	-	
Lineage 2 – tribal lineages					
Sisyphini	0.74	52.7 (early Eocene)	32.5 (Oligocene)	-	
Onitini	0.71	50.3 (Eocene)	31.1 (Oligocene)	-	
Onthophagini****	0.66	47.2 (Eocene)	29.2 (Oligocene)	-	
Oniticellini****	0.66	47.2 (Eocene)	29.2 (Oligocene)	-	
Basal node within tribal lineage					
Phanaeini	0.35	25.2 (Oligocene)	15.6 (Miocene)	(10.5,	6.5)
Eucraniini	0.33	23.5 (Oligocene)	14.5 (Miocene)	(12.2,	7.5)
Eurysternini	0.46	32.8 (Oligocene)	20.3 (early Miocene)	(5.9,	3.7)
Gymnopleurini	0.44	31.3 (Oligocene)	19.3 (early Miocene)	(12.2,	7.6)
Scarabaeini	0.49	34.9 (late Eocene)	21.5 (early Miocene)	(10.7,	6.6)

Taxa	Relative age (0-1 scale)	Absolute age (my)*		Tribe age minus basal node age**	
		Slowest rate	Fastest rate		
Sisyphini	0.42	29.8 (Oligocene)	18.4 (Miocene)	(22.9,	4.1)
Onitini	0.55	38.9 (late Eocene)	24.0 (Oligocene)	(11.4,	7.0)
Onthophagini****	0.54	38.4 (late Eocene)	23.7 (Oligocene)	(8.8,	5.4)
Oniticellini****	0.61	43.2 (Eocene)	26.7 (Oligocene)	(4.1,	2.5)

* Confidence limits would lie many millions of years either side of these estimated values.

** Tribal age minus age of basal internal node (my)

*** Origin of combined Phanaeini / Eucraniini lineage is 45.2 (Eocene) or 27.9 my (Oligocene).

**** Age estimates for Oniticellini include basal "onthophagine" genera (*Proagoderus*, and other onthophagines) which show closest relationships to "oniticellines".

No ages are provided for the intermingled generic groups of contentious basal tribes (Canthonini, Dichotomiini, Coprini) for which topology is changeable and resolution of group membership is mostly poor when using different analytical methods.

15.2 DIRECT FOSSIL EVIDENCE

Do trace fossils or fossil dung (coprolites), insect-worked coprolites, and underlying tunnels provide sufficient indirect evidence to predict the presence of a scarabaeine fauna in the Mesozoic? Could an earlier Mesozoic history be concealed by absence or poor substantiation of a fossil beetle record, or, would the existing record indicate a Cenozoic diversification for the subfamily?

Trace or ichnofossils are represented by various structures that include fossil tunnels and coprolites. The abundance of complex trace fossils in Cretaceous and Cenozoic palaeosols is held to reflect the diversification of modern insect groups, including dung beetles (Buatois *et al.* 1998). They occur together with coprolites that have a history extending throughout the fossil record (Thulborn 1991). The main problem with such fossils is that their identity relies strongly on interpretation and they cannot be easily linked to specific animal taxa (see Chapter 1.1).

Coprolites attributed to dinosaurs litter late Triassic, Jurassic and Cretaceous sedimentary strata, occurring randomly, at specific horizons, or occasionally as clusters of pellets that may represent single droppings (Thulborn 1991). It is a question of whether or not they occurred in sufficient density, with sufficient frequency, and were physico-chemically suitable to support a specialized dung beetle fauna. It is possible that they could support a dung fauna given the average size of coprolites at 8 ± 4 cm long and 4 ± 2 cm wide (Thulborn 1991).

Furthermore, assuming that the diet was not too fibrous, the action of the stone-filled dinosaur gizzard could have produced a sufficiently fragmented, moist dung consistency although evidence for dinosaur gastroliths is limited, except in theropods (Wings 2007).

An ichnofossil from the Nearctic late Cretaceous furnishes the most convincing evidence for a Mesozoic dung fauna. This comprises a burrowed herbivorous dinosaur coprolite (Chin 1995) and associated dung-filled tunnels (Chin and Gill 1996). Although this dropping comprises wood fragments (Chin and Gill 1996), it may be noted that one extant Afrotropical scarabaeine genus, *Paraphytus*, specializes in nesting in rotting tree trunks in tropical forests (Cambefort and Walter 1985). However, surface markings on coprolites from as early as the Triassic (Krell 2006) are not conclusive evidence for a Mesozoic scarabaeine fauna. Neither is the tunnelling of putative dinosaur coprolites since the Cretaceous Nearctic setting of these fossils is at odds with the hypothesized history of the modern Nearctic scarabaeine fauna. This fauna is dominated by species level relationships that indicate recent derivation from Afro-Eurasian and Neotropical ancestors. Ancestors of other extant dung burying groups like the Geotrupinae could equally have been responsible for the tunnelled coprolites, especially since they and their fossils are primarily centred on the Northern Hemisphere (Schoolmeesters 2008a; Krell 2000; 2006). However, their substantiated fossil remains are entirely restricted to strata of Cenozoic age despite a suspected history stretching back to the Cretaceous that is weakly supported by fossils of doubtful affinity (Krell 2000).

Despite earlier claims for a fossil dung beetle record dating back to the Jurassic (Crowson 1981), a recent review suggests that the oldest fossil possibly attributable to the Scarabaeinae is from much younger Upper Cretaceous strata. This fossil genus *Prionocephale* Lin, from Zhejiang, China, is classified as a scarabaeine since it resembles extant tunnelling or ball-rolling dung beetles (Krell 2000; 2006). However, the presence of a Cretaceous scarabaeine fossil in the modern Oriental region would conflict with the hypothesized Gondwana origin of the subfamily as the Cretaceous predates linkage between Gondwana fragments and China.

The greatest diversity of beetle fossils that may be reliably attributed to the Scarabaeinae occurs in strata of Cenozoic age, primarily in the Northern Hemisphere with fewer from the Southern Hemisphere. These fossils mostly belong to extant Afro-Eurasian centred genera. Although the identifications of some German fossils from the Eocene (*Gymnopleurus*) and Oligocene (*Onitis*) are doubtfully correct (Krell 2000), those for other fossils from Oligocene to Pleistocene strata are considered reliable. These taxa (see Table 1.1) originate from relatively few centres in France (Oligocene: *Ateuchites*, *Onthophagus*), Germany (Oligocene: *Onthophagus*; Miocene: *Copris*, *Gymnopleurus*, *Oniticellus*, *Onthophagus*), China (Miocene: *Scelocopris*), Japan (Miocene: *Heliocopris*), and the USA (Pliocene: *Copris*, Pleistocene: *Copris*, *Onthophagus*, *Phanaeus*). The fossil dung beetle record in the Southern Hemisphere comprises just Miocene fossils from near Lake Victoria Nyanza in Africa (*Anachalcos*, *Metacatharsius*, *Copris*). However, there are also fossil dung balls that possibly date back to the Neotropical Cretaceous (Krell 2006) but are primarily of Cenozoic age. These include records from Africa, Antarctica, and the Oligocene of South America (Argentina) that are similar to the brood balls of the extant canthonine genus, *Megathopa* Erscholtz (Frenguelli 1938a; 1938b; Halffter 1972). Such dung ball fossils have also been recorded in North America and Asia in the Northern Hemisphere (Krell 2006).

Thus, a Mesozoic origin for the Scarabaeinae cannot be precluded although the fossil support is inconclusive and at odds with biogeographical evidence. This includes the single tentative scarabaeine beetle from the Chinese Upper Cretaceous that is the only direct evidence for a history predating the Cenozoic. However, although the early Cenozoic marked a diversification and increase in body size of mammals (Wing and Sues 1993), which was, presumably, matched by adaptive radiations in dung beetles, it should be noted that the coeval fossil record is mostly comprised of extant genera that occupy terminal positions on scarab phylogenies. Thus, there is no known fossil record of the earlier history. Given the inconclusive fossil and phylogenetic evidence, it is unclear if radiation of the modern fauna with Cenozoic mammal dung is derived from the descendants of an earlier Mesozoic scarabaeine fauna that survived extensive extinctions at the Cretaceous / Cenozoic boundary (mammals: Clemens 2001; plant-insect associations: Labandeira *et al*. 2002) or whether it originates in a divergence between the Aphodiinae and Scarabaeinae in the early Cenozoic.

15.3 EVIDENCE FROM THE VERTEBRATE FOSSIL RECORD, EVOLUTIONARY ECOLOGY, AND PHYLOGENY

When did the spatial density and temporal frequency of fresh droppings become sufficient to drive specialization to coprophagy and divergence to subfamily level? Could ectotherms have produced enough dung with sufficient frequency or would an increased rate of dung production by endotherms have been necessary? Therefore, did the origin of specialization in Scarabaeinae occur in the early Cenozoic with the radiation of endothermic mammals that was characterized in places by increase in body size (Wing and Sues 1993) and increased dung type diversity. Or, might there have been an earlier fauna that used dung from Mesozoic mammals, dinosaurs, or both?

The possibility of Cenozoic derivation from earlier ancestors cannot be excluded given that fossil tunnels in dinosaur dung indicate that it was treated as a resource. However, this would only be circumstantial evidence as the Nearctic tunnels were made by a taxonomically unidentified Mesozoic fauna, with an unknown degree of generalization or specialization to dung that was interpreted as originating from dinosaurs of unknown physiological condition. Presumably the amount and frequency of dung dropped by dinosaurs would have been greater if they were endothermic with its associated implications for a specialized dung fauna. However, its inclusion as a resource by a generalist detritus or saprophytic fauna might be more likely if the density and frequency of dung were lower, as they might be if dinosaurs were ectothermic.

There has been a long debate in support of endothermy in at least some dinosaurs. Arguments rest on characteristics of endothermic physiology and behaviour. These have been extrapolated from known character states and physiology of extant taxa in comparison with similar character states in dinosaur fossils. It has emerged that most of the evidence is ambiguous as it could equally characterize ectothermic or endothermic taxa. This is because none is directly linked to endothermy, other than the presence or absence of complex respiratory turbinates (Hillenius and Ruben 2004). These structures are housed in special broadenings of the nasal cavity that permit the increased oxygen uptake necessary to support an increased metabolic rate, with resulting heat production that may be regulated to achieve homeostasis and endothermic physiology (homeothermy), even at rest. These turbinates bear epithelial tissues on their expanded surface area that are directly involved in water retention and thermoregulation. Respiratory turbinates are characteristic only of endothermic taxa including most mammals and birds but not modern ectothermic reptiles (Hillenius and Ruben 2004). Fossil evidence for strongly ridged sites of turbinate mounting or broad nasal chambers, supports the early evolution of endothermy in mammals (late Triassic), and their direct Triassic ancestors (synapsids, cynodonts), with the independent evolution of endothermy in early to mid-Cretaceous birds implied by different lung structure, breathing apparatus, and phylogeny. The absence of such evidence in dinosaurs suggests that they were essentially ectothermic although some theropods may have had improved respiratory systems that facilitated air intake above that of modern reptiles but below that of modern endotherms (Hillenius and Ruben 2004).

However, inconclusive evidence continues to be quoted in support of arguments for endothermy in dinosaurs. Some of this evidence has its strengths and has been studied in detail, particularly bone structure and its use to predict growth rates. Two principal types of bone structure have been defined in these studies. Fibrolamellar bone is perforated by many haversian canals for the carriage of blood vessels. It occurs in many extant mammals and birds and has, therefore, been associated with endothermy and rapid growth rates. By contrast, lamellarzonal bone has few haversian canals and is especially characteristic of extant, ectothermic amphibians, and most reptiles. However, it has emerged that these observations cannot be used as conclusive support for the physiological state of dinosaurs as the accumulated evidence is now so contradictory (Hillenius and Ruben 2004). For instance, although fibrolamellar bone has been recorded in many dinosaurs, some species show both fibrolamellar and lamellarzonal bone, like some extant ectothermic reptiles, whereas extant shrews and other small mammals are characterized by lamellarzonal-type bone despite their endothermy (Reid 1984). Furthermore, although fast growth rates in some dinosaurs are closer to those in extant, endothermic eutherian mammals (Erickson *et al* 2001) than to those in many extant ectothermic reptiles, the rate of growth is more rapid in extant, juvenile, ectothermic crocodilians than some mammals (Ruben 1995). It is now clear that particular bone structure and faster growth rates are not necessarily associated with endothermy (Starck and Chinsamy 2002; Chinsamy and Hillenius 2004).

Other evidence for endothermy in dinosaurs is less convincing, e.g. walking speed, predator / prey ratios, brain size, posture (Bakker 1986), and heart structure (Fisher *et al.* 2000). As higher pressure circulation may be achieved by a four chambered heart as in endothermic mammals, the discovery of a putative, fossil, four-chambered dinosaur heart has been cited as evidence of endothermy (Fisher *et al.* 2000). However, extant ectothermic crocodilians also have a four-chambered heart (Hillenius and Ruben 2004). Even so, stronger circulation would be useful in large animals, particularly those with erect posture, as in dinosaurs. Large brain size relative to body mass has also been cited as evidence of endothermy in some small theropod and ornithopod dinosaurs (Bakker 1986) since a large brain requires high rates of oxygenation. Fossil evidence indicates that some theropods did have respiratory systems that would have permitted increased oxygen uptake but at a level below that of mammals (Hillenius and Ruben 2004). Predator / prey ratios calculated from extant animal communities and the fossil record have also been used as evidence for endothermy. To permit a high but sustainable predation rate, a high ratio is shown by dinosaurs and by extant endothermic mammals with their high energy requirements compared to a low predation rate and a low ratio for ectotherms with their low energy requirements (Bakker 1986). However, bias in the fossil record renders this evidence unreliable (Farlow 1980). Evidence derived from the calculation of a fast walking speed from fossil dinosaur footprints

(Bakker 1986) is negated by the observation that even modern ectotherms may move rapidly for short periods although this is not sustainable unlike in many endothermic mammals. It has also been suggested that some dinosaurs could have shown mixed ectothermic and endothermic character by virtue of large body volume and solar heat retention (termed gigantothermy) (Seebacher 2003). Evidence from the extant heterothermic marsupial mouse, *Sminthopsis*, indicates that although radiant heat from the sun may be used to increase body temperature, it results in relatively modest increases in basal metabolic rate of about 25% (Geiser and Drury 2003) and would not be expected to appreciably increase energy requirements, food uptake, or the rate of dung production. Thus, the possibility of such a physiologically cheap derivation of body heat in dinosaurs could have had an insignificant effect on the rate of dung production.

As the evidence is equivocal for endothermy and copious dung production in dinosaurs, could the evolution of specialization to coprophagy have been in response to the dung of Mesozoic mammals? Or, could a combination of both mammal and dinosaur dung have achieved sufficient density for the evolution of a specialized dung fauna? Throughout their 250 my history as a separate taxon, Mesozoic mammals probably remained endothermic with possibly higher dung production rates than ectotherms. However, although they have a history stretching back to the Triassic coeval with much of the dinosaur history, they remained small-bodied and mainly arboreal during most of the Mesozoic (Lillegraven 1979). The largest-bodied, Mesozoic mammal fossil recorded to date was only recently recovered from Chinese late Mesozoic sediments (Hu *et al.* 2005) and was a dog-sized predator. Thus, Mesozoic mammal droppings would have been largely small and may or may not have supported a scarabaeine fauna. Although the molecular origin of extant mammal subclasses and orders has been traced back to the Mesozoic (Penny *et al.* 1999; Murphy *et al.* 2001), it is likely that radiation in the modern dung beetle fauna occurred with the increase in mammal body sizes and, presumably, their dung types in the early Cenozoic (Davis *et al.* 2002a) as defined by the dating of the recognisable fossil record of these modern mammal groups. However, the possibility of an earlier limited or extensive dung beetle radiation that was a victim of mass extinction events at the Cretaceous / Cenozoic boundary (Twitchett 2006) cannot be discounted, even though there is no fossil evidence for southern counterparts to the probably different regional taxon responsible for burrowed dinosaur dung in the Northern Hemisphere.

In conclusion, it is unclear if evolution of a specialized dung fauna is dependent on a terrestrial vertebrate fauna with a high proportion of taxa with high metabolic rate, self-generated heat, high energy demand, high food intake, rapid digestion, and frequent dung production of suitable size and composition, or whether the presence of dung from large-bodied ectotherms would be sufficient. There is inconclusive support for endothermy in dinosaurs and a generally small body size recorded for Mesozoic mammals. Evidence for a specialized dung fauna in the Mesozoic is meagre and inconclusive with only a single fossil record of a tunnelled dinosaur dropping and buried dung in the Nearctic Cretaceous (late Mesozoic) (Chin 1995; Chin and Gill 1996). If dinosaurs were not endothermic, this observation brings one back to the question, "could ectothermic dinosaurs have supported a specialized dung fauna or were the insects responsible for the observations, unspecialised organic matter feeders, even if the buried dung material has been interpreted as specialized behaviour (Chin and Gill 1996)?". It is useful to juxtapose this question to the observation that the modern scarabaeine fauna of Panama is associated with mammal rather than ectothermic, lizard dung (Young 1981), although it is unclear if this pattern is related to the density of reptile dung or some other reason. Thus, at present, any resolution of the questions on the drivers and age of specialization to coprophagy remain precluded by limitations and contradictions in the available evidence.

15.4 BIOGEOGRAPHICAL EVIDENCE

Can the modern distribution of the traditional tribes now be used in support of a hypothesized Mesozoic subfamily origin on Gondwana as implied from the shared presence and centring of basal Canthonini, Dichotomiini and Coprini on the fragments of this southern supercontinent? Considering the disarray in the traditional classification resulting from non-supportive phylogenetic evidence, the short answer is "no" since, without a reliable tribal level classification, one is unable to reliably link patterns of generic distribution that reflect the older history of the subfamily. It is not currently possible to construct an alternative classification system that satisfies both morphological and molecular phylogenetic findings since there are only partial analyses of generic relationships. These show no consistency in results using different methods as reflected by changes in topology for the same data when using different analytical methods. There is also no reliable absolute age to determine how any divergence patterns might relate to tectonic and other dated, possibly influential, historical events. However, it is possible to adapt the traditional classification to align more closely to the phylogenetic findings. Also, more recent Cenozoic history is still able to be implied using generic and species patterns since, with regard to species membership and generic status, revisions have generally been much less radical than those that will be necessary at tribal level.

15.5 CONCLUSIONS

Although a Mesozoic origin for the Scarabaeinae cannot be entirely discredited, there is only limited circumstantial fossil support for such a viewpoint. Even molecular evidence for a Cenozoic origin hinges on phylogenetic topologies and age estimates that are sufficiently variable to cast doubts on their validity. It is likely that a consensus viewpoint will only be achieved by expansion of data sets and refinement of the analytical methods.

CHAPTER 16

CLASSIFICATION, PHYLOGENY, SPATIAL PATTERNS AND BIOGEOGRAPHICAL HYPOTHESES

Recent phylogenetics research has questioned parts of the "traditional" tribal classification, thus undermining confidence in spatial patterns based on this system, particularly those pertaining to the polyphyletic basal tribes (Canthonini, Dichotomiini, Coprini). As tribal, generic, and species-level patterns differ from one another and may represent patterns of different evolutionary age, it is necessary to have a classification at each level for a balanced understanding of the subfamily biogeography, particularly as each level is, potentially, the origin of different spatial hypotheses. Thus, in the absence of a revised tribal level classification, what are the precise implications of inconsistencies between phylogenies, estimated ages, and higher classification for the global or regional spatial patterns and biogeographical hypotheses defined by Davis *et al.* (2002a)?

16.1 RATIONALIZING CLASSIFICATION AND PHYLOGENY

Because it is impossible to fully re-assess the historical biogeography of the Scarabaeinae in the absence of a valid classification system, it is a matter of urgency to revise the higher-level systematics, particularly that of the contentious basal tribes. Although Montreuil (1998) and Vaz de Mello (2008) have partly redefined the systematics and classification of the Dichotomiini (redefined as Ateuchini and additional Coprini), some canthonine genera have been shown to have relationships interspersed between genera of these basal tunneller-dominated tribes (Monaghan *et al.* 2007). Thus, it is clear that problems in the classification of the basal taxa cannot be resolved by analyses that examine generic relationships within the constraints imposed by the old tribal classification system. What is needed is a revised study of morphological systematics and classification that considers all members of the three basal tribes simultaneously.

This may be tested for consistency using molecular systematics. Such an analysis would determine overall phylogenetic relationships including those that lie outside of each current tribal division. Such results would also permit rigorous statistical analysis and generate a much greater understanding of the ancient biogeographical history of the subfamily. At present, missing genera from older events may be one reason for the lack of resolution of relationships between basal taxa that is shown when using different methods (Bayesian or maximum likelihood – Monaghan *et al.* 2007). As the three basal tribes comprise 60% of the genera, an overall study would require great effort. However, there is no obvious alternative. What are, perhaps, first needed are generic scale phylogenies for more species-rich genera to provide group divisions for selection of representative taxa for inclusion in tribal and subfamily scale phylogenies. This method would permit the selection of taxa that are as representative of the total history of the Scarabaeinae as can be provided by extant elements.

However, this reassessment will take time, so what is possible for a current biogeographical analysis of current spatial patterns, and does this diverge from Davis *et al.* (2002a)? Limited recent revisions have little effect on basic patterns based on genera and species. However, a tribal level classification is necessary to link areas with highly or entirely endemic generic-level faunas. Such endemism often involves basal tribal elements and without this linkage the older historical patterns will not be represented in analyses. Therefore, in the absence of a revised tribal classification we have collapsed the three contentious basal tribes into a single "Gondwana" entity. This is supportable since, although the genera of basal tribes are intermingled on recent phylogenies, they form a cohesive assemblage of taxa that are basal overall, basal on derived clades, or occur in derived clades that parallel those of nine other tribes but are entirely comprised of "Gondwana" genera. We have retained the nine well supported tribes with slight adjustments to membership (Monaghan *et al.* 2007) in that the three basal onthophagine genera (*Proagoderus*, *Digitonthophagus*, *Phalops*) have been transferred to the Oniticellini, which can no longer logically be divided into subtribes since two (Oniticellina, Drepanocerina) lack support. This is justified since the membership of these lineages is consistent with the current classification system and all are terminal to any included "Gondwana" group taxa. For overall summary of global patterns, we first analyzed the spatial patterns shown by these 10 tribal units (Fig. 16.3). We used the results of this analysis to further collapse the tribes into three units showing different biogeographical centring, i.e. (1) widespread, basal Gondwana-centred genera and their derived descendants that presumably retain plesiomorphic characterization, (2) derived tribes endemic to the Americas, and (3) derived Afro-Eurasian-centred tribes. So, do the results yielded by such analyses diverge radically from previous findings?

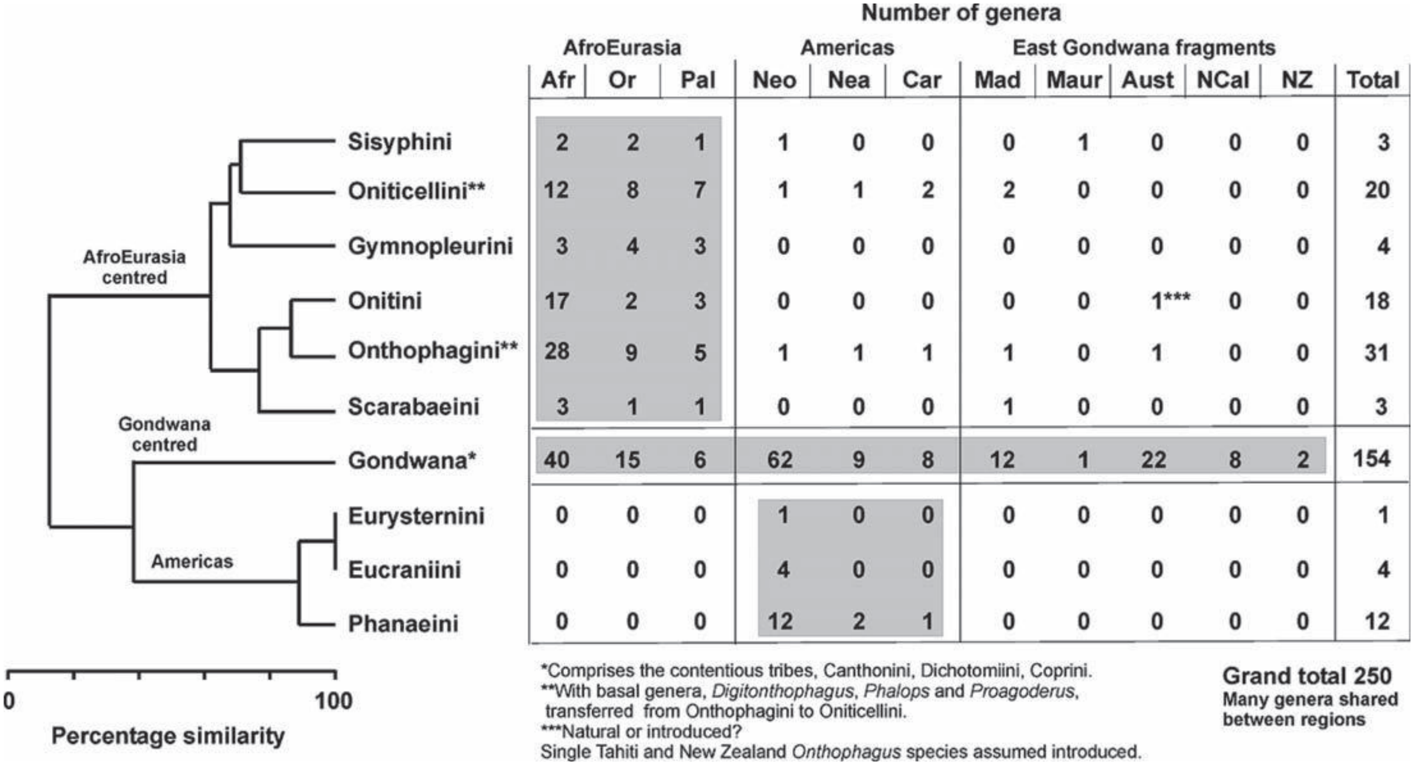
16.2 BETWEEN-REGION SPATIAL PATTERNS: TROPHIC, BEHAVIOURAL AND TAXON DIVERSITY

The biogeography of the Scarabaeinae has been driven by both spatial and trophic criteria (Davis and Scholtz 2001; Davis *et al.* 2002a). The relative influence of the different factors has not been determined. Therefore, they are discussed as a series of independent subjects. Regional differences in taxonomic structure and endemism result from historical differences in isolation by geographical barriers versus faunal intermingling by dispersal or range expansion from different regions. However, current eco-climatic conditions also have some influence on the taxonomic structure of assemblages and certainly strongly influence the overall numbers of taxa occurring in different regions. The historical biogeography of Scarabaeine has also been driven partly by co-evolution with mammal droppings and, by default, the historical biogeography of mammals. Between-region differences in mammal body size, dropping size, diet, and digestive system may have all been important evolutionary drivers of dung beetle biogeography together with behavioural responses by dung beetles in the manner of dung exploitation. Whereas some spatial correlations remain valid, previous correlations between geographical differences in taxon and dung type diversity (Davis and Scholtz 2001) are rendered uncertain due to unresolved questions concerning tribal level classification (Philips *et al.* 2004b; Monaghan *et al.* 2007), although this cannot be considered as invalidating the hypotheses on co-evolution between mammals and dung beetles. In general, re-analyses of data produce patterns that differ little from those described by Davis and Scholtz (2001) and Davis *et al.* (2002a).

As in Davis and Scholtz (2001) and Davis *et al.* (2002a), the present account discusses global patterns in relation to major biogeographical regions and does not consider spatial scales that are finer than major within continent eco-climatic regions. We use the zoogeographical regions as modified by Cox (2001). These differ from the standard zoogeographical classification in that Arabia is considered to be part of the Palaearctic and Australasia is considered to be separated from the Oriental region at the Wallace Line. This differs slightly from the biogeographical regions used by Davis *et al.* (2002a) in which the Nearctic / Neotropical boundary bisected the Isthmus of Tehuantepec. The zoogeographical boundary of the Nearctic used, here, follows the base of highland regions and the edge of arid northern regions of Mexico, so that all low, hot, wet regions of this country are now included in the Neotropics. Similarly, all other land barriers between regions are imposed primarily by high mountains or changing climate such as increasing aridity or coolness, i.e. the limit of winter rainfall influence separates the Palaearctic and Afrotropical regions in arid North Africa (differs slightly from the boundary suggested by Cox (2001)), the Oriental / Palaearctic boundary is defined by arid western climate, mountains along the central margin, and cool climate type VI (Wallter and Lieth 1964) to the northeast. Sea barriers separate all other regions, i.e. Americas from Afro-Eurasia at the Bering Straits and North Atlantic, Oriental from Australasia at the Wallace Line, with all other regions comprising sea-isolated islands, Madagascar, Mauritius, Caribbean Archipelago, New Caledonia, and islands of New Zealand.

The taxon-centred and region-centred patterns yielded by new biogeographical analyses (Figs 16.1, 16.2) are essentially similar to those shown by Davis *et al.* (2002a), even though the Coprini genera are now included in the combined "Gondwana" group instead of the Afro-Eurasian tribes. The regional patterns again show that the Afro-Eurasian centred tribes numerically dominate the generic and species-level faunas of the Afrotropical, Oriental and Palaearctic regions. In contrast, widely-represented Gondwana taxa numerically dominate in the Americas and at generic level in most East Gondwana fragments. At species level, Afro-Eurasian tribes are well-represented or dominate in those East Gondwana fragments that are closest to Afro-Eurasia (Madagascar, Mauritius, Australia) and are absent from those that are most distant (New Caledonia, New Zealand). Single *Onthophagus* species listed for New Zealand and Tahiti (Schoolmeesters 2008a; 2008b) are assumed non-native like *Epirinus aeneus*, a known introduction into New Zealand from South Africa (Emberson and Matthews 1973).

Patterns of generic endemism to biogeographical regions are related to the historical evolutionary process of isolation and taxon divergence. Levels of endemism are lower in northern biogeographical regions (Nearctic, Caribbean, Palaearctic) and greater in southern biogeographical regions (Afrotropical, Neotropical), particularly those that have been long isolated by sea barriers (Australia and New Guinea, Madagascar, Mauritius, New Caledonia, New Zealand) (Davis *et al.* 2002a; Table 16.1). Although Davis *et al.* (2002a) showed that proportional regional endemism was correlated with the number of continents with which links were shared during the Cenozoic, it is suggested that the northern continents may also show low endemism since they were only recently populated by Scarabaeinae, primarily from the continents lying directly to their south. Table 16.1 indicates the relative endemism and the proportional contribution of non-endemic genera shared with other regions. The Americas faunas have been primarily influenced by endemic or shared genera of the Americas with little sharing of genera with Afro-Eurasia. Afro-Eurasia has been influenced primarily by endemic or shared genera of Afro-Eurasia with few genera shared with the Americas (and these probably of Afro-Eurasian origin). The East Gondwana fragments show primarily endemic generic faunas with little



Number of genera

	AfroEurasia			Americas			East Gondwana fragments					
	Afr	Or	Pal	Neo	Nea	Car	Mad	Maur	Aust	NCal	NZ	Total
Sisyphini	2	2	1	1	0	0	0	1	0	0	0	3
Oniticellini**	12	8	7	1	1	2	2	0	0	0	0	20
Gymnopleurini	3	4	3	0	0	0	0	0	0	0	0	4
Onitini	17	2	3	0	0	0	0	0	1***	0	0	18
Onthophagini**	28	9	5	1	1	1	1	0	1	0	0	31
Scarabaeini	3	1	1	0	0	0	1	0	0	0	0	3
Gondwana*	40	15	6	62	9	8	12	1	22	8	2	154
Eurysternini	0	0	0	1	0	0	0	0	0	0	0	1
Eucraniini	0	0	0	4	0	0	0	0	0	0	0	4
Phanaeini	0	0	0	12	2	1	0	0	0	0	0	12

*Comprises the contentious tribes, Canthonini, Dichotomiini, Coprini.
**With basal genera, *Digitonthophagus*, *Phalops* and *Proagoderus*, transferred from Onthophagini to Oniticellini.
***Natural or introduced?
Single Tahiti and New Zealand *Onthophagus* species assumed introduced.

Grand total 250
Many genera shared between regions

Fig. 16.1. Dendogram showing similarities in the percentage distribution between 11 regions of dung beetle genera in 10 tribal level units (clustering of Bray-Curtis similarity matrix by group average linking) and the numbers of genera recorded in each (Afr = Afrotropical, OR = Oriental, Pal = Palaearctic, Neo = Neotropical, Nea = New Guinea, NCal = New Caledonia, NZ = New Zealand).

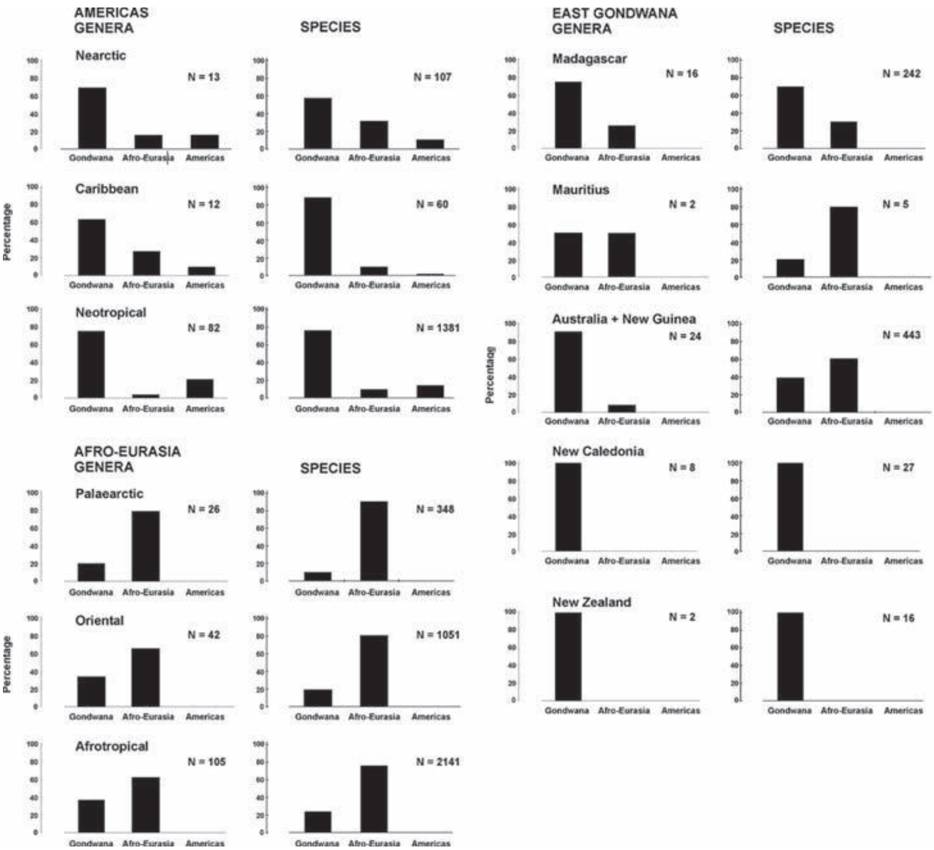


Fig. 16.2. Proportional occurrence in 11 regions of genera and species belonging to three groups of tribes defined in Figure 16.1.

sharing of genera with Afro-Eurasia although the globally distributed genus, *Onthophagus*, has radiated in Australia to numerically dominate the species-level fauna (Fig. 16.2). The relatively low generic richness in the Nearctic compared to that in the Palaearctic is a result of inflated totals in Eurasia due to marginal occurrences by about half the genera in Arabia, southern central Asia, or Eastern Asia at the edge of the Afrotropical or Oriental regions. Those genera and tribes that are more widespread, occur particularly in north / south paired continental units (41 genera out of 250) with only five genera shared in an east west direction mainly in the north (*Onthophagus*, *Sisyphus*, *Liatongus*, *Euoniticellus*, *Copris*). Species are primarily endemic to major regions. Only a few that are arid adapted or cool temperature tolerant, occur either side of barriers between major biogeographical regions.

Table 16.1. Global generic richness and proportional generic distribution patterns between biogeographical regions harbouring endemic genera.

Biogeographical Region	Number of genera	Percentage of genera showing distribution**					
		endemic	Amer.	Afro-Eur./Amer.	Afro-Eur./E. Gond.	Global	Total %
Palaearctic	26	7.7	-	15.4	73.1	3.8	100
Oriental	42	28.6	-	7.1	61.9	2.4	100
Afrotropical	105	70.5	-	3.8	24.8	1.0	100
Australia + New Guinea*	24	91.7	-	-	4.2	4.2	100
Madagascar	16	87.5	-	-	6.3	6.3	100
Mauritius	2	100.0	-	-	0.0	0.0	100
New Caledonia	8	100.0	-	-	0.0	0.0	100
New Zealand	2	100.0	-	-	0.0	0.0	100
Nearctic	13	7.7	69.2	15.4	-	7.7	100
Caribbean (+Trinidad)	12	16.7	66.7	8.3	-	8.3	100
Neotropical	82	79.3	17.1	2.4	-	1.2	100

*Includes the Moluccas.

**Amer. = Americas distribution; Afro-Eur. / Amer. = Afro-Eurasian and Americas distribution; Afro-Eur. / E. Gond. = Afro-Eurasian distribution with a few genera shared with nearby East Gondwana fragments; Global = Occurring in most regions (*Onthophagus* Latreille only) with single recorded species in New Zealand and Tahiti probably introduced.

Overall global distribution of generic and species numbers for the subfamily Scarabaeinae are presumably constrained by functional ecological processes as they are strongly correlated with area of suitable climate (Davis and Scholtz 2001, using the climatic classification of Walter and Lieth 1964). Correlations are strong with climate type I (wet tropical, either aseasonal or with limited seasonality imposed by rainfall patterns), particularly strong with type II (moist subtropical or warm temperate with greater seasonality imposed by rainfall and temperature patterns), and fairly strong with type III (tropical to warm temperate and arid). However, the most extreme correlation for both generic and species numbers (Davis and Scholtz 2001) is with a combination of climate types I, II and IV (IV = warm temperate Mediterranean-type winter rainfall). Other prominent correlations involve various combinations of climate type I to V (V = warm temperate with aseasonal to bimodal rainfall). Such correlations remain true despite subsequent taxonomic revisions and additions of new taxa (Table

16.2). However, at lower taxonomic scale, patterns of species distribution shown by individual, identified genera of Afro-Eurasia have clearly been primarily influenced by history since they mostly diverge from the numbers of species one would predict on the basis of correlation with area of suitable climate (Davis *et al*. 2002a). Thus, whilst overall taxon numbers may be influenced by current ecological factors, the identity of those taxa is largely the result of past history.

Three major biogeographical centres are indicated by analyses of spatial distribution patterns shown by both overall generic composition of continental faunas and generic composition of local assemblages (Davis *et al*. 2002a; Fig. 16.3). The centres comprise Afro-Eurasia, Americas, and East Gondwana fragments that include Australia. In the case of local assemblage composition, there is clear separation between these three centres with distinct eco-climatic

Table 16.2. Taxon richness, area of most suitable climate (I-V after Walter and Lieth 1964) in bigeographical regions, and taxon-area correlations.

Biogeographical Region	**Number of**		**Area of climate type (km^2 x 10^5)**				**Represented climate types**
	genera	**species**	**I, II, II, III, IV, V**	**I, II, IV, V**	**I, II IV**	**I, II**	
Afrotropical	105	2141	265.64	179.25	179.20	178.87	I, II, III, IV, V
Neotropical	82	1381	149.21	144.92	128.53	127.83	I, II, III, IV, V
Oriental	42	1051	86.47	83.33	74.12	74.12	I, II, III, IV, V
Australia + New Guinea*	24	443	77.96	42.93	39.37	32.85	I, II, III, IV, V
Nearctic	13	107	50.90	42.57	20.89	14.49	I, III, IV, V
Palaearctic	26	348	8.72	8.65	8.18	0.00	I, IV, V
Madagascar	16	242	5.73	5.73	5.73	5.73	I, II
Caribbean (+Trinidad)	12	60	1.43	1.43	1.43	1.43	I, II
New Zealand	2	16	1.05	1.05	0.00	0.00	V
New Caledonia	8	27	0.19	0.19	0.19	0.19	II
Mauritius	2	5	0.02	0.02	0.02	0.02	II
Correlation statistics**			r^2	r^2	r^2	r^2	
Genera N with climate area			0.908	0.939	0.964	0.957	
Species N with climate area			0.925	0.936	0.971	0.969	

*Includes the Moluccas. **All correlations significant at $P<0.001$.

grouping of sites within continents and, in some cases, eco-climatic grouping of geographically distant sites on different continents within a major region (Fig. 16.3). Overall eco-climatic groups comprise rainforest (Oriental / Afrotropical) plus highland grassland assemblages, savanna assemblages, and arid plus

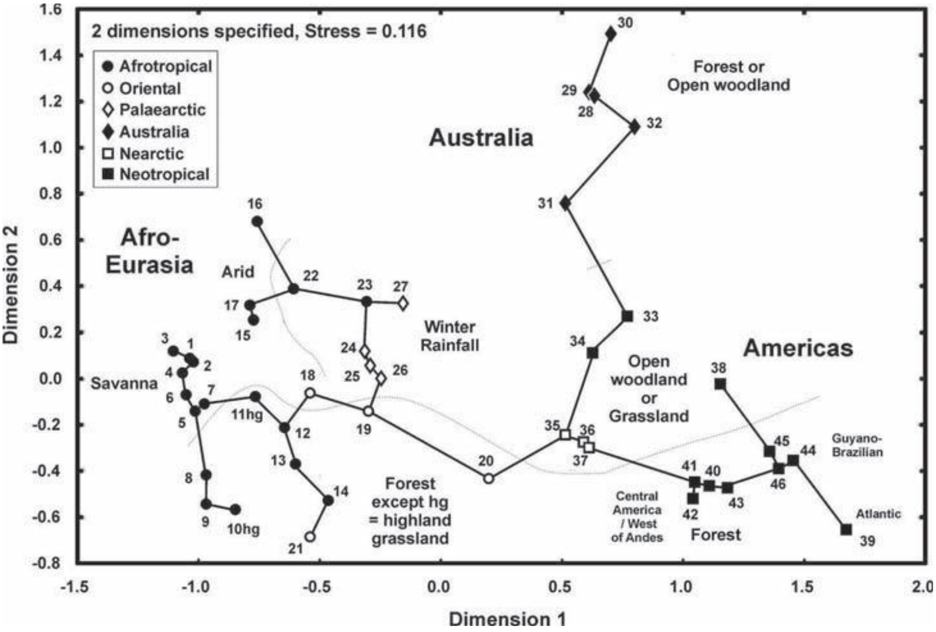


Fig. 16.3. Multidimensional scaling ordination plot showing the statistical grouping or separation of 46 local dung beetle assemblages from six major biogeographical regions based on generic representation (presence or absence). Local assemblages are linked by a minimum spanning tree calculated using Kruskal algorithm. Key to publications: Afro-Eurasia: 1. Davis (1994; 1996); 2. Doube (1991); 3. Kingston (1977); 4. Cambefort (1991c); 5. Van Rensburg *et al.* (1999); 6. Cambefort (1982); 7, 13. Walter (1978); 8, 9. Cambefort and Walter (1991); 10. Davis *et al.* (1999b) 1500 m and above; 11, 16. A.L.V. Davis and C.H. Scholtz (unpublished data); 12. Davis *et al.* (2002b) natural forest; 14. Nummelin and Hanski (1989); 15. Rougon and Rougon (1991); 17. Steenkamp and Chown (1996); 18. Mittal (2000); 19. Hanski (1983); 20. Hanski and Krikken (1991); 21. Davis (2000); 22, 23. Davis (1990; 1993) shrubland habitats; 24. Kirk and Ridsdill-Smith (1986); 25, 26. Lumaret (1980; 1983); 27. Ruiz *et al.* (1993); Australia: 28, 30, 31, 32. Matthews (1972; 1974; 1976) with a subregional example from each of the major geographical clusters defined for scarabaeine tribes by Allsopp (1955); 29. Hill (1996); Americas: 33. Walsh and Cordo (1997); 34. De Grosso *et al.* (1999); 35. Fincher *et al.* (1970); 36. Nealis (1977); 37. Peck and Howden (1985); 38. Morelli and Gonzalez-Vainer (1997); 39. Louzada and Lopes (1997); 40, 41. Halffter *et al.* (1992); 42. Peck and Forsyth (1982); 43. Gill (1991); 44. Howden and Nealis (1975); 45. Klein (1989); 46. Andresen (1999).

winter rainfall assemblages (Palaearctic / Afrotropical) in Afro-Eurasia; grass / open woodland assemblages in the Americas (Nearctic / Neotropical) with the separation of forest regions in the Americas. Figure 16.3 is based on the presence or absence of genera in 46 local assemblages, which diminishes the effect of differences in trapping protocol between ecological studies. It yields better eco-climatic grouping for Afro-Eurasia than the multidimensional scaling of Davis *et al.* (2002a) based on 4th root transformed percentage number of species per genus of the same 46 local assemblages and is closer to the eco-climatic grouping results shown by parsimony analysis of endemism of the same presence / absence data in Davis *et al.* (2002a), a method that has been criticised by Brookes and van Veller (2003) on the basis of its underlying methodological assumptions. But, in some cases, there are poorer results in Figure 16.3 for inter-regional linking of extremely dissimilar faunas that are based on the idiosyncratic occurrence of single genera in common. Further work needs to be done to provide and collate basic assemblage data for wider geographical analysis. There is also a need to incorporate phylogenetic relatedness data to circumvent anomalies produced by the purely descriptive results in Figure 16.3. Thus, although historical factors have a strong influence on taxonomic structure of assemblages at large spatial scales, group identity may also be structured by similar current ecological factors not only in connected habitat but also in isolated similar habitats where the most recent sharing of fauna has occurred, within Afro-Eurasia or within the Americas.

As the modern dung beetle fauna is dominated by association with mammalian dung with specialization to particular dung types (Young 1981; Davis 1994; Tshikae *et al.* 2008), it has been suggested that this fauna has co-evolved with the droppings of mammals so that the historical biogeography of Scarabaeinae has been partly driven by that of mammals (see Chapter 1.3). In particular, increase in mammal body size ranges is associated with diversification in diet and digestive system, so that four types may be recognized: pellets from small-bodied herbivores; small odorous droppings from omnivores and carnivores; large fibrous dropping of large monogastric herbivores; and large fine-fibred moist pads from large ruminant herbivores. The number of categorical dung types varies between regions according to average body size (Table 16.3). Davis and Scholtz (2001) showed correlations between categories of dung type diversity on different biogeographical regions and both number of tribes and generic diversity within tribes but not with numbers of genera or species or species diversity within genera. Since, in general, one is looking further back into evolutionary history at each successive taxon level, this was interpreted as suggesting some historical influence of dung type in tribal diversification and generic level diversification within tribes, high in

Table 16.3. Terrestrial mammal body size*, dung type diversity (four categories, see text) and indices for dung beetle taxon diversity (species per genus) in biogeographical regions harbouring endemic genera.

Biogeographical Region	Average mammal body mass (kg)	Number of dung types	Dung beetle taxon diversity indices		
			Simpson (1/D)	Berger-Parker (1/d)	McIntosh D (D)
Neotropical	9.3	3	15.86	7.94	0.76
Afrotropical	62.2	4	6.51	2.71	0.61
Caribbean (+Trinidad)	2.0****	2	5.64	2.73	0.61
Madagascar	1.5	2	5.16	3.32	0.59
Nearctic	25.4	3	5.11	3.03	0.59
New Caledonia***	0.0	0	3.28	1.93	0.49
Oriental	58.5	4	2.86	1.72	0.42
Australia + New Guinea**	2.2	2	2.62	1.65	0.40
Palaearctic	31.6	4	2.39	1.87	0.46
Mauritius***	0.0	0	1.67	1.25	0.35
New Zealand***	0.0	0	1.14	1.07	0.12

*Indigenous mammals only excluding aquatic mammals and bats. **Includes the Moluccas. ***Indigenous homeothermic vertebrate fauna of birds and bats only. ****Estimated.

Afro-Eurasia (high mammal body size and dung type diversification), lower in the Americas (limited diversification), and least in East Gondwana fragments (little diversification). However, the partial questioning of tribal level classification undermines confidence in this finding and it cannot be updated without an accepted revised tribal classification system. Furthermore, these series of gross generalizations could do with refinement. Patterns are dependent on taxon number that are, in turn, dependent on classification that is itself, dependent on taxonomist's decisions. Thus, correlations could be an artefact of the construction rather than a real association.

The history of subfamily classification is underpinned by emphasis on the importance of different behavioural habits in constraining morphology, which is the basis of the group taxonomy. This "traditional" classification has now been partly unravelled by the advent of statistical morphological analysis and molecular systematics. Not only do partial analyses of relationships within the subfamily question the generic composition of basal tribes by showing extensive polyphyly, they also suggest great behavioural plasticity with multiple origins of the same two dominant behavioural patterns and their associated morphological modifications.

Thus, although Davis and Scholtz (2001) have shown a correlation between dung type diversity and dominant behavioural patterns, either tunnelling or ball rolling, this is a generalization as behavioural traits were defined by tribal membership in the absence of direct observations for most taxa. Behavioural traits vary from tunnelling, ball rolling, to kleptocoprids, with some traditional ball rolling tribes containing "carriers", tunnellers, and leaf litter specialists. It is unclear if the findings of a more refined analysis would differ radically from those of Davis and Scholtz (2001) in which regions with low dung type diversity (small dung types from small-bodied mammals) (Table 16.3) favoured high proportions of ball rollers (genera & species), and high dung type diversity (range in dung types and sizes from large to small mammals) favoured high proportions of tunnellers.

Although current simple analyses indicate that there is behavioural and dung type influence at higher taxonomic level, indicating historical co-evolution, is this true or merely influenced by the now contentious construction of the classification system for basal Scarabaeinae? Correlations need to be strengthened by refining data beyond a simple categorical classification of dung type and the use of suspect classification systems for taxa. Considering the complexity of trophic and behavioural traits in the subfamily, all trait data need to be based on detailed observations and quantitative data, not estimations. Furthermore, more sophisticated analyses need to be developed using phylogenetic relatedness in conjunction with dung type association and behavioural data.

16.3 IMPLICATIONS OF RECENT RESEARCH FOR BIOGEOGRAPHICAL HYPOTHESES

The question of dung beetle origins is part of a wider debate on the overall origins of the southern flora and fauna from Gondwana vicariance, by subsequent dispersal, or by a combination of the two processes. Although Sanmartin and Ronquist (2004) indicate that animals of southern continents originated mainly by vicariance, these results are at odds with the majority of recent molecular systematic evidence (de Queiroz 2005). There is more frequently than not an incompatibility between younger molecular aging and the older timescale of vicariant events. This has driven a general swing away from vicariance towards dispersal (de Queiroz 2005) as the default, and dominant, process to explain current patterns.

Such a change in perception is no less true of dung beetles even though the recent molecular-aging-driven swing away from vicariance towards dispersal may be based on uncertain support. Even so, a consideration of the evidence suggests that the origin of the Scarabaeinae may post-date the fragmentation of Gondwana and the age of the dinosaurs although it will be difficult to support how the basal taxa populated some of the fragments by dispersal given the evidence for tectonic plate positions and wide sea barriers at the Cretaceous / Cenozoic boundary (Reeves and de Wit 2000; Sanmartin and Ronquist 2004). Therefore, this section briefly recaps the development of recent historical biogeographical hypotheses for the Scarabaeinae. It then discusses the implications of recent molecular systematics research. It concludes that many of the patterns described by Davis *et al*. (2002a) and other authors need little modification. Only the hypotheses for the processes and routes of origin for earlier taxa require reconsideration.

16.3.1 Vicariance, dispersal or range expansion hypotheses, routes, and timescale

Recent analyses of global spatial patterns shown by the Scarabaeinae have been used to develop hypotheses on the biogeographical and evolutionary processes that were responsible. Cambefort (1991b) divided the global genera into old, intermediate and modern taxonomic groups on the basis of historical biogeographical pattern and body size. This approach was coupled with a discussion of possible origins of patterns in dispersal by rafting or range expansions across land links. Vicariance was not explicitly cited as a possible origin of taxa showing a Gondwana distribution. By contrast, Davis and Scholtz (2001) and Davis *et al*. (2002a) provided descriptive statistical analyses of current global distribution patterns at different traditional taxonomic levels, whose origins were interpreted according to tectonic, orogenic, and climatic / vegetation history. Vicariance was explicitly hypothesized as the origin of basal Gondwana tribes with subsequent regional evolution and Cenozoic range expansions hypothesized for both basal and derived taxa.

The literature on plate tectonics was also used to hypothesize routes, both for early patterns due to Gondwana fragmentation in the Mesozoic and later patterns due to the later Cenozoic reconnection of southern Gondwana fragments with their northern Laurasian counterparts (Davis *et al*. (2002a). Basal tribes (Dichotomiini, Canthonini) were hypothesized to have evolved in Gondwana and to have expanded their ranges throughout this southern supercontinent. Divergence to generic or tribal level following vicariant fragmentation of Gondwana was hypothesized to account for the high generic endemism in modern southern continents.

Selective dispersal or expansion of range to northern continents was hypothesized to have followed divergence during a long period of isolation on southern continents. These events were hypothesized to have occurred in the Cenozoic via re-established land links or due to convergence of terrestrial parts of tectonic plates. One principal route was from Africa to Eurasia (Eocene to West Europe, Miocene onwards to Eurasia) to the Nearctic via Beringia (Miocene, Pliocene) or to Australia by dispersal. A second principal route was provided by the Great American Interchange between the Nearctic and Neotropical (Pliocene onwards). These patterns were characterized by species level divergence.

Molecular phylogenies have thrown doubt on the origin of southern elements by vicariance due to the lack of concurrence between dating of sequence divergence and tectonic events (e.g. Wirta *et al.* 2008). Although Monaghan *et al.* (2007) considered that the African endemism of the basal taxa was inconsistent with the vicariance / dispersal hypotheses of earlier authors, this conclusion may be a little precipitate as there is no consistency in detail between the various partial morphological and molecular phylogenies. However, there is some similarity in general topology that may provide support for some historical patterns (see Section C). Each phylogeny shows a variable number of basal generic lineages currently included in the Canthonini or Dichotomiini followed by a split into two major lineages. Major lineage (1) consistently comprises more derived membership of traditional tunnelling or ball-rolling "basal" tribes (Dichotomiini, Canthonini) with representatives on all southern continents, two tunnelling or food-carrying Americas endemic tribes (Phanaeini, Eucraniini), and Afro-Eurasian centred ball rolling tribes (Scarabaeini, Gymnopleurini). Major lineage (2) consistently comprises Afro-Eurasian centred tunnelling tribes (Onthophagini, Oniticellini, Onitini) and the ball rolling Sisyphini, whose Americas (not Onitini) and Australian membership (not Sisyphini, Oniticellini) is related primarily at species level. Current biogeographical hypotheses cannot entirely account for these major patterns of divergence, particularly the inclusion of the Afro-Eurasian-centred Scarabaeini and Gymnopleurini in Major lineage 1. Complications also emanate from major differences in detail. In particular, relationships are unresolved for the Coprini (polyphyletic and sited variously in basal groups, lineage 1 or lineage 2 in different analyses) and Eurysternini (sited with lineage 1 in morphological analyses and lineage 2 in molecular analyses with the latter probably the better assessment). The position of some mainly Australian, Madagascar or African canthonine and dichotomiine genera also needs clarification. These occur in basal groupings in analyses of morphological data and of molecular data using maximum likelihood, but are basal in major lineage 1 in analyses of molecular data using the bayesian 7-partition method. Perhaps the exclusion from analyses of many linking genera representing the survivors of old history is a reason for lack of resolution.

Although topology varies between phylogenies, the generic membership of the contentious basal "Gondwana" tribes (Canthonini, Dichotomiini, Coprini) are consistently: (1) derived from the basal lineages; (2) comprise basally-derived taxa in some of the most derived clades in which the terminal genera are classified in other tribes; or (3) comprise the entire membership of a few of the most derived clades. If one combines these results with those for patterns of generic endemism or generic sharing, it is still possible to create useful hypotheses for the origin of the patterns, the routes followed, and the relative timescale. As indicated by Davis *et al.* (2002a), basally derived genera (1) or clades entirely comprising membership of former "Gondwana" tribes (2) tend to show east-west regional endemism centred on southern continents and would represent, respectively, old patterns of indeterminate age followed by within-region divergence. The most derived clades (2 and 3) include most of the genera which show north-south sharing between continental groupings and, in some cases, east west sharing primarily centred on northern continents. This would represent later, within region divergence, followed by more recent Cenozoic faunal intermingling between regions. In order to support hypotheses for the processes responsible for the patterns (vicariance, dispersal or range expansion across land links), it is necessary to provide accurate and independent dating for phylogenies, tectonic events, and tectonic plate positions as suggested by Waters and Craw (2006).

The current global spatial patterns are the culmination of a long evolutionary history. Divergence and extinction events have continued throughout this history so that the extant fauna comprises only the surviving lineages. Dispersal / vicariance analysis (Monaghan *et al.* 2007) and molecular clock analyses (Sole *et al.* 2005; Orsini *et al* 2007; Wirta *et al.* 2008) suggest that this fauna is dominated in character by the evolutionary influence of relatively recent Oligocene or Miocene, Pliocene and Pleistocene events as suggested by Cambefort (1991b). However the ultimate origins of the lineages lay in relatively much older events (Monaghan *et al.* 2007). It is a case of determining a reliable absolute age for these basal events.

Currently, aging of divergence events in Scarabaeinae suggests a history post dating Gondwana fragmentation. If the dating is inaccurate, a halving of the average rate of sequence divergence could conceivably place divergence of early lineages at time of Gondwana fragmentation but dung type drivers may have been absent at that time unless an earlier fauna was supported by the dung of ectothermic dinosaurs or earlier, largely small-bodied mammals. Another possibility is origin by vicariance at a date post-dating the absolute basal origin of the subfamily. However, the membership of the two major clades resulting from relatively basal divergence does not fit biogeographically (though see the discussion of the Oriental fauna below). If late Cretaceous or Eocene dates of origin (Tables 1.1, 15.1) are accurate then dispersal is the only likely origin for basal genera. Perhaps this could have occurred via land connections, due to the proximity of land masses, or via island arcs (see regional discussions below). However, all is currently highly speculative and nothing is resolvable.

CHAPTER 17

OUTLINES OF COMPOSITION, SPATIAL PATTERN AND HYPOTHETICAL ORIGINS OF REGIONAL DUNG BEETLE FAUNAS

Outline discussions of regional faunas consider their general composition and current distribution centres in relation to (1) processes important to the origin of basal lineages and (2) processes important in generating the different spatial patterns shown by more derived lineages. For the purposes of this discussion, basal lineages are defined as all genera belonging to the contentious tribes Canthonini, Dichotomiini and Coprini. Derived lineages are defined as comprising the generic membership of all other current tribes even though the derivation and diversification of some terminal dichotomiine, canthonine and coprine lineages are essentially parallel and coeval with these so-called derived lineages. We consider two main questions. What evidence is there to support dispersal as a major determinant of spatial patterns in basal lineages if vicariance was not the dominant process, particularly as dispersal is invoked by default if Gondwana fragmentation long preceded the timescale for early scarabaeine evolution on isolated southern continents? On the other hand, is it necessary to modify hypotheses for range expansion across re-established land links between southern and northern continents (Davis *et al.* 2002a) as the dominant determinant of spatial patterns shown by some members of derived lineages and terminal clades of basal lineages (Afrotropical / Eurasia / Nearctic / Neotropical and Neotropical / Nearctic tracks), with dispersal only remaining important for the Oriental / Australia track? In view of the voluminous literature, the outlines developed below mostly consider only recent reviews and those findings pertaining to dung beetles, in particular.

17.1 AFRO-EURASIA

Afro-Eurasia forms a cohesive biogeographical unit owing to the relict status of many, though certainly not all, taxa classified in basal tribes and the relative dominance of genera and species classified in derived tribes that are centred in Afro-Eurasia.

17.1.1 Afrotropical

The Afrotropical dung beetle fauna is the most generic and species rich of the global regional faunas (Table 16.1). It comprises 40 genera currently classified in three contentious basal tribes and 65 genera in mostly well-supported, more derived tribes, many of which (8 + 22 genera) are shared with Eurasia. Members currently classified in the basal tribes include the four most basal genera overall (*Coptorhina*, *Sarophorus* – Dichotomiini or Ateuchini (Montreuil 1998); *Dicranocara*, *Odontoloma* – Canthonini) in morphological and molecular phylogenies (Philips *et al*. 2004b; Monaghan *et al*. 2007) leading Monaghan *et al*. to suggest an African origin for the subfamily Scarabaeinae.

Africa is considered to have been largely isolated from the mid-Cretaceous until the early Miocene (Gheerbrant and Rage 2006). Although the vertebrate fossil record supports some interchange via filter routes, these were primarily to Eurasia, firstly to Western Europe and, later, to the Irano-Turanian region in the middle Eocene. Therefore, what import might these findings have for the origin of basal dung beetle taxa in other southern continents? As a generalization, vicariance was found to be the dominant most parsimonious explanation for the origin of animal taxa in the southern continents (Sanmartin and Ronquist 2004). However, the late Cretaceous to early Cenozoic timescale suggested for molecular evolution of the subfamily Scarabaeinae (Table 15.1) would discredit vicariance as a mechanism for the populating of other Gondwana fragments by basal scarabaeine taxa. This leads to the question, what evidence is there for routes of dispersal from Africa across marine barriers in the late Cretaceous or early Cenozoic? In theory, late Cretaceous early Cenozoic passage to Gondwana fragments may be explained: (1) by past trans-oceanic dispersal as discussed by de Queiroz (2006); (2) by dispersal along hypothesized and now submerged island chains situated on submarine ridges that link continental fragments, e.g. Africa to South America via hypothetical island chains on the Rio Grande-Walvis Ridge (Rage 1981) and then to Australia via land links across a then warmer Antarctica (see Australian discussion below); or (3) by dispersal due to greater past proximity between major continental fragments than indicated by geological findings, e.g. Africa to India (Briggs 2003). In practise, early Cenozoic evidence for direct exchanges from Africa to Gondwana fragments is severely limited (but see Neotropical and Madgascar discussions). Nevertheless, basal elements of the Scarabaeinae occur on all major and some minor Gondwana fragments and the subfamily is considered monophyletic (Philips *et al.* 2004b) with a bootstrap value of 100% (Monaghan *et al.* 2007). It may be noteworthy, that few basal elements, classified in the Canthonini and Ateuchini (Montreuil 1998) occur in Eurasia, either as extant representatives or as fossils, despite fossil evidence for early faunal interchanges between Africa and Eurasia during the Eocene (Gheerbrandt and Rage 2006). These interchanges predate the Miocene closure of a sea barrier between east and west Europe that resulted in a major immigration of African and West Asian mammals at 15 my (Mein 1979). They also predate the enduring land connection between Africa and Eurasia that was already well-developed at 17.5 to 15 my (Potts and Behrensmeyer 1993) and, presumably, led to further extensive interchange of derived tribal dung beetle lineages, which now dominate the modern Afro-Eurasian faunas.

Although the basal Afrotropical genera with known habits comprise specialists (*Coptorhina* – widespread with mycetophagous associations (Frolov *et al.* 2008), *Dicranocara* – severely range restricted in the arid southwest with hyrax midden associations (Frolov and Scholtz 2003; Deschodt *et al.* 2007)), the mainstream of scarabaeine evolution has been dominated by dung association. Although, the Afrotropical forest faunas of the early Cenozoic presumably contained higher proportions of basal taxa, all ecoregion dung faunas (Fig. 16.3) are now dominated by derived taxa. The origin of derived tribes was probably partly driven by the early Cenozoic diversification of mammal groups and dung types, and the subsequent history of mammal dispersal or range expansion between regions. Dung type evolution on the continent has, presumably, progressed from the coarse-fibred dung of elephant and the omnivore dung of primates that are represented by early Cenozoic fossils (Maglio 1978) to the pads of ruminant Bovini that enter the African fossil record only in the late Miocene (Maglio 1978) from the Oriental region. As an illustration of dung type as a driver of specialization, the Onitini comprise 18 genera of which 15 are species-poor African endemics mostly recorded from elephant, rhinoceros, or, occasionally, horse dung (Davis *et al.* 2002a). Evolution with dung type has occurred coeval with the opening out of the early Cenozoic forests following the northwards drift of the continent (Axelrod and Raven 1978) and the development of cooler drier climates (Potts and Behrensmeyer 1993). Recent Pleistocene oscillations in areal extent of forest versus savanna in response to wetter versus drier climate induced by high latitude interglacial / glacial cycles (Jahns *et al.* 1998; Dupont *et al.* 2000), and past restriction of forest to small refugia, may explain the dominance of derived taxa in modern Afrotropical forest faunas. Most basal forest relicts are centred in the east where moist forests, presumably, persisted on the mountains due to Pleistocene Indian Ocean temperatures that remained warm (0-2 °C cooler) compared to much greater oscillation of 2-8 °C cooler in the Atlantic Ocean to the west (Prell 1980; Trend-Staid and Prell 2002). Thus, as a result of historical events, the bulk of the Afrotropical Canthonini and Ateuchini (Montreuil 1998) genera now have restricted distributions in the forests, shaded situations or highland grassland of the south-east or in moist to arid shrubland regions of the southwest (20 genera) or are centred in those regions (2 genera). Few Canthonini and Ateuchini show widespread tropical distributions (5 genera) unlike most Coprini (including coprines transferred from the Dichotomiini like *Heliocopris* – Montreuil 1998) and most of the genera of derived tribes.

The modern Afrotropical dung beetle fauna may be divided into five principal eco-climatic groups (Fig. 16.3) that comprise forest (1) and cool highland grasslands (2) resulting mainly from late Cenozoic uplift around the continental periphery (Meyers *et al.* 1998; Griffiths 1993; Kampunzu *et al.* 1998) that commences in the Miocene (Lavier *et al*. 2001) following the collision of the Africa / Arabia Tectonic Plate with Europe. Coevally, extensive opening into savanna (3) resulted from a cooling, drying trend in response to ocean currents modified from circum-latitudinal to north-south (Parrish 1987), increasing global latitudinal thermal stratification (Laporte and Zihlman 1983) and polar glaciation at 34 my (Barker *et al*. 2007a). The probable Miocene commencement (± 15 my) of cold current upwellings (Wigley and Compton 2006) from the glaciated poles resulted in aridification in the Karoo-Namib region (4) with the Pliocene onset of winter rainfall climate (5) across the southwestern Cape (Deacon 1983) resulting from the northwards shift of climatic systems at ± 3 my. Genera from all eco-climatic groups (Fig. 16.3) have been extensively shared with the Oriental region with filtering of elements shared with the Australian, Nearctic and Neotropical regions. The African fauna may have remained the most diverse fauna owing to the great diversity of mammals and dung types with little loss of large dung types during Pleistocene extinctions unlike in the Australian, Nearctic and Neotropical regions (Martin 1984).

17.1.2 Oriental

At generic level, the extant Oriental fauna (42 genera) shows great similarity to that of the Afrotropical region owing to the dominance of a subset of 28 taxa that are shared between the two regions. In general, these show eastern forest-centred distributions (e.g. *Proagoderus*, *Paraphytus*), western savanna-centred distributions (e.g. *Scarabaeus* (*Kheper*), *Phalops*, *Tiniocellus*) or both (e.g. *Copris*, *Onthophagus*). The principal difference to Africa results from 13 endemic genera, which mostly show forest distributions. Most of these genera are classified in the contentious basal tribes (Canthonini, Dichotomiini) or they are known or possible ant associates classified in the Onthophagini. A few further endemic genera in different derived tribes comprise *Paragymnopleurus* (Gymnopleurini), *Sinodrepanus* and *Yvescambefortius* (Oniticellini). One further difference to the Afrotropical region results from the more widespread genus, *Synapsis* (Coprini) that is shared with the Palaearctic region and shows a disjunction between south central Asia and eastern China to Sumatra. Over much of the eastern Oriental region, the effects of widespread habitat fragmentation may be producing species assemblages that comprise a subset of the former forest or dense woodland faunas, which are tolerant of opened out vegetation cover (see Shahabuddin *et al.* 2005).

As ancient (Cretaceous) northern origins are unlikely considering the uncertain fossil evidence (see above) and southern centring of generic endemism (Table 16.1), the composition of the present Oriental dung beetle fauna has been hypothesized to be, variously, by Cenozoic expansion of range from Africa via the present-day Palaearctic region (Davis *et al.* 2002a) or through land links from the subcontinent of India (e.g. Krikken and Huijbrechts 2007) after its drift across the ocean and collision with Asia. This collision is variously considered to have occurred at 55 my in the early Eocene (Epard and Steck 2007), or from 55-42 my (Briggs 2003), becoming fixed at 35 my in the Miocene, with India / Asia faunal exchanges commencing at the earliest date (Ali and Aitchison 2008).

The possible involvement of India depends on its tectonic history, which has remained in dispute (Ali and Aitchison 2008). The hypothesized split from Madagascar at 96-84 my (Briggs 2003) or 90-85 my (Ali and Aitchison 2008), would precede the mean dated origin of the subfamily Scarabaeinae, assuming that this is accurate (Table 15.1). However, the presence of dung beetles in early India cannot be discounted since some of the different viewpoints on the subsequent history of the subcontinent (Ali and Aitchison 2008) may provide indirect evidence for their occurrence through dispersal if not by vicariance. These viewpoints may be summarized as north-eastwards drift of India close to Africa versus relative oceanic isolation and limited (vertebrates in general) versus marked endemism (frogs) of fossils depending on the study group. Based on a perceived limited endemism in the Indian fossil vertebrate fauna, Briggs (2003) argues for a route of drift close to Africa that was open to dispersal. This close proximity is disputed by Ali and Aitchison (2008) on geological evidence who suggest an alternative Madagascar / India dispersal route via possible land exposures along the Seychelles / Mascarene ridge. In addition, citations of similarities between present or past distribution of particular vertebrate faunal groups between India, Madagascar and South America (Briggs 2003; Yoder and Nowak 2006) lead one to ask if the apparent biogeographical inconsistencies in the dung beetle phylogeny of Monaghan *et al.* (2007) could be resolved by a hypothesized dual origin. Under such a scenario, derived Afro-Eurasian centred dung beetle tribes originate from either the Afrotropical (Sisyphini, Onitini, Onthophagini, Oniticellini – major clade 2) or the Oriental regions via India (Gymnopleurini, Scarabaeini – major clade 1 together with derived Neotropical, and Australasian taxa), despite the current greatest species diversity of these tribes in Africa. It has been further suggested (Krikken and Huijbrechts 2007) that origin in India accounts for the forest litter pattern of distribution from India, through south-east Asia, to west Sundaland shown by the species rich, endemic, basal canthonine genus, *Ochicanthon*. However, in the absence of phylogenetic support, a Sundaland origin with range expansion to India is an equally plausible possibility, particularly as first contact between India and Asia, is hypothesized to have been with Sumatra (Ali and Aitchison 2008). Krikken and Huijbrechts (2007) also discuss relationships between *Ochicanthon* and Madagascar taxa, as indicated by molecular analysis (Monaghan *et al.* 2007), in support of a route via India. This is, however, all somewhat speculative. So far, convincing molecular support for Out-of-India origin in extant taxa is limited to a single plant group (Conti *et al.* 2002).

Although *Ochicanthon* is a member of the contentious basal tribe Canthonini, some other members of basal tribes are shared between the Afrotropical and Oriental regions, e.g. *Panelus* (Canthonini), *Delopleurus*, *Paraphytus* (Dichotomiini). Likewise, many members of all derived tribes are also shared. So, would the Oriental fauna be derived from a dual origin via range expansions from India and Africa or just a single origin from Africa, or would it represent one end of an interchange of taxa between Africa and the Oriental region? Would the age of the shared fauna be more recent since it is still at species level similarity or is age of the elements masked by selective sharing of taxa (i.e. all generic level elements are of relatively older age but some are shared whereas others have remained endemic at generic level)? Also, by how much may past routes have been masked by orogenics and late Cenozoic climate change?

Orogenics resulting from the collision of India with Asia created the mountain barriers that delimit most of the Oriental biogeographical region (Acharyya 2000). Geological data indicate that structural re-development through metamorphosis in the western Himalayan region commenced in the Eocene with uplift dating from 48 my (Epard and Steck 2007) with deformation of similar Eocene age in Yunnan in the east (Sato *et al.* 2001). It seems that uplift and the development of barriers were already well advanced by the Oligocene since there is fossil evidence of tropical trees in central Pakistan mixed with pollen of different origins, some of which indicates a nearby high altitude flora centred at around 2000-2500 m (de Franceschi *et al.* 2008). This uplift induced great regional climatic change by the late Miocene, comprising a rain shadow to the north and the development of air currents responsible for the monsoon to the south (Zheng *et al.* 2004). These events were coeval with the post Eocene global cooling and drying trend (Allen and Armstrong 2008) that, especially, affected dung beetle occurrence in the Palaearctic culminating in north / south climatic oscillation in response to glacial / interglacial cycles. This trend lead to the current cool northeast and arid western boundaries of the Oriental region, the latter possibly very recent as, ecologically, in the Saharo-Sindian region, the Sahara was a dry savanna region only 5000 year ago (Pachur and Hoelzmann 2000) with a strong inclusion of woody elements in the Arabian flora of similar age (Parker *et al.* 2004).

The effects of late Cenozoic cooling and drying may be, jointly, indicated by the fossil record and preserved in some modern faunal patterns. Southward retreat due to late Cenozoic cooling is indicated by the loss of *Heliocopris* from Palaearctic Japan known as a Miocene fossil (Fugiyama 1968) and the loss of *Eodrepanus* (Barbero *et al.* 2009) from Palaearctic England, which is known as an Eemian age, interglacial, Pleistocene fossil (cited as *Drepanocerus*) (Coope, 2000). A relict disjunct pattern is shown by *Synapsis* with one species to the north of the mountains in the central Asian arid region and the remaining species in east China to Sumatra. Perhaps the Saharo-Sindian pattern of distribution is a relict of past connection between Africa and the Oriental region with isolation of the dryer Indian savanna more recent than that of the south-eastern rainforests. Penetration into Afghanistan river valleys by *Catharsius* and *Phalops* species may also represent a relatively recent pattern. Thus, the effects of uplift limit the Oriental region primarily to the southern mountain edge with penetration up river valleys whereas a derived Sino-Tibetan Palaearctic fauna occurs in the high altitude mountain region to the north with little penetration into the Oriental region.

17.1.3 Palaearctic

At generic level, the extant Palaearctic fauna (26 genera) is almost completely shared with that in the Afrotropical and Oriental regions as it comprises only two endemic genera, *Paroniticellus* (Irano-Turanian) and *Bubas* (Mediterranean to Irano-Turanian). Patterns may be related variously to relicts of historical range expansion routes, relicts of range contraction, and ecological adaptation enabling taxa to survive in or re-colonize the southern part of the Palaearctic region despite late Cenozoic cooling and drying events. Some of the shared genera (10) are widespread across the main centres of the southern Palaearctic from the west (Mediterranean, Madrean), to the centre (Irano-Turanian, Sino-Tibetan) and the east (East Asiatic) (e.g. *Copris*, *Onthophagus*, *Caccobius*) whereas some are more biased to the drier centre and west (e.g. *Cheironitis*, *Euonthophagus*, *Onitis*, *Scarabaeus*). The remainder of the genera (14) represent marginal occurrence in the extreme southwest in an arid Saharo-Sindian or Saharo-Arabian pattern (8 genera) (e.g. *Proagoderus*, *Cleptocaccobius*, *Heliocopris*, *Phalops*, *Catharsius*), in the arid extreme central south to the north of the Himalayas (3 genera) (*Phalops*, *Catharsius* in Afghan river valleys, *Synapsis* in south central deserts) or in the moist extreme south-east of the East Asiatic region (5 genera) (e.g. *Panelus*, *Paragymnopleurus*, *Liatongus*, *Strandius*), including Japan (Schoolmeesters 2008a; 2008b), which has been isolated by a sea-barrier since the early (Jolivet *et al.* 1994) or late Miocene (Itoh *et al.* 1999).

Despite its hypothesized derived status, the Palaearctic fauna clearly has a long history since fossils of extant and extinct genera genera have been recorded from several places in Western Europe. These have been dated to ages varying from Eocene to Pleistocene although the earliest fossils confidently identified as Scarabaeinae are of Oligocene age. Some of these genera no longer occur in the Palaearctic or their modern range is far to the south of their fossil occurrence, presumably due to global or local extinction (*Heliocopris* in Japan, *Eodrepanus* in U.K. – see above) or southwards retreat in response to Plio-Pleistocene glacial cycles. Except for marginal occurrence of *Panelus* species in the east, the Palaearctic lacks representatives of basal taxa currently classified in the Canthonini or as ateuchine Dichotomiini. As the Eocene, Oligocene, Miocene, and Pliocene of the lower Rhine (Germany) show a trend from tropical (ca 25 °C – mean temperature early Eocene) through warm temperate (ca 17 °C – early to mid Miocene) to cool temperate palaeoclimates (ca 10 °C – Pliocene) based on floral fossils (Bechtel *et al.* 2008), the current Palaearctic fauna apparently represents the relict of a warmer adapted fauna that has become adapted to current cooler temperate climates, is restricted to warmer seasons of these climate types, or has been able to recolonize the region from warmer climates to the south following the Plio-Pleistocene glacial cycles. As a result it may have diverged from possible closer similarity to the faunas of the Afrotropical and Oriental regions.

The origin of the Palaearctic and Oriental faunas may be indicated by the molecular relationships of the most widespread genus, *Onthophagus* (Emlen *et al.* 2005b) that forms mostly consistent biogeographical groups. Other onthophagine genera and *Onthophagus* from Africa are clearly the basal group with most Palaearctic / Oriental and Australian taxa forming one terminal clade and the Nearctic plus Neotropical taxa the other terminal clade. An early Cenozoic colonization of Western Europe is indicated by the fossil dung beetle record (Krell 2000; 2006) but this region remained isolated from the rest of the Palaearctic until the Miocene when an influx of eastern mammal elements is indicated (Mein 1979). The age and routes followed to the east by the modern dung beetle faunas are unclear since the current major patterns Mediterranean, Saharo-Sindian, Irano-Turanian, East Asiatic, and Sino-Tibetan distribution, are the result of more recent history.

17.2 AMERICAS

The Americas form a cohesive biogeographical unit owing to the continuing dominance of genera and species in basal and endemic derived tribes although some recent addition of Afro-Eurasian taxa occurred via Beringia with decreasing representation southwards from the Nearctic to the Neotropical regions.

17.2.1 Nearctic

At generic level, the Nearctic fauna (13 genera) is almost completely shared with those of Afro-Eurasia and the Neotropical region as it comprises only a single endemic genus (*Melanocanthon*) with Neotropical affinities (Kohlmann and Halffter 1991). One pattern would, presumably, result from Miocene to Pliocene range expansions that added three Afro-Eurasian genera from the Palaearctic across a land link at Beringia, followed by southwards retreat and range expansion across the Central American land link to the Neotropics during the Great American Interchange (Webb 1976). A fourth Afro-Eurasian genus, *Sisyphus*, has, presumably, retreated southwards as it is now restricted to the Central American part of the Neotropical region. The other pattern would result from Plio-Pleistocene range expansions that added nine genera from the Neotropical region during the Great American Interchange. Largely similar patterns are seen in modern Nearctic mammals (Potts and Behrensmeyer, 1993) with a combined 80% exotic derivation from Afro-Eurasia or the Neotropics.

If Afro-Eurasian elements entered North America via Beringia, faunal ranges would have extended much further north in the warmer past and have, presumably retreated south as a result of Plio-Pleistocene cooling. Invasion from genera represented in the East Asiatic region may be supported by the molecular relationships of the Afro-Eurasian component to Palaearctic / Oriental ancestors of the genus *Onthophagus* (Emlen *et al.* 2005b). Furthermore, the presence of two taxonomic groups in American *Copris* that are not duplicated in Afro-Eurasian taxa (Matthews 1961) may indicate two waves of invasion by the genus. Similar patterns are recorded in relict but formerly widespread Cenozoic floras that are now restricted to warmer humid refugia in south-eastern and western North America, East Asia, and south-west Eurasia (Milne and Abbott 2002). Two clusters of divergence times at 10 (Late Miocene) and 5 my (Pliocene), that are duplicated in disjunct East Asian and North American Cenozoic floral relicts, may reflect a hiatus in connectivity across Beringia during a cold period at 6 to 8 my before marine incursion broke this Nearctic – Palaearctic land link at around 5 my.

The modern Nearctic dung beetle fauna is centred primarily in the lower altitudes of the warmer south-east USA, in the arid southern USA, and in northern Mexico (Schoolmeesters 2008a; 2008b). Even so, some genera have penetrated further northwards (Neotropical affinities: *Melanocanthon*, *Phanaeus*) or have, presumably, recolonized cooler northern regions following Pleistocene glaciation (Afro-Eurasian affinities: *Onthophagus*). Northernmost records now occur, variously, from Connecticut westwards to Wisconsin although at least one *Copris* species occurs as far north as Ontario in eastern Canada. By contrast, one genus, *Liatongus*, is centred in western forests and is represented by two mycetophagous species. Routes from the south followed by dung beetles have passed either side of the mountains of the Mexican Transition Zone along the Pacific or Atlantic seaboards (Kohlmann and Halffter 1988). Faunal ranges were, presumably, much further north in the past. However, effects of climatic change since the Pleistocene are reflected in the range changes indicated by fossil dung beetles from Rancho La Brea on the Pacific coast (California). These records suggest a warmer climate at the time of fossilization as they comprise species whose ranges are now far to the east or far to the south in the warmer climate of Mexico. Some are even possibly globally extinct as they have not been recorded in any modern faunas (Miller *et al.* 1981; Miller 1983).

17.2.2 Neotropical

Generic (82) and species richness of the Neotropical fauna is second only to that of the Afrotropical region but, in comparison, the Neotropics are somewhat depauperate in large-bodied mammal species subsequent to Pleistocene extinctions (Martin 1984). The dung beetle fauna is numerically dominated by 61 genera currently classified in three contentious basal tribes. Some of these genera (e.g. *Canthon*, *Deltochilum*) are clearly derived from older elements (Monaghan *et al.* 2007) as are a further 17 genera classified in three derived tribes endemic to the Americas. The remaining four genera have, presumably, been gained via the Nearctic during the Great American Interchange as they belong to Afro-Eurasian centred tribes (Oniticellini, Onthophagini, Sisyphini) or to basal tribes (Coprini) with Afro-Eurasian affiliations. Three of these genera remain shared with Afro-Eurasia whereas one is endemic (*Attavicinus*). Only one of the four has penetrated deeply into South America reaching as far as Argentina (*Onthophagus*) (Schoolmeesters 2008a; 2008b). The others are restricted to Central America (*Sisyphus*, *Attavicinus*) or occur only as far as the forest to the west of the Andes (*Copris*), which is limited to the south by the Atacama Desert that results from a western rain shadow induced by the Andes.

The origin of the Neotropical dung beetle fauna is contentious in a region that was essentially isolated for most of the Cenozoic until orogenics and sea level changes created the modern link to the Nearctic region across the Central America isthmus in the Pliocene. As South America was already separated from Africa at 110 my (Sanmartin and Ronquist 2004), origins in vicariance may be discredited since separation pre-dates molecular age data for dung beetles (Table 15.1). However, this conclusion is dependent on the validity of data that are insufficiently exact to determine if an alternative origin in dispersal could have occurred prior to the Eocene diversification of indigenous South American mammal groups (Simpson 1980**)** or as late as the Oligocene coeval with the arrival of rodents and monkeys as determined from their appearance in the fossil record (Simpson 1980).

Thus, what evidence is there for an origin of early Neotropical dung beetles at least by the Eocene with divergence partly driven by all of the main events in the mammal faunal history, viz. Eocene divergence of indigenous groups, Oligocene addition of monkeys and rodents, Plio-Pleistocene Great American Interchange followed by Pleistocene extinctions? Fossil remains of both South American monkeys and basal rodents first appear in Neotropical deposits of Oligocene age. Both groups have been demonstrated to be most closely related to African groups by molecular systematics (Mouchaty *et al.* 2001; Schrago and Russo 2003). The absence of earlier fossils or related fossils on other continents has been used to infer trans-oceanic dispersal directly from Africa. Coeval Oligocene dispersal of dung beetles to the Neotropics from Africa would fit with the younger estimated age scale for earliest divergences of Neotropical elements but not the older scale. The latter would indicate prior occurrence and earlier commencement of radiation coeval with indigenous Eocene radiations and increase in body size of indigenous mammal groups (Wing and Sues 1993). These groups decline from the Oligocene, following the arrival of rodents, and are now extinct (Notoungulata, Lipopterna) or outnumbered (Xenarthra) by more widespread groups. An effect would also be expected from the addition of other Afro-Eurasian mammal groups in the Plio-Pleistocene Great American Interchange (Simpson 1980) as well as the loss of others in Pleistocene extinctions (Martin 1984), including the mastodon. It is unknown what these effects might be.

The modern Neotropical dung beetle fauna comprises relatively older genera genera classified in contentious basal tribes, derived genera still classified in these basal tribes, derived genera in endemic American tribes, and genera with Afro-Eurasian affiliations added during the Great American Interchange in the Plio-Pleistocene. The latter are a relatively small part of the fauna and decline in representation beyond Central America (Davis *et al.* 2002a) unlike the greater northwards penetration by Neotropical elements into the Nearctic where there may have been fewer warm adapted competitors in the absence of a long-established scarab fauna. Thus, genera of basal tribes still dominate at both generic and species level unlike in most other regions. The history of this fauna may be ascribed jointly to mammal history (Eocene diversification, Oligocene and Plio-Pleistocene additions, Pleistocene losses) and to physical factors, particularly climate change associated with uplift of the Andes, which commenced in the late Oligocene (Tassara 2005). By the early Miocene (± 22 my), uplift reached sufficiently high altitudes to induce speciation of potato nematodes in the Central Andes with a trend to progressively later speciation to the north (Picard *et al.* 2008).

Early radiations in basal dung beetle tribes have clearly now been overlain by later radiations in these tribes and in derived indigenous tribes (Monaghan *et al.* 2007) since all are now distant from the single known southern genus that is considered to show closer relationships to the Australian rather than Neotropical fauna (Vaz de Mello and Halffter 2006). In tropical isolation, dichotomiines, canthonines, phanaeines, eucraniines and eurysternines evolved coeval with derived Afro-Eurasian tribes that are known as Oligocene fossils in Western Europe (Krell 2000; 2006). This history leads to the present major divisions in a primarily forest-centred fauna, which may have persisted with limited change because pollen samples indicate that Pleistocene vegetation oscillations were between montane and tropical forest (Colinvaux *et al.* 2000) rather than between savanna and forest as in Africa (Jahns *et al.* 1998; Dupont *et al.* 2000). Based on faunal structure, major forest regions (Fig. 16.3) comprise: Central America and the west of Andes in South America; the Guyano / Brazilian basin in the east; the winter rainfall Atlantic forest on the east coast; and Andean cloud forest which, in Colombia, is distinguished by highland assemblages at and above 1750 m (Escobar *et al.* 2005), with endemic highland species centred at and above 2000 m (Escobar *et al.* 2006). The drier southeast is a region apart characterized in particular by the eucraniines. The modern distribution of this tribe to the east of the Andes in the southern rain shadow area of Patagonia indicates evolution in response to increasing aridity driving behavioural changes from tunnelling to pellet carrying habits functionally similar to but phylogenetically distant from *Pachysoma* in arid southwest areas of Africa (Philips *et al.* 2002; 2004a; Ocampo and Philips 2005). Whereas the divergence of the phanaeine / eucraniine lineage may have pre-dated Andean uplift, the one estimate of Eucraniine / phanaeine divergence at 22 my (Table 15.1) would be coeval with the achievement of high altitude in the central Andes.

17.2.3. Caribbean

At generic level, the Caribbean fauna (12 genera) including Trinidad, is largely shared with those of the Neotropical (8 genera) and Afro-Eurasian regions (2 genera). The shared Afro-Eurasian genera comprise endemic species whose distribution patterns indicate possibly different origins via Nearctic (*Euoniticellus* – Bahamas, Cuba, Jamaica) and Neotropical routes (*Onthophagus* – Lesser Antilles, Hispaniola, Cuba). There are only two endemic genera, one with Afro-Eurasian affinities (*Anoplodrepanus* – Jamaica) and one with Neotropical affinities (*Canthochilum* – Cuba, Hispaniola, Puerto Rico). There is species level endemism in some Neotropical genera (*Canthonella*, *Sulcophanaeus*, *Uroxys*), mixed island endemism and Neotropical sharing in others (*Anomiopus* – in Trinidad only, *Ateuchus*, *Canthon*, *Pseudocanthon*), and complete sharing with the Neotropics in one genus (*Ontherus* – to Trinidad only).

The faunal history of the Caribbean islands clearly reflects that of the neighbouring major biogeographic regions as it is dominated by Neotropical elements but also contains Afro-Eurasian taxa. Whether the origins are by vicariance, dispersal, or both, is open to conjecture as in mammals (Dávalos 2004). The major islands of Cuba, Hispaniola and Puerto Rico are considered to have been emergent by the late Eocene and isolated by the late Oligocene (Iturralde-Vinent and McPhee 1999) and this is where 31 endemic species of *Canthochilum* and *Canthonella* are centred. Jamaica has a differing history having been submerged in the Oligocene (Robinson 1994) and uplifted by post-Oligocene eastwards movement of the Caribbean Tectonic Plate (Perfit and Williams 1989) and this is reflected by its quite different dung beetle fauna (single species of *Euoniticellus*, *Pseudocanthon*, *Sulcophanaeus*, two species of *Anoplodrepanus*). The remaining islands were also uplifted by similar tectonic movements between the Miocene and early Pliocene (24 to 5 my), except the Bahamas with a Quaternary origin due to sea level changes (Hearty 1998). Cladistic biogeographical analysis of extant and fossil terrestrial mammal distribution during the Cenozoic indicates two principal distribution patterns (Bahamas, Cuba, Jamaica, versus Lesser Antilles, Puerto Rico, Hispaniola) (Dávalos 2004). Patterns in the dung beetles (excluding *Canthochilum* and *Canthonella*) reflect the former distribution pattern in Afro-Eurasian Oniticellini (*Anoplodrepanus*, *Euoniticellus*) whereas the remaining eight genera treated as a group are represented in Trinidad / Lesser Antilles (19 species), Hispaniola (6), with none in Puerto Rico but several in Jamaica (2) and Cuba (2).

17.3 EAST GONDWANA FRAGMENTS

The fragments of East Gondwana remain dominated by basal tribes at generic level and may be divided into islands whose faunas have been influenced by proximity to Africa (Madagascar) and those which have been influenced by proximity to the Oriental region after northward continental drift (New Guinea, Australia). Of several derived Afro-Eurasian tribes that have reached these fragments (includes ball rolling Scarabaeini and Sisyphini), diversification is numerically dominated by small tunnellers of the sister tribes Oniticellini (Madagascar) or Onthophagini (Australia).

17.3.1 Madagascar

At generic level, the highly endemic dung beetle fauna of Madagascar is dominated by members of the polyphyletic basal tribe, Canthonini. Out of a total of 16 genera, 14 are endemic with 12 classified in the Canthonini and two others as an endemic subtribe, Helictopleurina, in the derived Afro-Eurasian tribe, Oniticellini. The remaining two genera also belong to derived Afro-Eurasian tribes and comprise *Scarabaeus* (Scarabaeini – represented by three flightless species in the dry southwest) and *Onthophagus* (Onthophagini – represented by six species). The dung beetle fauna is limited on an island on which mammals are represented by an endemic set of relatively small-bodied primates, rodents, insectivores and carnivores (viverrids / mongooses) dropping small dung types, with pygmy hippos extinct (Hanski *et al*. 2008).

Madagascar has been in its present position relative to Africa since 130-118 my (Seward *et al*. 2004) and isolated since the split with India, possibly at around 88 my (Yoder and Nowak 2006). Davis *et al*. (2002a) suggested that the dung beetle fauna originated by vicariance. However, rigorous recent molecular analysis of the Helictopleurina suggests a more recent origin from African ancestors in the late Eocene to Oligocene at 37 to 23 my (Wirta *et al*. 2008), which postdates all estimates of separation of the island from Africa and would, by default, indicate an origin in dispersal as suggested by Paulian (1987). Similarly, less detailed analyses of relationships between canthonine lineages suggest recent separation primarily in the Miocene (Orsini *et al*. 2007). Although these results likely reflect in situ evolution and would not provide an age of origin for this basal tribe on Madagascar, given the isolation of Madagascar, dispersal would be the only possible process of origin assuming that the timescale in Table 15.1 is valid. The majority of the modern Madagascar biota shows affinities to that of Africa and it has been suggested that dispersal may have been assisted by the past presence of an island arc or land bridge extending south-eastwards from east Africa to Madagascar during the mid-Eocene to early Miocene at 45 to 26 my (McCall 1997). In recent years, origin through dispersal during the Cenozoic has been claimed for various other groups on Madagascar (Yoder and Nowak 2006) including lemurs at 66-62 my (Yoder *et al.* 2003). It is suggested that radiation of the Helictopleurina has paralleled that of the lemurs (Wirta *et al* 2008).

Yoder and Nowak (2006) hypothesize that the drier south-west vegetation belts are older than the eastern rainforest and western woodlands and are relicts of drier past Palaeocene / early Eocene climate when Madagascar lay further to the south. Although this precedes the hypothesized arrival date of helictopleurine dung beetles that are dominated by forest associations (Hanski *et al.* 2008), it does not sit well with Madagacar as a late Cretaceous / early Cenozoic dispersal route to other Gondwana fragments for basal dung beetle taxa that are also predominantly forest associated, variously in Madagascar (Paulian 1987), the Neotropics and Australia (Matthews 1972).

The extant fauna remains primarily centred on the eastern forests (~80% of species) (Paulian 1987) where there is high regional species turnover (Hanski *et al.* 2008) although a minority (~20% of species) occurs or also occurs in the drier vegetation in the west (Paulian 1987). Many forest species were not re-recorded in a recent survey of Madagascar (Hanski *et al.* 2008) and the likelihood of their rediscovery was predictable on the basis of coincidence between known distribution and known forest fragmentation within the past 50 years (Hanski *et al.* 2007). Rampant habitat fragmentation also obscures some of the natural patterns, particularly in the west of the island, which has been highly modified since the arrival of man some 1500 years ago resulting in known extinctions of endemic mammals (Burney *et al.* 2004). Other anthropogenically linked changes include recent resource shift to cattle dung and range expansion into cleared areas by three open vegetation tolerant *Helictopleurus* species as determined from molecular allele structure of populations (Hanski *et al* 2008).

17.3.2 Mauritius

The Mauritius dung beetle fauna comprises only two genera, one belonging to a contentious basal tribe, Canthonini (*Nesovinsonia*, one species), and the other to an Afro-Eurasian centred tribe, Sisyphini (*Nesosisyphus*, four species). As these genera are endemic to an oceanic island of volcanic rather than Gondwana origin with earliest volcanism dated at only 7.8 to 6.5 my (Debajyoti *et al.* 2007), dispersal is, presumably, the only process by which fauna could have colonized the island. This may explain the unusual tribal structure of the dung beetle fauna. Diversification is limited but appreciable for a small island where there are no indigenous terrestrial mammals other than bats. It may result from the isolated mountain forest distributions shown by the species of *Nesosisyphus* (Vinson 1951; Cambefort 1991b; Motala and Krell 2007) although these separations may be an artefact of forest fragmentation (Vinson 1951).

17.3.3 Australasia – New Guinea and Australia

Generically, the combined dung beetle faunas of Australia and New Guinea (24 genera) are dominated by members of polyphyletic basal tribes, from which 14 genera are endemic to Australia, three are endemic to New Guinea (*Oficanthon*, *Paraphacosomoides*, *Penalus*) and five are shared between Australia and New Guinea (*Amphistomus*, *Coptodactyla*, *Lepanus*, *Temnoplectron*, *Tesserodon*). Some shared genera are also found on outlying islands, including *Amphistomus*, which is represented by one endemic species on the Moluccas (Krikken & Huijbrechts 2007; Schoolmeesters 2008a; 2008b) just east of the Wallace line. Two Afro-Eurasian genera (*Onitis*, *Onthophagus*) have, also reached New Guinea and Australia, presumably by more recent dispersal from the Oriental region as supported by molecular relationships to Eurasian taxa (Emlen *et al*. 2005b). One species of *Onitis* is both shared with the Oriental region and is restricted to Irian Jaya, whereas *Onthophagus* is now found throughout New Guinea (74 endemic species) and Australia (188 endemic species with two shared with New Guinea) where it has diversified and now dominates the dung beetle fauna in terms of numbers of species.

Although some of the basal Australasian genera are, apparently, more recently derived within the region, including the New Caledonian and New Zealand faunas, some are clearly of relatively older origin (Monaghan *et al*. 2007). If Gondwana vicariance is discredited as the process of their origin, how might they have dispersed or expanded their ranges to the island continent within the timescale suggested by Table 15.1? Answering this question is problematical considering the various published hypotheses and findings. For instance, late Cretaceous dispersal routes from India / Madagascar to Antarctica are hypothesized along the Gunnerus and Kerguelen ridges (Yoder and Nowak 2006) and these may account for similarities between Indian, Madagascan and Neotropical fossil faunas until 80 my. Although, separation of Australia from east Antarctica had already commenced at 90 my, it remained partly connected at Tasmania until 35 my (Sanmartin and Ronquist 2004; Barker *et al*. 2007a) and the Neotropics were connected to the West Antarctic Peninsula until at least 41 my and possibly up until 6 my (Barker *et al*. 2007a). Although some ancient links between Madagascar and Australia are indicated by molecular data for sister fish taxa (Sparks and Smith 2004), the modern biota of Madagascar mostly shows closest relationships to Africa (Yoder and Nowak 2006) and Matthews (1974) states that the Australian dung beetle fauna shows closer links to that of the Neotropical region than to that of Madagascar. Links between Australia and the Neotropical region would be possible only via an Antarctic route. During the Late Cretaceous and the later Palaeocene, Antarctica and adjacent islands were much warmer than at present as indicated by fossil marsupials (Reguero *et al.* 2002) and fossil forest trees (Poole *et al.* 2005). However, passage to Australia via Antarctica would, necessarily, be an early Cenozoic event, or earlier, since this route was cut before the mid Cenozoic by climatic and marine barriers. These barriers comprise: complete isolation of Australia to the south of Tasmania at around 35 my (Sanmartin and Ronquist 2004; Barker *et al.* 2007a); coupled with Antarctic cooling in the Eocene indicated by cool-adapted fossil trees (Poole *et al.* 2005); followed by some evidence for full glaciation at around 33-34 my (Barker *et al.* 2007a); and strong evidence for full glaciation from the early (East Antarctica) or late Oligocene (West Antarctica) (Barker *et al.* 2007b). Furthermore, although the modern Araucarian region of South America is largely too cool for dung beetles, one endemic genus (*Tesserodionella*) has recently been described from the northernmost Chilean part of this austral region with affiliations closer to Australian than other Neotropical elements (Vaz de Mello and Halffter 2006). This would lend support to a past austral route for dung beetles between Australia and the neotropics.

Since the early Cenozoic, the New Guinea-Australia Tectonic Plate has drifted northwards, reaching its present position close to the southeast island archipelagos of the Oriental region by 25 my (Hall 2002) in the Oligocene. This has resulted, especially, in the probable dispersal of *Onthophagus* to New Guinea and Australia where it is now represented by at least 34 species groups (Matthews 1976). The Australian species studied by Monaghan *et al.* (2007) form one clade of eight species with basal node divergence at 38.4 or 23.7 my and basal internal node divergence at 28.1 or 17.3 my. The younger ages are comparable to the dates for plate tectonics. One outlier Australian species, sister to an Oriental species with a divergence age of 22.4 or 13.8 my, supports Matthews' (1976) contention of more than one dispersal event to Australia. There is currently no evidence for exchanges in further dung beetle taxa to or from Australasia.

Distribution patterns shown by the current Australian dung beetle fauna result largely from the drying trend that has proceeded in steps from the mid Cenozoic associated with rapid expansion events in south polar glaciation (Crisp and Cook 2007). These occurred at 34 (Eocene), 14 (Miocene) and 3 my (Pliocene) and caused progressive retreat of forest and its replacement by woodland and more open vegetation, especially since the Miocene and after intensification of aridity in the Plio-Pleistocene (Hope 1984; Kershaw 1984; Potts and Behrensmeyer 1993). At the present time, the basal dung beetle taxa mostly occupy forest ranges in New Guinea and eastern Australia (84% of Canthonini: Matthews 1972) or ranges in the southeast and southwest including sclerophyllous vegetation. As shown for plants (Crisp and Cook 2007), this southeast / southwest separation would result from central Australian aridity. It is characterized by four dung beetle genera endemic to the southwest, nine endemic to the northeast and east, with seven shared, including *Onthophagus*. The latter genus is represented in forest but has also radiated into more open vegetation so that it now occupies all 17 biogeographical areas defined for Australia by Allsop (1995) and dominates the fauna in terms of numbers of species.

17.3.4 Australasia – New Caledonia

The dung beetle fauna of New Caledonia is represented by eight genera classified in the polyphyletic basal tribe, Canthonini. Molecular relationships of seven genera form a derived clade with sister relationahips to both New Zealand and Australian taxa (Monaghan *et al.* 2007). An age of 41.1 my or 25.4 my may be estimated for the divergence of New Caledonia dung beetle genera from other regions. These ages are roughly consistent with the cited separation of New Caledonia and New Zealand at 40-30 my (Sanmartin and Ronquist 2004). Diversification has occurred in the absence of an indigenous terrestrial mammal fauna other than bats.

17.3.5 Australasia – New Zealand

The dung beetle fauna of New Zealand comprises only two endemic genera currently classified in the polyphyletic tribe, Canthonini. On an island lacking indigenous terrestrial mammals other than bats (McDowall 2008), the fauna shows saprophagous habits (Paulian 1987), or may be found on bird or introduced mammal droppings (Cambefort 1991b). One South Island genus is larger-bodied and monotypic (*Saphobiamorpha*). The other genus (*Saphobius*) is more species-rich but very small-bodied with specimens recorded during the hottest, driest season by surface pitfalls or in leaf litter of natural forest localities (McColl 1975). An early vicariant origin may be discredited as, phylogenetically, *Saphobius* species are embedded in a derived clade with both Australian ancestors and descendents. Furthermore, an age of 38.4 my or 23.7 my may be estimated for the divergence of New Zealand dung beetle genera using the aging methods of Table 15.1. This long postdates the supposed isolation of the New Zealand island archipelago at 80 my in the late Cretaceous (Trewick *et al.* 2007), which was, in any case, by separation from West Antarctica rather than from Australia or New Caledonia. Other problems for a hypothesized origin in Gondwana vicariance are the marine sediments that underlay all studied parts of New Zealand and indicate marine incursions at some time during the Oligocene (Waters and Craw 2006). Although this may not indicate total inundation, there is also no evidence that some parts of New Zealand always remained above water during this submergence at ~25 my (Campbell and Landis 2001; Trewick *et al.* 2007). Evidence from the highlands is unobtainable as the relevant strata have eroded away (Waters and Craw 2006) but, in any case, uplift seems to postdate drowning (Trewick *et al.* 2007). As with dung beetles, much of the modern New Zealand fauna shows strong biogeographical relationships with Australia (McDowell 2008) and New Caledonia.

Thus, by virtue of the phylogenetic, geological, biogeographical, and dating evidence, recent reviews of New Zealand have swung away from vicariance in favour of faunal origins dominated by dispersal (McGlone 2005; McDowell 2008), which may have been partly assisted by a chain of islands linking New Zealand to New Caledonia along the now submerged Norfolk Ridge (Trewick *et al.* 2007). This would be consistent with the indication of a common ancestor for New Caledonian and New Zealand dung beetles (Monaghan *et al.* 2007).

CHAPTER 18
CONCLUSIONS

The question of the historical events that drove specialization of the Scarabaeinae to coprophagy remains largely speculative owing to the inability to develop an acceptable absolute timescale for evolution of the subfamily. Past suggestions have placed the origin of the Scarabaeinae in the Mesozoic when dinosaurs were the dominant, large-bodied, terrestrial dung providers or the early Cenozoic when mammal diversification resulted in both increased body size and dung type diversity. There is limited circumstantial evidence for the former, which is weakened by the inconclusive Cretaceous fossil evidence for a Gondwana centred group and the probable ectothermic character and low rate of dung production in dinosaurs. Evidence for the latter fits better with modern observations of specialization to the copious amounts of dung produced by endothermic mammals that increase in body size from the early Cenozoic. The latter is also supported by a tentative age scale extrapolated from molecular systematics results that places scarabaeine origin in or close to the commencement of the Cenozoic.

Re-analysis and re-assessment of biogeographical patterns is rendered difficult owing to: (1) the current disarray in basal tribal classification resulting from phylogenetic analyses; and (2) the lack of reclassification in the face of variable topology. However, a compromise approach adopted, here, suggests that many of the basic patterns described for dung beetles in recent accounts of their historical biogeography remain supportable.

Although the Gondwana vicariance hypotheses proposed for the origin of Scarabaeinae (Davis *et al*. 2002a) are weakened by the findings of molecular phylogeny, the derivation and variability of molecular ages are themselves subject to criticism. Even so, a halving of the current slowest published rate of substitution and divergence for insect CO1 sequences would be necessary to push the origin of Scarabaeinae back to the age of Gondwana fragmentation. In view of general swing away from vicariance to dispersal that has been driven by molecular systematics research, alternative processes are considered for the populating of Gondwana continents by basal taxa in the outlines of regional biogeography, including those for outlying islands harbouring endemic genera.

However, until there is an acceptable consistency between a well-resolved phylogeny and a restructured classification with accurate absolute age data, there is little possibility of strongly supporting particular biogeographical hypotheses either for the origin of spatial patterns or for the forces that have driven the phylogeny of the Scarabaeinae.

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Section E

CONSERVATION OF DUNG BEETLES

Ute Kryger

In this section we will review the importance of dung beetles, their major threats, and their use as bio-indicators.

CHAPTER 19

THE IMPORTANCE OF DUNG BEETLES IN ECOSYSTEMS

A book chapter with the title "Conservation of dung beetles" must first of all elaborate on why these organisms should be conserved. Besides the all-encompassing, altruistic ethical argument that all components of biodiversity intrinsically deserve equal conservation efforts by the human race in charge of this planet's fate, there are more pragmatic and very egoistic reasons for us to conserve these animals. Mankind in its very existence depends on an intact biosphere with functional ecosystems (Daily 1997, Reid *et al.* 2005a, b). Contrary to general public opinion, many invertebrates are exceptionally important for the functioning of most ecosystems and especially the ecosystem services provided by insects are vital components in the complex natural interactions that remove waste and put food on our tables (Losey and Vaughan 2006). During his speech at his acceptance of the TED 2007 Prize, the well-known scientist Edward O. Wilson summarized these facts rather succinctly in the statement that insects are "the small things that run this world". This section of the book will explore the many ways in which dung beetles contribute to "running this world".

19.1 ECOLOGICAL FUNCTIONS

In terrestrial ecosystems, insects contribute significantly to the ecological processes of nutrient cycling, bioturbation, pollination and seed dispersal (Nichols *et al.* 2008). Dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae) fulfil these and other vitally important functions in many different ecosystems, especially in tropical savannas and forests (Hanski and Cambefort 1991e). Through their dung consumption and relocation activities, dung beetles are involved in the ecological functions of parasite suppression, secondary seed dispersal, nutrient cycling and bioturbation (Andresen 2001, 2003; Losey and Vaughan 2006; Nichols *et al.* 2008; Shepherd and Chapman 1998; Stokstad

2004; Waterhouse 1974). Furthermore, dung beetles may also function as pollinators (Ratcliffe 1970). One dung beetle species, *Canthon virens* (misidentified as *C. dives sensu* Borgmeier 1937), fulfills another ecological function by predating on leaf-cutter ants (*Atta* sp.) and thus potentially regulating the population dynamics of one of the principal herbivores of the Neotropics (Nichols *et al.* 2008). These beetles provision their larvae with leaf-cutter queens that they capture during the queens' nuptial flights (Forti *et al.* 1999; Halffter and Matthews 1966; Hertel and Colli 1998; Silveira *et al.* 2006). It has been estimated that a single *C. virens* individual could be able to predate dozens of *Atta* queens in a single reproductive period (Forti *et al.* 1999); this would represent up to 10% of the hatched *Atta* queens at a given time. On the other hand, it has been observed that 61.8% of all *Atta* nest establishment failure events caused by predation were due to *C. virens* (Vasconcelos *et al.* 2006a). Given the significant impact of *Atta* ants on plant community structure and dynamics as well as soil properties and nutrient cycling in the Neotropics (Farji-Brener 1992; Hull-Sanders and Howard 2003; Moutinho *et al.* 2003), the population regulation of this group of animals by dung beetle predation may also be an important ecological process (Nichols *et al.* 2008).

19.2 ECOSYSTEM SERVICES

Ecosystem services are those ecosystem functions that directly benefit human society (De Groot *et al.* 2002). It has been proposed that labeling an ecological process "important" to human beings is highly subjective and dependent on temporal, spatial and ethical considerations (McCauley 2006; Srivastava and Velend 2005; Wallace 2007). While this may be valid at the quantitative level, it is indisputable that at the qualitative level human beings are not capable of existing outside of a functioning ecosphere but heavily depend on viable natural systems providing ecosystem functions that directly or indirectly serve and support human life in countless ways. This also includes ecosystem services provided in agro-ecosystems; especially so since humanity has developed a pastoral lifestyle.

The Millenium Ecosystem Assessment (Reid *et al.* 2005a) warned that 15 out of 24 ecosystem services that directly contribute to mankind's well-being are in decline, as a consequence of ecosystem changes brought about by mankind. While we teach dogs not to bite the hand that feeds them, we ourselves seem to have missed that lesson. Reid *et al.* (2005b) divided ecosystem services into four categories: supporting, provisioning, regulating, and cultural. As this chapter shall illustrate in more detail, dung beetles are directly involved in supporting (nutrient cycling and soil formation), regulating (disease regulation and pest suppression, flood/drought regulation via bioturbation), and cultural (recreational, aesthetic, spiritual and educational) ecosystem services. One could argue that their activities indirectly also contribute to the provisioning of healthy beef grown on pastures.

19.2.1 Suppression of dung breeding pests and parasites

In an article titled "The Biological Control of Dung", Waterhouse (1974) was one of the pioneers (along with G.F. Bornemissza of the Australian CSIRO) explaining the importance of dung beetles for a balanced ecosystem. The well-known "crusader for biological control" (as he has been called by Cullen and Sands in their dedication of the First International Symposium on Biological Control to Douglas Frew Waterhouse in 2002) illustrated the crucial ecological role of dung beetles using Australia as an example. Before the import of cattle by European settlers in 1788, the large herbivore fauna of Australia consisted of marsupials producing relatively small, dry, fibrous dung pellets. The indigenous dung beetle fauna had adapted to this dung type and thus marsupial dung would never accumulate in Australian ecosystems. The dung pads of the imported cattle, however, were much larger and moister and hence unattractive to native Australian dung beetles. Thus they remained in the pastures unchanged, even for years, until rotting and weathering or trampling by livestock would eventually disintegrate them. This led to a number of negative consequences from obliterating pastures (Bornemissza 1976) to increasing the populations of dung-breeding insect pests (compare Dadour and Allen 2001).

Besides pasture fouling under the persisting dung pads, Waterhouse (1974) observed zones of tall rank herbage at their periphery that would be avoided by cattle (Anderson *et al*. 1984). Since a single adult bovine produces an average of 12 dung pads per day and in the mid 1970s there were around 30 million cattle in Australia, the negative effect of the accumulated unprocessed dung pads became severe and the effective loss of pasture land was considered to be enormous (Ferrar 1975; Waterhouse 1974). Bornemissza (1960, 1976) estimated that the unattended cattle dung deposits in Australia reached a staggering 33 million tons annually. Following the cumulative amount of unprocessed cattle dung pads over many years, many dung breeding pest species exploded in numbers in Australia (Hughes 1975). Globally, many dung-breeding fly species have followed livestock introductions, among these the pestiferous *Musca autumnalis*, *M. vetustissima*, *Haematobia thirouxi potans*, *H. irritans exigua*, and *H. irritans irritans* (Nichols *et al*. 2008). Especially the pestiferous bush fly (*M. vetustissima*) and the buffalo fly (*H. irritans exigua*) became exceedingly abundant and a major nuisance for people and livestock in Australia alike (Waterhouse 1974). In general, fly infestations diminish livestock productivity and livestock hide quality (Guglielmone *et al*. 1999; Haufe 1987); and consequently are thought to lead to substantial financial losses to livestock producers (Byford *et al*. 1992).

Waterhouse (1974) documented the biological control measure taken by Australia: the import of "foreign" dung beetle species attracted to ruminant dung. Not an entirely new idea then, as already in the year 1923 Hawaii imported three dung beetle species from Mexico and a bit later the Afro-Asian species *Onthophagus gazella* in order to aid in the biocontrol of the horn fly (*Haematobia irritans*). Apparently that approach worked out and the number of horn flies fell markedly in Hawaii after the dung beetles became abundant (Waterhouse 1974). In Australia, the South African dung beetle *Onthophagus depressus* had already been established before 1900. But only in 1967 were the first deliberate and organized beetle releases undertaken in Australia, and over the following three years 275,000 specimens belonging to four different dung beetle species were imported into northern Australia (Waterhouse 1974). The tunneller species *Onthophagus gazella* has been a particularly successful colonizer, dispersing over distances as far as 18 miles across sea. But also the tunnellers *Euoniticellus intermedius* and *E. africanus* increased in numbers swiftly in Australia. Between 1968 and 1982, some 55 "foreign" dung beetle species were introduced to Australia, most were species from southern Africa. Several of these introduced species are by now widely distributed over Australia's livestock producing regions (Elphinstone 2006), and eight species are considered to be successfully established (Macqueen and Edwards 2006). Hughes (1975) reported early on that the introduction of these ruminant adapted dung beetles into Australia swiftly led to a 4% reduction of the pasture area physically covered with cattle dung. Considering that 6-12% of the pasture area surrounding each dung pad is also avoided by grazing livestock, a reduction of dung-pad-covered pasture area by 4% represents a significant gain in available grazing area affected through the dung removal services of dung beetles (Fincher 1981; Weeda 1967). The economic returns of this were estimated to amount to hundreds of thousands of dollars per annum by Waterhouse (1974).

Besides the increase in available grazing, dung beetle activity also leads to parasite and pest population suppression. Waterhouse (1974) stated that in experiments, the efficient breaking up and burial of cattle dung pads by one of the imported dung beetle species (*Onthophagus gazella*) led to a 80-100% reduction in bush fly populations. Only a few fly maggots were found to survive the dung processing by the beetles, and they matured into stunted flies with reduced or totally suppressed fecundity. Waterhouse (1974) speculated that fly eggs and maggots were destroyed or discarded by the beetles during dung ball formation, due to the fact that neither of these was ever found in beetle brood balls. Nichols *et al.* (2008) listed a number of studies that reported elevated fly mortality in artificial dung pads due to dung beetles (Bishop *et al.* 2005; Blume *et al.* 1973; Bornemisszа 1970; Doube 1986; Feehan *et al.* 1985; Hughes *et al.* 1978; Macqueen and Beirne 1975b; Moon *et al.* 1980; Ridsdill-Smith 1981; Ridsdill-Smith and Hayles 1987; 1990; Ridsdill-Smith *et al.* 1986; Ridsdill-Smith and Matthiessen 1984, 1988; Wallace and Tyndale-Biscoe 1983). Furthermore, several studies experimentally simulating field conditions found clearly reduced fly abundances due to dung beetle presence in individual dung pads (Hughes *et al.* 1978; Ridsdill-Smith and Hayles 1990).

It seems that dung beetle activity elevates fly mortality through a combination of various factors: (i) dung beetle brood ball production constitutes resource competition with older fly larvae (Hughes 1975; Ridsdill-Smith and Hayles 1987, 1990), (ii) dung beetle feeding leads to direct mechanical damage of fly eggs and early instars (Bishop *et al.* 2005; Ridsdill-Smith and Hayles 1990), and (iii) dung beetle-induced dung disturbance leads to a microclimate in the dung pads that is unfavourable for fly eggs and larvae (Ridsdill-Smith and Hayles 1987).

While these dynamics are easily proven in experimental set-ups, the situation in natural field settings is much more complex (Nichols *et al.* 2008). For instance, it was shown by Tyndale-Biscoe and Walker (1992) that experimentally elevated densities of the dung beetle species *Onthophagus australis* negatively influenced survival and size of pupae in the bush fly. *In situ*, however, the populations of this dung beetle did not reach the necessary densities to effectively suppress bush fly populations during spring, the critical period of bush fly population growth (Nichols *et al.* 2008). Factors influencing the effectiveness of dung beetle induced suppression of fly populations include temporal and spatial habitat use. Therefore, studies investigating the effect of entire dung beetle communities are much more likely to find a negative effect on fly populations, rather than studies concerned with single dung beetle species (Nichols *et al.* 2008).

Consequently, the two field studies assessing the impact of intact dung beetle assemblages on fly populations both measured massive reductions of fly survival due to the beetles (Fay *et al.* 1990; Horgan 2005).

Phoretic macrochelid mites may play an additional role in this context: dung beetles ordinarily carry numerous individuals of these predatory mites (of which there are hundreds of different species) with them. While the mites are entirely harmless to the beetles, and in fact depend on the dung beetles for transport between the dung pads (Krantz 1998), they attack and consume large quantities of small maggots and fly eggs and larvae in the dung pads (Axtell 1963; Doube 1986; Wallace *et al.* 1979; Waterhouse 1974). While Waterhouse (1974) started to wonder whether Australia should also import the phoretic mites besides dung beetles for effective pest control, Dadour (2006) mentioned anecdotal reports from Australia suggesting superior fly control in dung pads with both mites and beetles.

It has been suggested for a long time that dung beetles play a major role in the suppression of enteric parasites in humans as well as in livestock. Hingston (1923) already established that dung beetles in rural India interred 40-50 thousand tons of human faeces over just two months of peak dung beetle activity. And Miller (1954) speculated that dung beetles played a crucial role in controlling human endoparasites. However, empirical support for this plausible speculation remains to be gathered (Nichols *et al.* 2008).

In early laboratory studies, Miller *et al.* (1961) revealed that the ingestion and digestion of dung by dung beetles led to a significant reduction of the abundance of protozoan cysts and viable helminth eggs (among them *Ascaris lumbricoides*, *Necator americanus*, *Trichuris trichura*, *Entamoeba coli*, *Endolimax nana*, and *Giardia lamblia*). Mathison and Ditrich (1999) found the same to be true for the protozoan *Cryptosporidium parvum*. It was shown by Miller *et al.* (1961) that the feeding action of four species of dung beetles belonging to the genera *Canthon* and *Phanaeus* almost entirely suppressed the passage of hook- and roundworm eggs.

Experiments in South Africa and Australia have shown that dung beetle activity leads to a tremendous reduction in the number of infective larvae of intestinal worms (helminths) in cattle reaching pastures from dung pads – the number of worm larvae was reduced by 48 to 93% in cattle dung pads attacked by dung beetles in comparison to intact pads (Waterhouse 1974). Bryan (1973, 1976) observed that the activity of the dung beetle species *Digitonthophagus gazella* decreased the number of emergent strongyle nematode larvae in dung pads on Australian cattle pastures significantly. In the United States, Fincher (1973) could prove that a 5-fold elevation of dung beetle numbers in cattle pastures led to a 3.7-fold reduction of *Ostertagia ostertagi* (the "small brown stomach worm", probably one of the most important nematode parasites in cattle in temperate zones) emergence in comparison to pastures with natural dung beetle abundance. Fincher (1975) found further that calves grazed on dung beetle free pastures carried four times more endoparasites (*Ostertagia* and *Cooperia*, the small intestinal worm) than calves grazed on pastures with natural beetle numbers. When elk dung was worked by dung beetle communities, Bergstrom (1983) measured an 84.7% reduction in the emergence of elk lungworm larvae (*Dictyocaulus hadweni*). Gormally (1993) reported reduced numbers of *Pilobolus sporangia* – an exploding fungus that forcefully disperses its spores and along with them nematodes – due to dung beetle activity. It is known that male dung beetles of the species *Canthon cyanellus cyanellus* are able to produce an antifungal compound that protects the brood balls; but it remains unclear whether this form of chemical protection is widespread and whether it may possibly be considered for biocontrol of fungi (Cortez-Gallardo and Favila 2007).

19.2.2 Secondary seed dispersal

In temperate and tropical ecosystems, seed dispersal strategies of many plants involve vertebrates as primary seed dispersers (Howe and Smallwood 1982; Jordano 1992; Willson *et al.* 1990). Frugivorous mammals or birds typically swallow the seeds of the plants they feed on along with the fruits, and later excrete these seeds intact and viable but at a different place (deFigueiredo 1993; Garber 1986). There are numerous risks for the seeds between deposition in vertebrate dung and final seedling emergence, including unsuitable placement for future germination, pathogens, and predators (Chambers and MacMahon 1994). Especially in tropical forests, as much as 90% of the excreted seeds that remain on the soil surface may be eaten by seed predators such as rodents (Chapman 1989; Estrada and Coates-Estrada 1991; Sanchez-Cordero and Martinez-Gallardo 1998). For this reason it is important for the recruitment of many seed plants that their seeds get buried after deposition by the primary seed disperser; a service almost entirely accomplished by dung beetles (Estrada and Coates-Estrada 1991). Examples of this dung beetle driven secondary seed dispersal are known mainly from the Neotropics (e.g. Stokstad 2004) and Afrotropics (Shepherd and Chapman 1998). Andresen (2001 and 2003) reported on the positive effect of dung beetles burying the seeds of *Micropholis guyanensis* (Sapotaceae) in Central Amazonia - a significantly higher number of seedlings established from buried seeds in comparison to seeds that remained on the soil surface (Fig. 19.1). Andresen (2003) further demonstrated that seeds of the plant genera *Micropholis, Pouteria* and *Pourouma* had a much better chance to germinate and establish when buried with dung buried by dung beetles than when they remained without dung and / or not buried by dung beetles (Fig. 19.2). The author attributed the benefit of secondary seed dispersal through dung beetles to enhanced avoidance of seed predation as well as to the provisioning of a more moderate and less variable microclimate for the germinating seeds in the soil. Shepherd and Chapman (1998) examined whether the burial by dung beetles affected the survival and germination success of seeds of *Monodora myristica* (Annonaceae), *Mimusops bagshawei* (Sapotaceae), *Uvaria* sp. (Annonaceae), *Cordia abyssinica* (Boraginaceae), and *Aframomum* sp. (Zingiberaceae) in frugivore dung in Kibale National Park in Uganda. These authors found that dung

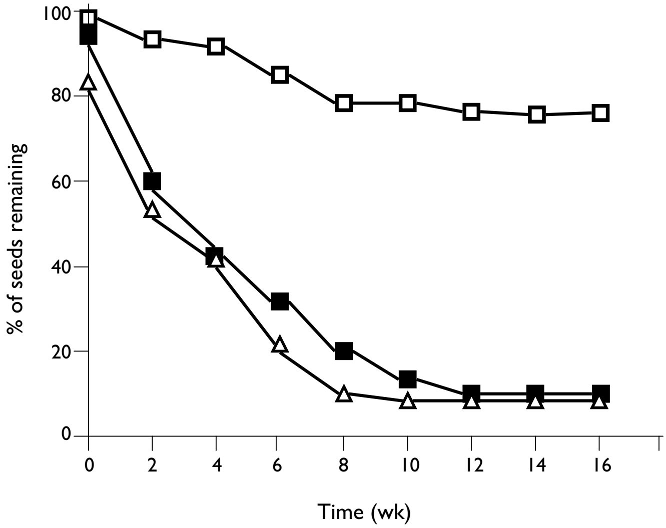

Fig. 19.1. Percentage of *Micropholis* seeds remaining over time (in weeks), time 0 represents 1 day after setting out the seeds. Filled squares represent seeds placed on the forest floor without dung, open triangles represent seeds placed with howler monkey dung but not buried by dung beetles, open squares represent seeds placed with dung and buried by dung beetles. (Adapted from Andresen 2001).

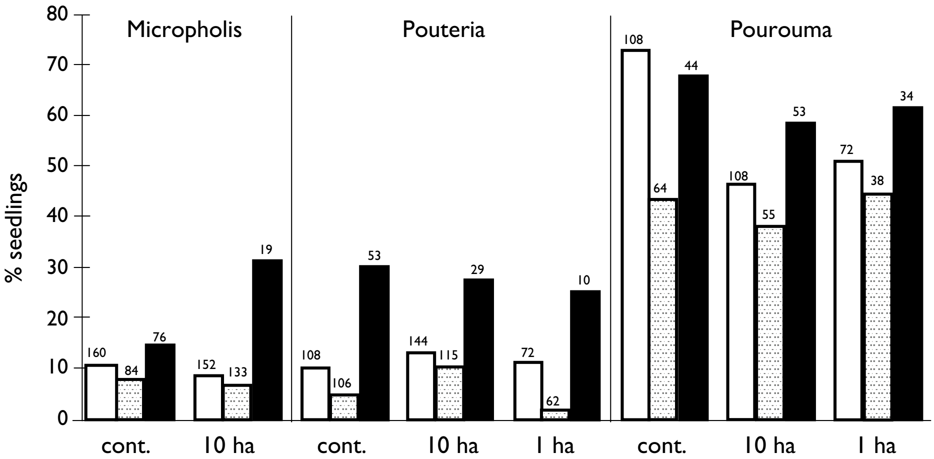

Fig. 19.2. Percentage of seedlings of three plant species establishing themselves in three different habitats in central Amazonia: continuous forest (cont.), 10-ha forest fragments (10 ha), and 1 ha forest fragments (1 ha). Numbers above the bars represent the actual numbers of seeds. Seeds are either deposited without dung (white bars), with dung but without being buried (dotted bars), or with dung and buried by dung beetles (black bars). (Adapted from Andresen 2003).

beetles facilitated seed survival by dispersing the seeds to locations with lower predation risk and higher germination potential.

When dung beetles bury dung, the plant seeds contained in the dung defecated by vertebrates are usually also buried (Halffter and Matthews 1966, Hanski and Cambefort 1991, Estrada *et al.* 1991); despite the fact that to the beetles the seeds actually represent unpalatable contaminants in the resource dung. It has been speculated that dung beetles bury the seeds along with the dung due to time constraints arising from competition for the available dung. Sometimes dung beetles purposefully "clean" the dung from any contaminant seeds before burying it (Andresen and Feer 2005). This seed burial activity by the dung beetles enriches the soil and helps the involved plant species to successfully disperse and to start a new generation by facilitating germination. Many of these plant species may be important food sources for fruit-eating mammals (Estrada and Coates-Estrada 1991), or micro-habitats to epiphytes and numerous invertebrate and vertebrate species. In this fashion, the functional integrity of entire ecosystems may directly be linked to a healthy dung beetle community fulfilling this role of secondary seed dispersal (Vulinec 2000).

While tunnelling dung beetle species relocate the seeds along with the dung in a vertical direction, rolling species also relocate the seeds horizontally (Nichols *et al.* 2008). Secondary seed dispersal by tunnellers and rollers in combination impacts positively on seed survival (and consequently plant recruitment) in a three-fold manner. Firstly, seed mortality through pathogens and seed predation is reduced (Andresen 1999; Andresen and Levey 2004; Chambers and MacMahon 1994; Estrada and Coates-Estrada 1991; Feer 1999; Shepherd and Chapman 1998). Secondly, seed clumping as well as density dependent seed mortality, seedling competition and predation risk all decrease (Andresen 1999, 2001; Andresen and Feer 2005; Howe 1989; Peres *et al.* 1997). And lastly, the relocation of the seeds underground represents a movement into a more favourable microclimate for germination and emergence (Andresen and Levey 2004).

Dung beetles bury 6-95% of the seeds found in a dung deposit; with exact percentages varying greatly between studies: 6-75% found by Andresen (2002), 35-48% in Andresen (2003), 26-67% in Andresen and Levey (2004), 13-23 % found by Feer (1999), and 47-95% in Shepherd and Chapman (1998). Roughly 5-44% of available seeds are moved horizontally by dung beetles (Andresen 2001; 2002, Andresen and Levey 2004).

Horizontal secondary seed dispersal distances by dung beetles observed in the literature range from 6-17 cm (Andresen 2002), 18 cm (Andresen and Levey 2004), 82-112 cm (Andresen 1999), 200-500 cm (Halffter and Matthews 1966) to a maximum of 10.6 m in the Neotropics (Halffter and Matthews 1966) and 15 m in the Afrotropics (Heymonds and von Lengerken 1929). It seems that the probability and distance of a seed's horizontal dispersal through dung beetles depends on the composition of the beetle community as well as the size of the seed (Andresen 2002). Furthermore, the probability and depth of a seed's vertical dispersal through dung beetles is a function of the composition of the dung beetle community (Andresen 2002; Slade *et al.* 2007; Vulinec 2002), the amount and type of dung (Andresen 2001, 2002; Ponce-Santizo *et al.* 2006), and the seed's size (Andresen and Levey 2004). There is a trade-off between the benefits gained by deeper seed burial depths in terms of decreased rodent detection and predation (Andresen 1999; Estrada and Coates-Estrada 1991; Shepherd and Chapman 1998) and the benefits of a more shallow burial depth that still allows the seed to germinate and emerge (Andresen and Feer 2005; Dalling *et al.* 1995). Usually dung beetles bury seeds at depths of 1-5 cm (Andresen and Feer 2005). For most seeds, the emergence success declines drastically when the burial depth exceeds 3 cm (Feer 1999; Hingrat and Feer 2002; Pearson *et al.* 2002). Shepherd and Chapman (1998) documented the depth of seed burial by dung beetles for the following Ugandan plant species, *Monodora myristica*, *Mimusops bagshawei* and *Uvaria* sp. They found that most seeds of the first two species were buried about 1-2 cm below the soil surface, while those of *Uvaria* sp. were buried as deep as 18 cm below the surface (Fig. 19.3).

Larger beetles are more efficient at seed burial because they bury larger amounts of dung and also bury larger seeds at greater depths simply due to their body size (Andresen 2002; Slade *et al.* 2007; Vulinec 2000). Furthermore, beetles of the burrower guild bury small seeds better than those of the roller guild (Vulinec 2000).

Stokstad (2004) referred to studies undertaken in tropical forests in Venezuela, where habitat fragmentation led to a decline of beetle diversity and consequently, with fewer seeds being buried, to a threat to forest diversity as a whole. It has even been proposed that the loss of just one single species (of dung beetles acting as secondary seed disperser) may lead to a breakdown of ecosystem integrity; and large dung beetle species seem to be most sensitive to extinction and most important for seed dispersal at the same time (Fransen, in Stokstad 2004). Andresen (1999), Estrada and Coates-Estrada (1991), Feer (1999) and Vulinec (2000) speculated that secondary seed dispersal and burial by dung beetles may be an essential element in reforestation. In support of this idea are the results of a study by Chapman and Chapman (1999) that had shown that rodent density in secondary growth areas was quite high, seed predation posed a major threat for unburied seeds and a swift burial would therefore be advantageous to a seed. Additionally, Vulinec (1999) and Estrada *et al.* (1999) found elevated dung beetle abundances in areas of secondary growth in comparison to clear-cuts.

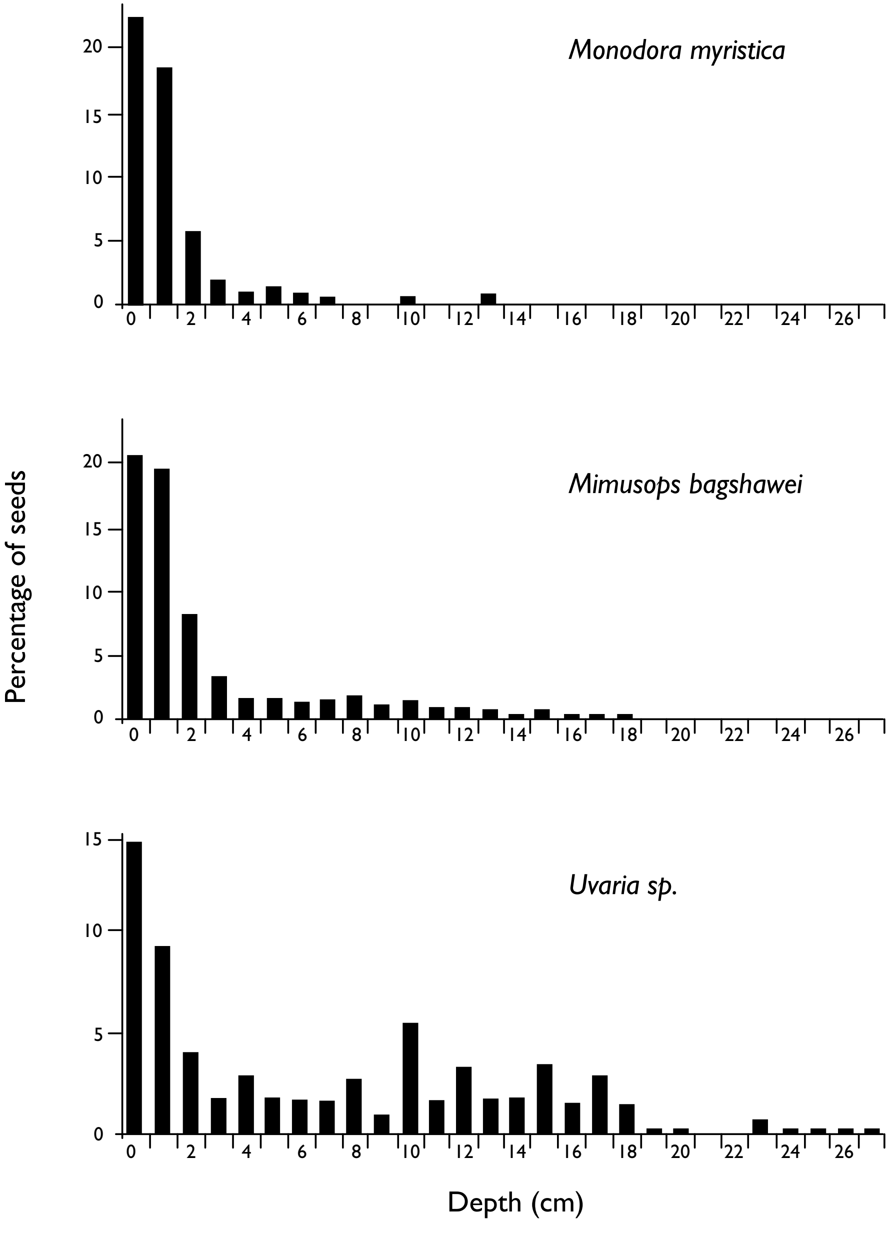

Fig. 19.3. Mean percentage of the total number of seeds found in Kibale National Park, Uganda, at various depths after burial by dung beetles. Per species 28 experimental buckets were used. In *Monodora myristica* 8 seeds were allocated per bucket with a mean seed length of 19 ± 1.7 mm (SE). In *Mimusops bagshawei* 15 seeds were allocated per bucket with a mean length of 16 ± 1.6 mm (SE). In *Uvaria* sp. 20 seeds were allocated per bucket with a mean length of 10 ± 1.6 mm (SE). (Adapted from Shepherd and Chapman 1998).

19.2.3 Pollination

For some plant species, dung beetles are crucial (and sometimes obligate) pollinators; this is the case for some decay-scented flowers belonging to the plant families Lowiaceae and Araceae (Nichols *et al.* 2008). One of the first scientific observations of dung beetle dependent pollination of a carrion-scented plant (*Typhonium tribolatum*, Araceae) by Gleghorn in India was cited in Arrow (1931); the dung beetles involved are *Onthophagus tarandus* and *Caccobius diminituvus*. In the Lebanon, it was reported by Gibernau *et al.* (2004) that the two dung beetles species *O. ovatus* and *O. sellatus* pollinate the dung/carrion-scented plant *Arum dioscordis* (Araceae) and Meeuse and Hatch (1960) observed beetle pollination in the plant genera *Dracunculus* and *Sauromatum* (Araceae).

Four different carrion-feeding *Onthophagus* species (*O. waterstradti, O. fujii, O. aurifex, O. vulpes*) and two species of *Paragymnopleurus* (*P. pauliani*, *P. striatus*) were also found to be obligate pollinators of *Orchidantha inquei*, a Bornean carrion-scented member of the highly relictual plant family Lowiaceae (Sakai and Inoue 1999). This flower does not secret any nectar and the visiting beetles do not seem to receive any other reward. The beetles presumably follow the dung-like odour of the flower and then search the flowers for dung. Since the flower does not provide any reward in form of food or protection to the beetles, this form of pollinator attraction has been called "deceit pollination" (Sakai and Inoue 1999).

19.2.4 Nutrient cycling

Vertebrate excreta contain a significant proportion of the nutrients originally consumed by the vertebrates (Steinfeld *et al.* 2006). For the productivity of an ecosystem it is crucial that a large amount of these nutrients is returned to the plant growth cycle (Nichols *et al.* 2008). Dung beetles bury dung and carrion as food for themselves and for their offspring and thereby relocate nutrient rich organic material into the upper soil layers. Furthermore, they instigate chemical and micro-organismal changes in the soil (Yokoyama *et al.* 1991a). The beetles' activity of incorporating animal faeces into the soil may therefore increase the rate of nutrient cycling (Bornemissza and Williams 1970; Halffter and Matthews 1966; Nealis 1977) and thus improve soil fertility and consequently plant productivity (Bornemissza 1976; Fincher 1981, 1990; Halffter and Edmons 1982; Hanski and Cambefort 1991). It is known that herbivore dung is rich in phosphorus, calcium and nitrogen, but contains only little potassium (Hutton *et al.* 1967). Of all these nutrients, nitrogen seems to be the critically limiting component structuring plant productivity (Vitousek *et al.* 1997). Plants can make the most efficient use of faecal nitrogen if the fresh dung is relocated beneath the soil surface (Bang *et al.* 2005). By transferring the freshly deposited vertebrate excreta below the soil surface, tunnelling and rolling dung beetles increase the available nitrogen for plant uptake through mineralization (Yokoyama *et al.* 1991a). Among the coprophagous arthropods, dung beetles are most capable of accelerating the return of nitrogen and other nutrients into the soil (Stevenson and Dindal 1987). By altering the environmental conditions in the dung pads and brood balls during feeding and nesting, their activity affects microbial populations and accelerates the growth of bacteria populations involved in ammonification, nitrification, denitrification, and nitrogen fixation (Breymeyer *et al.* 1975; Yokoyama *et al.* 1991b). It has been suggested that the activities of dung beetles elevate the carbon and nitrogen levels in the upper soil layers thus fostering bacterial growth of (among others) ammonifier bacteria that effect a continued nitrogen mineralization (Yokoyama and Kai 1993; Yokoyama *et al.* 1991a,b). Principally through brood balls production, dung beetles inhibit NH_3 volatilization significantly (Yokoyama *et al.* 1991a). The casings of these brood balls have been found to contain high concentrations of amino acids that are thought to accumulate as a consequence of fixation of gaseous nitrogen through microorganisms living in the digestive tract of scarbaeine larvae (Rougon *et al.* 1990).

Moreover, the beetles may reduce the nitrogen volatilization by physically diluting the concentration of accessible inorganic nitrogen by incorporating it into the soil compartment; this possibly enhances nitrogen-fixation by increasing the availability of decomposable organic matter (Yokoyama *et al.* 1991b).

In agro-ecosystems, it has been found that 80% of the nitrogen in the deposited manure that remains on the pasture surface is lost by (NH_3) volatilization unless sufficient numbers of dung beetles bury the dung swiftly and thus reduce the loss of nitrogen through volatilization to 5-15% (Gillard 1967). Even a more modest recent estimate of a volatilization loss of 12 of a total of 30 million tons of nitrogen excreted by extensive livestock production in the mid-1990s (Steinfeld *et al.* 2006) is still drastic.

Besides nitrogen, other soil nutrients have been shown to increase in dung beetle-exposed soils; among these are phosphorus, potassium, calcium and magnesium (Bertone 2004; Galbiati *et al.* 1995; Lastro 2006; Yamada *et al.* 2007). Furthermore, Bertone (2004) found a dung beetle mediated increase in soil pH and cation exchange capacity.

19.2.5 Bioturbation

The physical rearrangement of the soil profile by organisms exploiting the solum for food and shelter is called bioturbation. Especially burrowing animals and insects change the soil morphology by displacing and mixing sediment particles and thus creating passageways for air and water. During nesting, tunnelling dung beetles move large quantities of soil to the surface (Mittal 1993) and thereby increase soil aeration and water penetration (Nichols *et al.* 2008). Most tunnellers construct tunnels underground that may be up to more than one metre deep, and that branch into brood chambers. The depth of these tunnels, as well as the amount of soil displaced, are directly dependent on the body size of the beetles (Edwards and Aschenborn 1987; Halffter and Edmonds 1982; Lindquist 1933). The transmission of liquid and gas through the soil is proportional to the size and continuity of pore space in the soil (Bang *et al.* 2005). Larger beetles would therefore create larger tunnels (= pore space in the soil) and would consequently increase soil permeability most markedly. Bang *et al.* (2005) found in a study involving three Korean paracoprids that only the largest of these, *Copris ochus*, significantly increased soil permeability to 0.56 cm/h (in comparison to 0.38 cm/h in the control) for air to a depth of 10 cm (Fig. 19.4); the study measured air permeability with a permeameter and did not examine the extent of any horizontal effects.

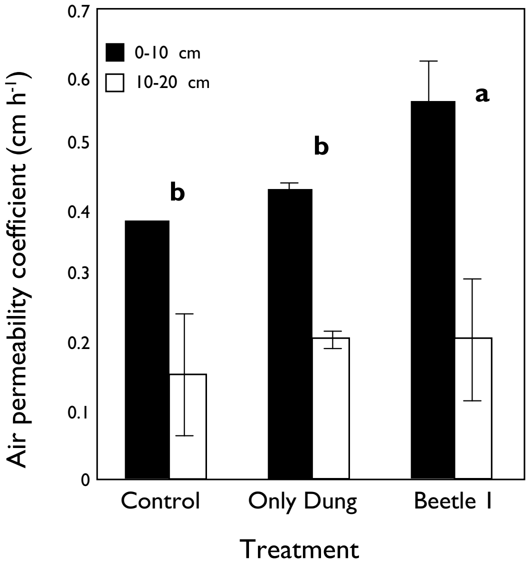

Fig. 19.4. Air permeability coefficients of soil cores from two different depths and three different experimental conditions in comparison: "Control" = no dung and no dung beetles, "Only Dung" = dung added but no dung beetles, "Beetle 1" = dung added as well as paracoprid beetle species *Copris ochus*. Measurements taken 172 days after dung burial by the paracoprid dung beetle species. Means with the same letter are not significantly different using ANOVA. L.S.D. (5%). (Adapted from Bang *et al.* 2005).

Richardson and Richardson (2007) reported that dung beetles buried two metric tons of wet manure per hectare in pasture land in Oklahoma and thereby increased water permeability by an average of 129% (ranging from 42-346% over six study plots). These authors further calculated that each extra inch of absorbed water adds 254.3 l/ha of water to the soil, thereby reducing the risk and extent of drought as well as flooding. This is in accordance with the report by Waterhouse (1974) that loamy soil worked by dung beetles required five times more water to get saturated than did undisturbed soil.

19.2.6 Enhancement of plant growth

The role of dung beetles in nutrient mobilization has been investigated by numerous authors by comparing biomass increase in plants grown in soil with dung worked by dung beetles in comparison to controls (Nichols *et al.* 2008). Different authors connected elevated protein levels (Macqueen and Beirne 1975a), increased grain production (Kabir *et al.* 1985), more above-ground biomass (Lastro 2006) as well as below ground biomass and corncob diameter (Galbiati *et al.* 1995), and increased plant height (Galbiati *et al.* 1995; Kabir *et al.* 1985) to the dung-burying and mixing works of dung beetles. Miranda *et al.* (1998, 2000) observed a time lag of several months before plants showed a dung beetle-related enhanced below and above ground biomass.

Waterhouse (1974) reported on laboratory experiments with Japanese millet plants that showed a marked increase in soil fertility through the presence and action of dung beetles: in comparison to plants growing in experimental pots without dung beetles, the plants in pots with dung and dung beetles showed a significantly increased yield, which the author attributed to the elevated uptake of sulphur, phosphorous and nitrogen by these plants. Waterhouse (1974) suggested that by dispersing the dung through the solum, dung beetles actually fertilize the soil. He further proposed that dung beetle activity leads to an improvement in soil structure and humus content, which in return would enhance plant growth. Other authors also proposed that the burying activity of dung beetles leads to increased pasture yields in various ways: it boosts the water-holding capacity and aeration of the soil and incorporates organic matter into the soil, thus recycling volatile nutrients contained in herbivore faeces (Bornemissza and Williams 1970; Gillard 1967; Macqueen and Beirne 1975a). (See Fig. 19.5).

Several authors have investigated the extent of dung beetle-mediated nutrient mobilization in comparison to the effects of chemical fertilizers. Macqueen and Beirne (1975a) observed that, against hand-mixed controls, crude protein levels in bearded wheatgrass were by 38% higher when dung beetles were al-

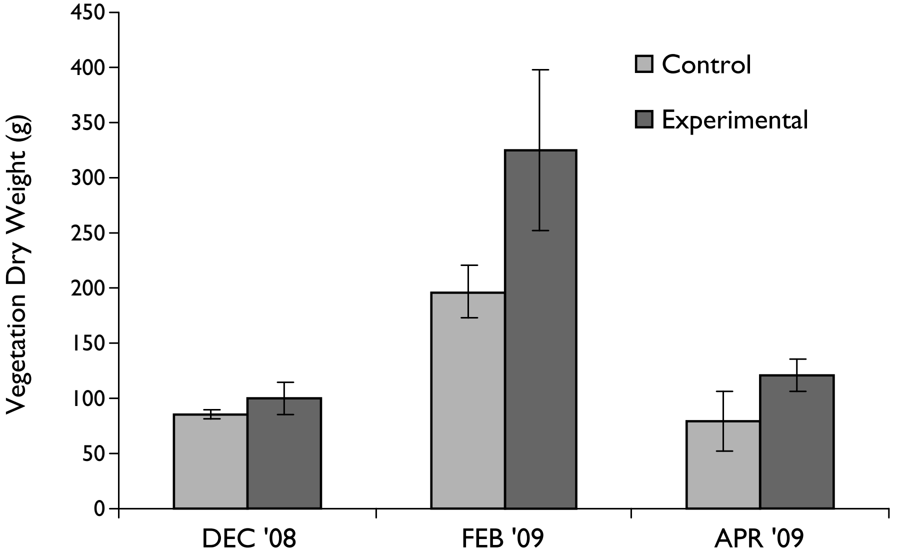

Fig. 19.5. Comparison of total dry weight of vegetation between 1 m^2 experimental and control plots. After vegetation was cut in December 2008, 3 kg of fresh cattle dung was applied to experimental plots and these were subsequently colonised by natural populations of dung beetles. The dry weight of cut vegetation on the plots was re-evaluated in February and April 2009. (Unpublished data, Jackie Brown, Scarab Research Group, University of Pretoria).

lowed to work the dung into the soil. However, these authors also found that chemical fertilizer applications at two different dosages (67 kg/ha and 269 kg/ha) increased crude protein levels much more significantly (by 95% and by 144% against the control, respectively). The *in situ* field study by Fincher *et al.* (1981) compared the increase in plant yield in Bermuda grass when cattle dung was naturally exposed to dung beetles to the increase in yield when ammonium nitrate was applied as a fertilizer (at two dosage levels: 112 kg/ha and 224 kg/ha). While the presence of dung beetles led to a significantly increased yield against the lower dosage of fertilizer and against a negative control, this higher yield was at the same level as achieved with the higher fertilizer application. Furthermore, Fincher *et al.* (1981) conducted three trials on wheat plants and found in one of these three trials that dung beetle activity significantly boosted the yield in comparison to chemical fertilizer treatments and unmixed dung set-ups. In a study by Miranda *et al.* (2000), plant height and leaf production were higher in plants with associated dung beetle activity than in plants exposed to a chemical fertilizer at an application of 100 kg/ha K_2O, 100 kg/ha P_2O_5, and 100 kg/ha N.

Bang *et al.* (2005) conducted greenhouse and field experiments to assess the effects of three Korean paracoprid dung beetles species (*Onthophagus lenzii, Copris ochus* and *C. tripartitus*) on the physical characteristics of the underlying soil as well as on the growth of pasture plants. Like in the experiments undertaken by Waterhouse (1974), the three different treatments in Bang *et al.*'s (2005) experiments consisted of a) controls without dung or dung beetles, b) treatments with dung beetles only, and c) treatments with dung plus dung beetles. The field experiments resulted in an elevated herbage yield in the treatments with the dung beetles (especially those with *O. lenzii*). The authors claimed an association of all three dung beetle species with elevated nitrogen content and higher herbage yields. Their laboratory experiments produced significantly increased total digestible nutrients contents and total crude protein contents in grass shoots that were grown in the presence of *C. tripartitus* and *C. ochus* compared to grass shoots from the controls. When *O. lenzii* was involved in the burying of faeces, the dry matter digestibility, dry intake and relative feed value of perennial ryegrass was highest (Bang *et al.* 2005).

Borghesio (1999) undertook *in situ* experiments with un-manipulated dung beetle abundances and natural vegetation in Italy and found a significantly increased net primary production of heathplants in comparison to controls without dung beetles or without dung.

19.2.7 Aesthetic, spiritual and religious relevance of scarab beetles

Besides material needs connected to our physical wellbeing, our species has long exhibited an intrinsic need for a spiritual life. The contents of this spiritual aspect of the human experience are myths regarding the origin and functioning of the world, including ourselves, and are also symbols that model desirable qualities and moral principles for us.

Scarab beetles have been important spiritual symbols dating back to prehistoric times (Cambefort 1994). Beetle-shaped artefacts are known from as early as the late Paleolithic epoch (10,000 until 20,000 years ago). The current ethnological hypothesis assumes that the significance of beetles stemmed from their importance as a food source as well as their ability to fly. This capability to fly was possibly related to the shaman's ability to "fly" into the upper spirit world and/or under world in dreams or in trance states and mediate there on behalf of his patient's health. Quite similarly the beetles were observed to be able to fly up into the sky and also to descend into the ground. And like the esteemed shamans, dung beetles were consequently also revered (Cambefort 1994). This may have especially been so with species that exhibited bright, metallic colourations, because their additional aesthetic-ornamental appeal may have enhanced the symbolic connection of the scarab beetle to the sun and luminous sky.

Among many shamanic societies today, there are still myths relating the world's creation to beetles. Some tribes from the Chaco (South America) see a large scarab named Aksak as the creator of humans - he is though to have shaped woman and man out of clay (Cambefort 1994). Obviously this symbolism is derived from the working of food and brood balls by scarabs.

Also in Taoism we find dung beetles as sacred beings that exemplify to us what we need to do in order to reach spiritual immortality (Cambefort 1994).

In ancient Egypt the scarab was also revered. The first use of scarab beetles by Egyptian culture dates back to the early first dynasty (approximately 3000 B.C.). The sacred scarab was primarily associated with the sun and the sun god, both the bright metallic species *Kheper aegyptiorum* as well as the black species *Scarabaeus sacer* feature among ancient Egyptian artefacts. The scarab god Khepri ("The Being") was regarded as the great god of the morning sun (it represented the rejuvenated sun that rises from the ground after having metamorphosed in the ground during the night), as well as the self-created creator of the universe. The scarab beetle was seen as the earthly representation of this god and powerfully symbolized the victory of life over death, of resurrection (Cambefort 1994). Due to Egyptian influence, the Phoenicians adopted the esteem of scarab amulets as auspicious ornaments and even added scarabs to the tombs of their dead. In Sardinia a thriving industry of producing scarab amulets existed. The habit to carve these ornamental scarabs spread to Etruria and later to Rome (Cambefort 1994). Also in the late ancient Greek civilization, the scarab was important as the "king of Pygmies" and in its association with the god Zeus (Cambefort 1994). In a transference of the idea of resurrection, scarab beetles and their relatives were even worshiped in Germany until the time of the artist Albrecht Dürer (1471-1528) who associated the stag beetle with Christ in several of his paintings (Cambefort 1994).

While most of these ideas are outdated today, still many contemporaries find great aesthetic pleasure in scarab beetles (one only needs to look at contemporary jewellery depicting scarabs), and the passion of some collectors is certainly reminiscent of religious dedication. Many wildlife enthusiasts are fascinated by the charismatic rollers and there are nature reserves in South Africa that successfully market their dung beetle fauna as a tourist attraction. Even if tourists were not interested in insects, the bountiful dung beetles of African savanna habitats are certainly an important food source that maintains some bird and small mammal populations that are valid attention-catching factors in wildlife tourism.

Thus it is still justified to claim that these beetles fulfil a service to us on a more spiritual or at least aesthetic level.

19.2.8 Estimated monetary value of ecosystem services delivered by dung beetles

We humans strongly depend on ecological services provided by natural systems; we are an integral part of the biosphere and are as such unable to exist in a "bio-vacuum". Following this fact and the peculiar modern-human motivation to only value something if it is possible to equate it to a monetary worth, Losey and Vaughan (2006) attempted to calculate US dollar values for the services delivered by beneficial insects each year. This was done in order to stimulate so far direly neglected conservation efforts for these insects. As was emphasized by Losey and Vaughan (2006), it is very difficult to assign an accurate economic value to ecological services in general. However, even rough estimates of the monetary equivalent of the various ecosystem services will be useful in establishing the relative priority for conserving the relevant organisms performing these services. This should then obviously be followed by a corresponding allocation of funds for specific conservation actions.

Losey and Vaughan (2006) investigated the economic value of vital ecosystem services maintained by wild (i.e., not domesticated and unmanaged) insects native to the USA and found available data to base their estimates on for the following four services: pollination, pest control, dung burial/decomposition, and maintenance of wildlife species involved in the recreation industry. With the goal of providing well-researched estimates, these authors defined "value" as the documented financial transactions (such as the purchase of goods) dependent on the relevant service. The value of the first three of the above mentioned services were calculated by Losey and Vaughan (2006) as the money paid to producers for a raw commodity connected to the particular ecosystem service. Their calculation of the insect support of game bird nutrition, on the other hand, was based on census data about how money was spent by US consumers (therefore reflecting the higher amount spent on value-added products, as opposed to usually much lower sums paid for raw commodities). As the overall annual value for the four investigated services together, they calculated a sum of over $57 billion in the United States; with $49.96 billion spent on recreation, $3.07 billion for pollination, $4.49 billion for pest control and $0.38 billion for dung burial.

The authors did not model an adjustment of the calculated values for service-dependent changes in quality or quantity of the connected commodities and the resulting effects on per-unit prices. Rather, the estimates were based on current service-levels, and are thus considered conservative. Furthermore, Losey and Vaughan (2006) emphasized that their estimates are "minimum estimates" of the economic value of the investigated ecosystem services. This, they attributed to the fact that a large fraction of the calculated values were not based on the real monetary equivalent of value-added products or actual wages paid to the producers of the relevant raw commodities, but only on the monetary charge of the raw commodities themselves. Furthermore, these authors only had data concerning a small fraction of the insect groups performing certain services (for instance their estimate for pollination is solely based on hymenopteran species thereby ignoring the large group of coleopteran pollinators and their additional contribution). In the calculation of averted economic losses as a result of accelerated dung burial of livestock faeces, Losey and Vaughan (2006) only included pastured beef and dairy cattle; however, dung beetles also avert economic losses by burying horse, sheep, goat and pig faeces. And, of course, the true economic worth of insects lies much higher than the calculated estimates by Losey and Vaughan (2006), simply because there aren't any available data to calculate the monetary equivalents of some very important ecosystem services such as soil improvement, decomposition of organic matter, seed dispersal and suppression of weeds and exotic invader species. These authors therefore stressed the point that a quantification of all these missing ecosystem services would add billions of dollars to their overall estimate.

Dung beetles are a very speciose group among the beneficial insects and play a dominant role in several of the ecosystem services for which Losey and Vaughan (2006) calculated corresponding economic values. Admittedly, the financial benefit to humans derived from dung beetle mediated pollination may be negligible. But dung beetles contribute significantly to pest control and are practically the only agents of dung burial, especially so in subtropical and tropical ecosystems. Referring to the framework of Losey and Vaughan (2006), the annual net value of ecosystem services delivered by dung beetles to the pastured beef cattle industry in the USA would be \$380 million (see Table 19.1). It is important to stress that this sum represents the postulated avoided costs of putative production losses due to forage fouling (averted annual losses of \$120 million), nitrogen volatilization (averted annual losses of \$60 million), livestock parasites (averted annual losses of \$70 million) and pest flies (averted annual losses of \$130 million). This means that the effective economic value of the dung burying activity by dung beetles is actually higher, due to the additional profit gained by more productive pastures (enhanced plant growth) and, as a consequence of better soil drainage reduced damage due to droughts and floods. As an example of how Losey and Vaughan arrived at these estimates see Table 19.2 for the calculation of the range fouling losses averted by dung beetles.

An (admittedly very simplified) application of the total estimate from the US beef cattle industry (with an estimated 100 million beef cattle) to a subtropical country with a striving beef cattle industry such as South Africa (with an estimated 13.5 million beef cattle) would lead to an annual averted

Table 19.1. Averted total annual economic losses (in million US $) due to dung beetle mediated burial of livestock faeces in the US. (Adapted from Losey and Vaughan 2006).

Cause of loss	**Estimated losses**		**Losses averted**
	Without dung beetles	**With dung beetles**	
Forage fouling	650	530	120
Nitrogen volatilization	310	250	60
Parasitism	980	910	70
Pest flies	1830	1700	130
Total losses averted			**380**

Table 19.2. Formulae used by Losey and Vaughan (2006) for the calculation of their estimates of dung beetle ecosystem services.

Formula used to estimate the number of cattle in the US producing dung that can actually be processed by dung beetles:	**Formula used to estimate the value of reduced forage fouling resulting from dung beetle activity:**
$\mathbf{C_p = (C_t \times P_r) \times P_{nt}}$	$\mathbf{V_{rf} = [V_c \times (C_p \times L_{nb})] - [V_c \times (C_p \times L_b)]}$
C_p = number of cattle producing dung that can be processed by dung beetles C_t = total number of cattle produced in the US per annum P_r = proportion of cattle raised on pastures and rangeland P_{nt} = proportion of cattle not subjected to avermectin treatment	V_{rf} = value of reduced forage fouling V_c = value of cattle (per kg body weight) C_p = number of cattle producing dung that can be processed by dung beetles L_{nb} = number of cattle lost without dung beetle activity L_b = number of cattle lost at current levels of dung beetle activity

economic loss of $51.3 million due to dung beetles burying cattle dung; at the current exchange rate (1 US$ = 8.53 South African Rand) this would equate a total sum of ZAR 437.59 million. When considering the additional 30 million sheep and goats in South Africa (with each of these producing one tenth the amount of manure of an average cow and therefore their totality producing the same amount of dung as 3 million cattle), and large numbers of wild animals on "game" farms, the overall financial benefit due to dung beetles' dung burying activity would rise to an annual sum of at least ZAR 534.83 million, a substantial amount for an emerging economy.

Steinfeld *et al.* (2006) estimated that 2.0 billion hectares of land, about 15% of the earth's ice-free surface, are utilized by human beings in the form of extensive pasture systems with livestock. Globally, vast areas are dedicated to livestock production in the economically motivated absence of chemical preventative or curative veterinary care. In these areas the sustainability of agriculture relies even more on dung beetles that drive the natural ecological processes responsible for prevention of pasture fouling, maintenance of forage productivity (by preventing nitrogen volatilization and enhancement of nutrient cycling) and suppression of livestock parasites and pests (Miranda 2006; Nichols *et al.* 2008). Moreover, in the absence of veterinary pharmaceuticals dung beetles will be able to process 100% of the deposited dung pats and thus the averted economic losses in terms of accelerated burial of livestock faeces will proportionally be even higher in these areas than in the US where 56% of cattle on rangelands are treated with pesticides (Losey and Vaughan 2006).

We humans most definitely derive substantial further financial benefits from dung beetle facilitated bioturbation (for instance in the form of averted flooding and droughts, see Richardson and Richardson 2007), and also from soil conditioning and nutrient recycling which lead to significantly increased plantation productivity and crop yields (see laboratory studies by Miranda *et al.* 2000 and Yokoyama *et al.* 1991b).

Secondary seed dispersal through dung beetles contributes to the profits of the timber industry and non-timber forest products industry as well as to the success of restoration and reforestation projects (Vulinec *et al.* 2007). While the monetary value of dung beetle mediated secondary seed dispersal to the profits of the timber and the forest products industries could probably be quantified, the economic worth of successful restoration and reforestation projects is more complex to calculate. However, it is obvious that human populations benefit directly economically in many tangible ways from such successful projects.

It has, furthermore, been suggested that the chemical compounds that suppress the growth of pathogenic fungi on dung beetle brood balls may have horticultural applications (Nichols *et al.* 2008). While this is not an ecosystem service as such performed by dung beetles in horticulture, but rather requires human intervention and application, the economic potential could be significant.

In modern times, recreation in nature (especially game viewing) has gained tremendously as an economic factor. In the US alone, the expenditure for recreational activities in nature that rely on ecosystem services provided by insects amount to an annual value of 49.93 billion dollars (Losey and Vaughan 2006). Admittedly, dung beetles won't contribute much to the expenditures for fishing or hunting included in this sum, but they certainly represent an important food source for insectivorous birds. Thus they probably play a large supporting role in the maintenance of bird biodiversity and consequently the bird watching industry. The annual expenditure for bird watching (adjusted to the proportions of birds that depend on insects for nutrition) in the US was estimated to amount to 19.76 billion dollars (Losey and Vaughan 2006). In countries such as the US, there is an additional expenditure for hunting of insectivorous galliform birds which was estimated to add an extra 1.48 billion dollars annually to the economic value of insects including dung beetles (Losey and Vaughan 2006). In other countries around the globe, especially tropical and subtropical countries with a flourishing eco-tourism industry (e.g. South Africa), game and bird watching is also a strong economic factor; with a much richer dung beetle community in such countries the contribution of dung beetles to the expenditure for recreation may be even higher than in the US. Large charismatic dung beetle species (e.g. large rollers such as *Circellium bacchus* in South Africa) themselves may even be objects of interest to game viewing (and paying) tourists.

19.3 CONCLUSION

While the above reported monetary estimates are considered conservative, they imply that it would be justified, and indeed necessary, to dedicate large sums of money to the conservation of these beneficial and beautiful insects in order to ensure the sustained economic and aesthetic benefits we derive from their sheer presence and their very useful activities. Unfortunately, the importance of insects in general has, until now, escaped popular awareness. They are commonly regarded as a nuisance and it comes as no surprise that their decline does not raise the grave concern that it should. Kremen *et al*. (2002) gathered evidence for the steady decline in beneficial insects and even localized severe declines in certain environments that suffer heavy degradation by human impact.

A combination of human-induced habitat destruction, influx of invader species and exposure to toxic chemicals poses an ever increasing threat to beneficial insects (Losey and Vaughan 2006). Alarmingly, Larsen *et al*. (2005) indicated that under certain conditions the most important species in terms of providing specific ecosystem services are the ones to be lost first. Generally, ecosystems are believed to possess a capacity to absorb a certain degree of perturbation without losing functionality. However, Schwartz *et al*. (2000) suggested that this capacity may be limited and an ecosystem may collapse swiftly once a threshold level of disruption is passed. This danger makes it even more important to take timely conservation action, especially for taxa such as dung beetles, on whose vital ecosystem services we depend. Losey and Vaughan (2006) made specific recommendations as to which concrete steps should be taken in this direction.

They suggested that conservation funding should pay specific attention to the ecological needs of insects and that the funds should be used to ensure that habitat is provided for beneficial insects in natural, semi-natural as well as agricultural landscapes. These authors further demanded that land-management decisions should take into account the essential ecosystem services provided by insects. This would imply that land management practices such as grazing, burning and pesticide use should be tailored in order to protect the highest degree of insect biodiversity, e.g. only treating small areas at a time or only using specific pesticides with a minimum of non-target effects.

CHAPTER 20
EFFECTS OF HABITAT DESTRUCTION AND FRAGMENTATION ON DUNG BEETLES

20.1 TERMS AND DEFINITIONS

There is one species that dominates all ecosystems on this globe (Vitousek *et al*. 1997) in ever growing population sizes and with ever stronger greed – this species is called *Homo sapiens*. Unfortunately the impact of this species on its environment generally leads to disruption of ecological processes and destruction of natural habitat. It is important to acknowledge that most components of earth's biodiversity are found in landscapes used by man (Halffter 2005). Thus it comes as no surprise that the primary cause for the current loss of biodiversity in general is habitat loss through human-induced destruction and fragmentation of natural ecosystems (Burgess and Sharpe 1981; Tscharntke 1992; Tscharntke *et al*. 2002a). This global biodiversity loss as a direct consequence of human alteration of natural landscapes occurs across all major taxonomic groups (Reid *et al*. 2005), from vertebrates to invertebrates, including dung beetles.

Often human land use leads to subdividing of a continuous habitat into smaller patches. This is frequently called "fragmentation" and it is thought to consist of three major components: overall area loss of the original habitat type, increasing isolation of the newly formed habitat fragments, and decreasing size of these fragments (Andren 1994). Originally, the species-area relationship of island biogeography was linked to the decline of biological diversity after fragmentation, arguing that the number of species and populations will decrease with decreasing area of suitable habitat (Connor and McCoy 1979; MacArthur and Wilson 1967; Preston 1960, 1962). However, all three components mentioned above are believed to lead to a decline in biodiversity (Wilcox 1980; Wilcox and Murphy 1985), and this not only accumulatively but even synergistically (Andren 1994; Gustavson and Parker 1992). Additionally, the creation of new habitat boundaries is followed by increased edge effects (Ewers and Didham 2006).

Many studies have assessed the effects of human land use on natural habitats and consequently on biodiversity. Within this bulk of literature the changes imposed upon habitats by humans are not always named consistently (Fahrig 2003). This has led to some contradictory results with some studies retrieving a positive effect of fragmentation on biodiversity (Belisle *et al.* 2001; Collinge and Forman 1998; McGarigal and McComb 1995; Villard *et al.* 1999). Fahrig (2003) therefore stressed the importance of clearly distinguishing between the terms "habitat fragmentation" and "habitat loss". While it is generally assumed that habitat fragmentation has a large negative effect on biodiversity and is therefore an aspect of habitat degradation (Haila 2002), this holds true only for the conceptualization of "habitat fragmentation" used as a synonym for "habitat loss" (as depicted in Fig. 20.1) (Fahrig 2003). Habitat fragmentation *per se* (Fig 20.2) is thought to have a much weaker effect on biodiversity that can be either negative or positive (Fahrig 2003).

Some authors conceptualize habitat fragmentation as a process during which an initially large area of a given habitat is broken up into smaller patches (of a total area smaller than the initial contiguous area) that are isolated from each other by a matrix of a changed or different habitat (Wilcove *et al.* 1986; also compare Fig. 20.1). Other scientists conceptualize habitat fragmentation quantitatively as a pattern characterized by four measurable effects: 1) a reduction in habitat amount, 2) increase in the number of habitat patches, 3) decrease in the size of the habitat patches, and 4) increase in patch isolation (Fahrig 2003). This second approach equates fragmentation with the loss of habitat (compare Fig. 20.2).

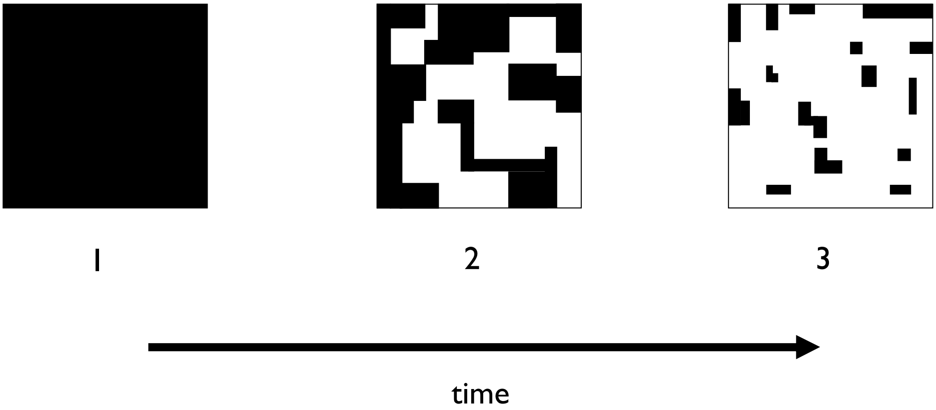

Fig. 20.1. Illustration of the process of habitat fragmentation as the transformation of one large area of habitat into several smaller patches that are isolated by a matrix of differing habitat(s); black areas represent habitat, white areas represent the matrix. (Adapted from Fahrig 2003).

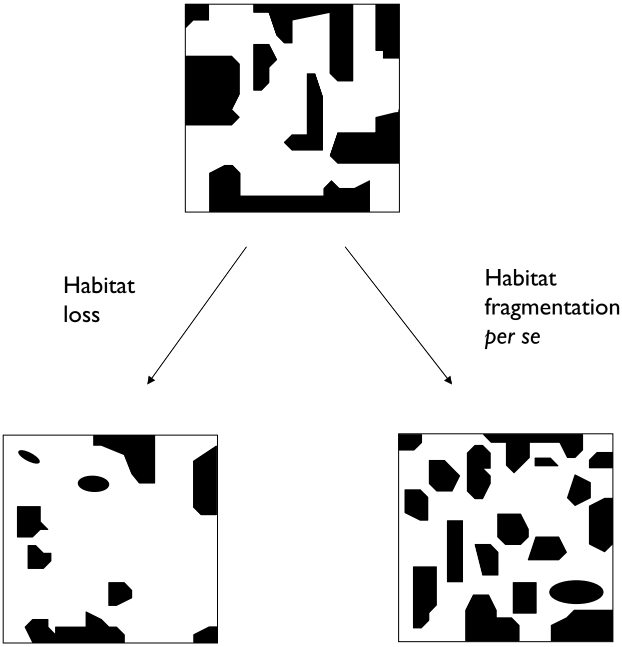

Fig. 20.2. Difference between habitat loss and habitat fragmentation *per se* (independent of habitat loss); both result in smaller patches. Patch isolation can actually decrease with habitat fragmentation *per se*. (Adapted from Fahrig 2003).

20.2 EFFECTS OF ANTHROPOGENIC HABITAT DESTRUCTION

Numerous studies have shown that habitat loss has significant, consistently negative effects on biodiversity. These reported negative effects apply to direct measures of biodiversity such as genetic diversity (Gibbs 2001), population abundance and distribution (Best *et al.* 2001; Gibbs 1998; Hanski *et al.* 1996), species richness (Gurd *et al.* 2001; Schmiegelow and Mönkkönen 2002; Steffan-Dewenter *et al.* 2002). But also indirect measures of biodiversity suffer under habitat loss (Fahrig 2003). Bascompte *et al.* (2002) predicted such negative effects on the growth rate of populations. Donovan and Flather (2002) found supporting evidence for this assumption in the fact that species with declining global abundances occurred in areas affected by high rates of habitat loss. Furthermore, it has been shown that habitat loss alters interspecific interactions (Taylor and Merriam 1995) as well as intraspecific social relationships and movements of individuals (Debinski and Holt 2000), reduces the abundance of large-bodied specialist species (Gibbs and Stanton 2001), and reduces trophic chain length (Komonen *et al.* 2000). Moreover, negative effects on predation rate (Bergin *et al.* 2000), competitor release (Debinski and Holt 2000), breeding success (Kurki *et al.* 2000), and dispersal success (Belisle *et al.* 2001) have been reported. It can exacerbate edge effects, modify nutrient flow (Bierregaard *et al.* 1992) and even affect the genetic composition of populations (Debinski and Holt 2000). Thus, through the negative impact of natural habitat destruction on patterns of diversity and biotic interactions ecosystem functioning and stability may be eroded (Lawton 1994; Naeem *et al.* 1994, 1995).

Ewers and Didham (2006) warned that other threats to biodiversity (such as climate change, invasive species, and human-altered disturbance regimes) may interact synergistically with habitat loss and the detrimental impact may thus be magnified. Additionally, the fact that anthropogenic fragmentation of natural habitat at a large scale is a recent phenomenon (in terms of evolutionary timelines) could imply that there are long-term negative impacts (such as changes in behavioural, morphological or genetic traits) that have not yet been observed but that will only become effective with a time-lag (Ewers and Didham 2006).

Ewers and Didham (2006) and Fahrig (2003) stressed that habitat fragmentation occurs at the landscape level and can therefore not be assessed at the patch level. Earlier, Law and Dickman (1998) suggested that in order to produce the largest positive biodiversity response, conservation management should protect landscape patterns that maintain the required habitat amount as well as the required habitat types. It has also been deduced from theoretical studies that the relationship between the amount of available habitat in a landscape and the number of individuals of a species that can be supported by this landscape is not proportional but rather characterized by an "extinction threshold". Should the amount of available habitat drop beneath this threshold level, the population would not be able to further sustain itself and therefore go extinct (Bascompte and Sole 1996; Fahrig 2001; Flather and Bevers 2002).

20.2.1 Severe impacts of habitat destruction on dung beetles and other insects

While the above described dynamics affect animals from all taxonomic groups, invertebrates are extraordinarily susceptible to the adverse effects of anthropogenic landscape changes. Experiments have shown that arthropods fitted the theoretical expectations of greater species richness and diversity on larger habitat areas and lowest species richness and diversity in smallest fragments better than other taxa (Debinski and Holt 2000; Laurance and Bierregaard 1996). Since insects have smaller home ranges and weaker dispersal capabilities compared to vertebrates, they are more affected by the isolation effect of fragmentation (Tscharntke *et al.* 2002b). And yet they remain overlooked all too often in studies or policies on habitat disturbance (Samways 1993; Dunn 2004a), despite the fact that they amount to more than 50% of all described living species and impact more strongly on terrestrial ecosystems than any other animal group (Kruess and Tscharntke 1994). In fact, insects are key players in many ecosystem processes and, consequently, it is possible that their loss will produce cascading negative effects throughout entire communities (Coleman and Hendrix 2000).

In recent years, forest fragmentation and deforestation have been some of the leading causes of species loss (Brooks *et al.* 2002; Wilson 2002). In forests, the biological processes that maintain ecosystem functioning (such as nutrient recycling, pollination and secondary seed dispersal) are largely driven by insects (Didham *et al.* 1996). Alarmingly, forest fragmentation-induced changes in abundance and species richness have been shown in many insects groups.

Vasconcelos *et al.* (2006b) reported significant differences in ant species richness and composition between continuous forest and forest fragments in the Brazilian Amazon. In forest fragments these authors retrieved on average only 85% of the ant species found in continuous forest, and significantly fewer rare species.

Klein (1989) investigated the effects of forest fragmentation in Central Amazonia on dung beetles and observed an almost complete turnover of species between continuous forest and clear-cut areas. In the same study, the author noted that species richness (Fig. 20.3) and population densities (Fig. 20.4) of dung beetles (and consequently dung decomposition rates) were significantly lower in the fragmented habitat and the resulting clear-cuts than in the continuous forest (Table 20.1). Moreover, the abundance of primary forest species declined dramatically in the forest fragments, to a level where they may be "functionally extinct" (Didham *et al.* 1996). Correspondingly, Vulinec (2000) detected negative effects on dung beetles, in terms of severely reduced biomass, through clearing and disturbance of primary forest in the Brazilian Amazon (Table 20.2). She suspected that this may have severe implications for seed dispersal and hence rainforest regeneration. Andresen (2003) reported on dung removal and seed burial rates being lower in fragmented forest patches (1-10 ha in size) than in continuous forest in Central Amazonia. As a possible explaining factor, this author also found that average beetle body size decreased with decreasing forest fragment size. The breaking up of natural tropical forests may have an especially dramatic impact on the biodiversity of dung beetles, because the vast majority of Neotropical dung beetles are forest dwellers (Gill 1991; Halffter 1991).

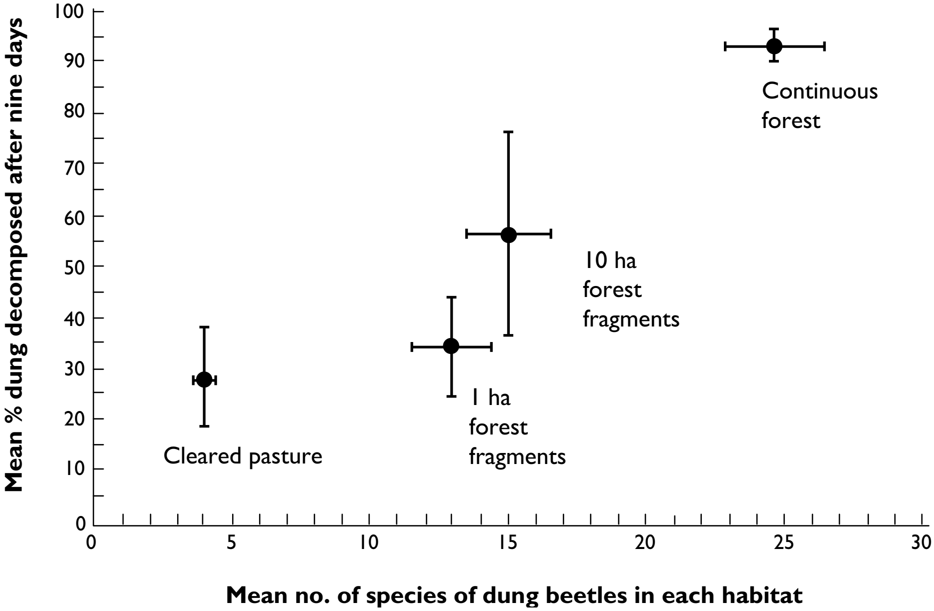

Fig. 20.3. Decline of mean (±SEM) species richness of dung beetles accompanied by a decline in the mean (±SEM) rate of dung decomposition in four habitat types in Central Amazonia, illustrating the effect of biodiversity loss on ecosystem functioning. Values are the means of three replicates for each habitat type. (Adapted from Klein 1989).

There are several studies from tropical and temperate systems that indicate a severe impact of local and regional-scale anthropogenic habitat changes on patterns of dung beetle abundance and species diversity (Nichols *et al.* 2008). The global modification, fragmentation and loss of tropical forest habitat are reported to lead to high local extinction rates across forest restricted dung beetle communities (Nichols *et al.* 2007).

Table 20.1. Comparison of dung beetle species richness and abundance between natural and primary forest and clear-cuts (A) or pastures (B) in Latin America. Data from original studies by 1 = Klein (1989), 2 = Medina *et al.* (2002), and 3 = Estrada *et al.* (1998), and table adapted from Davis *et al.* (2004).

Land	Species richness Forest	Species richness Transformed	Abundance Forest	Abundance Transformed
Brazil ^{1A}	43	12	1,369	717
Colombia ^{2B}	14	3	282	56
Mexico ^{3B}	30	8	10,060	729

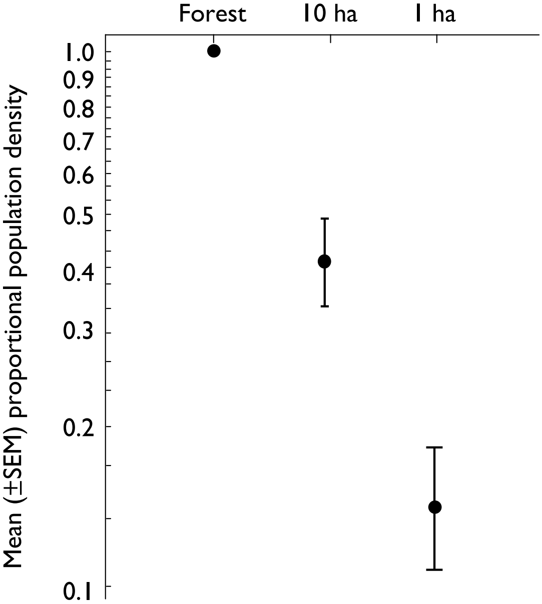

Fig. 20.4. Significant decrease in dung beetle population densities in forest fragments in Central Amazonia; adapted from Klein (1989). The drop in dung decomposition rates in smaller forest fragments may therefore be the consequence of decreased dung beetle population densities as well as reduced species richness.

A study by Halffter *et al.* (1992), investigating the effects of clearing of rain forest at Palenque, Mexico in 1965, also found a massive reduction of dung beetle richness, diversity and evenness in forest edges and clear-cut areas compared to original forest (Table 20.3).

Horgan (2006) found that dung beetle communities from deforested habitats near San Ramón in central Peru were characterized by drastically reduced

Table 20.2. Mean dung beetle biomass (SE) at three sites in Amazonia for three different habitat sites. Means with the same superscribed letter in each row are not significantly different (adapted from Vulinec 2000). Caxiuanã (student's t-test, $p < 0.001$), * = only three beetles caught; Ducke (Scheffes' multiple comparisons, $p \leq 0.003$) and Rondônia (Scheffes' multiple comparisons, $p \leq 0.002$).

Site	Primary forest	Secondary growth	Clear-cut
Caxiuanã	5.07 (2.65)^a	2.49 (1.66)^b	*
Ducke	9.85 (1.71)^a	7.03 (1.15)^a	0.41 (0.11)^b
Rondônia	36.55 (4.16)^a	19.78 (3.10)^b	0.58 (1.10)^c

Table 20.3. Dung beetle species diversity, richness and evenness in three different habitats in Palenque, Mexico. (Adapted from Halffter *et al.* 1992).

	Forest	Edge	Clear-cut
Species diversity	2.5	2.12	1.01
Species richness	27	11	5
Evenness	0.76	0.88	0.62

species richness as well as beetle biomass in comparison to communities from forested sites (Fig. 20.5).

Hanski *et al.* (2007) described how relatively low annual deforestation rates (1.4-2.0%) since 1953 led to the extinction of 43% of endemic forest-dwelling dung beetle species of the Oniticellinini subtribe Helictopleurina in Madagascar.

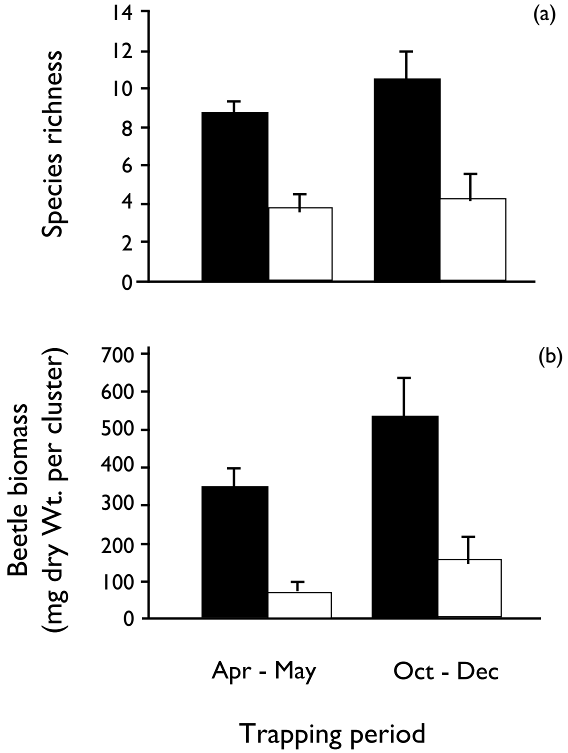

Fig. 20.5. Mean species richness (a) and mean total beetle biomass (b) with 1 SE (bars) per trap cluster at forested sites (solid bars) and deforested sites (open bars) near San Ramón, Peru during two rainy seasons (Apr–May) and (Oct–Dec) in 2002. (Adapted from Horgan 2006).

Similarly, a study examining dung beetle communities in a forest archipelago in French Guiana found that species diversity, composition and abundance of dung beetles was positively related to the size of forest fragments (Feer and Hingrat 2005). The archipelago in this study was created by flooding a rainforest and then investigating the impact of forest fragmentation on tropical invertebrates in a "true" island system. The authors found that islands had less diverse and less abundant coprophagous beetle communities than the mainland forest, and the smallest island harboured the community with the lowest diversity and evenness (Table 20.4). Besides area-effects, Feer and Hingrat (2005) attributed the reduced dung beetle species richness and densities on islands mainly to deleterious edge effects and collapsed populations of howler monkeys. Edge habitat is characterized by lower humidity and higher temperatures and is thus generally less favourable to the development and survival of invertebrates (Ehrlich *et al*. 1980). Estrada *et al*. (1998) likewise recorded that edge effects were responsible for a 57% reduction in species richness in dung and carrion beetles in forest fragments in Mexico. Another limiting factor for dung beetles is food resource (Heinrich and Bartholomew 1979; Peck and Forsyth 1982). In many Neotropical forests, howler monkeys are among the most important dung sources for dung beetles (Estrada *et al*. 1999, Gill 1991, Howden and Young 1981, Peck and Forsyth

Table 20.4. Features of the study sites and dung beetle communities at a French Guianan forest archipelago, Saint Eugene. For the three mainland and seven island study sites the total area, the distance to mainland and the number of mammal species are given. The features of the dung beetle communities at each study site are observed species richness, true species richness as measured by the incidence-based coverage estimator (ICE) in the EstimateS software package (Colwell 1997), species diversity as calculated with the *H’* Shannon-Wiener index (Lloyd *et al*. 1968), species evenness as calculated with Piélou's *J’* (Piélou 1975) and abunbance. (Adapted from Feer and Hingrat 2005).

	Mainland sites			**Island sites**						
	TF1	**TF2**	**TF3**	**2**	**103**	**15**	**13**	**16**	**9**	**102**
Study site										
Area (ha)	1500	1500	1500	38.3	25.5	8.0	4.5	3.9	1.4	1.1
Distance (m)	0	0	0	410	30	20	90	120	100	150
Mammal species	16	16	16	13	9	4	5	3	4	3
Scarab sample										
Observed species	32	34	28	24	30	31	22	22	11	15
ICE	34.2	42.9	36.7	28.7	36.3	36.4	28.8	28.1	20.3	21.4
Diversity *H’*	3.86	3.76	2.70	3.63	3.93	4.06	2.95	2.71	2.51	2.18
Evenness *J’* (%)	77.3	74.0	56.2	78.2	80.2	81.9	65.3	60.9	72.7	55.9
Abundance	651	648	644	400	335	363	469	361	57	480

1982). And Dadda *et al.* (1998) demonstrated in Mexican forest fragments that the volume of available howler monkey dung has a stronger influence on the dung beetle communities than fragment area. Earlier, Estrada *et al.* (1993) had shown that 16 species of dung beetles displayed a strong affinity for the droppings of howler monkeys. And Estrada *et al.* (1999) and Estrada and Coates-Estrada (2002) found that the fragmentation of tropical rain forests in Mexico led to the disappearance of howler monkeys and consequently dung beetles who utilize the droppings of these monkeys (Estrada and Estrada-Coates 1991).

In their long-term monitoring of the Los Tuxtlas fragmented landscape in Mexico, Estrada *et al.* (1998) initially inferred that a rich pool of forest dung beetle species would still exist in the forest fragments, and that, contrary to Feer and Hingrat's (2005) findings, isolating distance negatively affected dung beetle species richness of fragments.

However, Estrada and Coates-Estrada (2002) reported that forest fragments at Los Tuxtlas were indeed less diverse than continuous forest, a finding similar to that by Klein (1989). The least diverse habitat at Los Tuxtlas was shown to be cattle pastures (Estrada *et al.* 1998; Fig. 20.6). It had been suggested before that the conversion of wet tropical forest into pastures significantly decreases the number

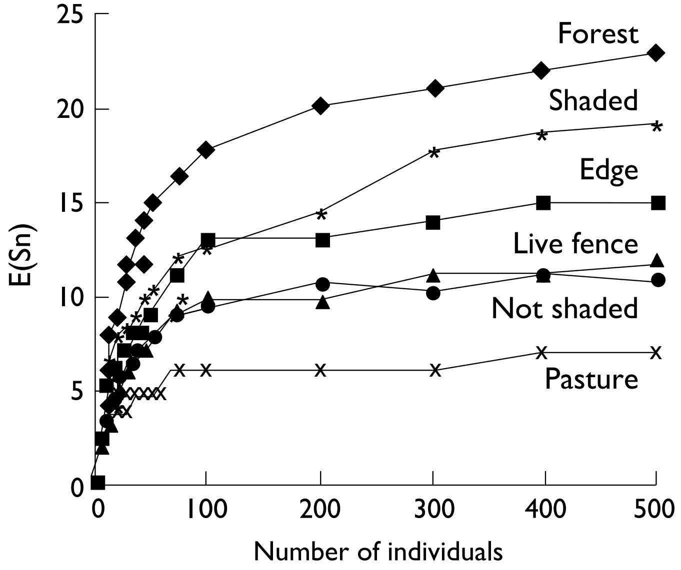

Fig. 20.6. Rarefaction curves of six different habitats at Los Tuxtlas, Mexico, where E(Sn) is the expected number of dung beetle species in a random sample of size n and S is the sum of the probabilities that each species will be included in the sample. Comparisons made at N=500 clearly show that forest habitat harbours the most speciose dung beetle community and pastures the least speciose. (After Estrada *et al.* 1998).

of carrion and dung beetle species (Howden and Nealis 1975; Klein 1989; Montes de Oca and Halffter 1995). A striking feature of the dung beetle community changes involved is the replacement of a rich native species assemblage by a few introduced dung beetle species. Montes de Oca and Halffter (1995) reported the swift southward range expansion of the African savanna specialist *Digitonthophagus gazella* as a consequence of large extensions of rain forest being converted into pastures. This species was originally imported from Africa into the USA and is since expanding its range into Meso- and South America (see Chapter 1.2).

Horgan (2007) examined the effect of the expansion of cattle pastures through Central America and found a regional decline of the native dung beetle diversity along with a proliferation of synanthropogenic species, among these also *D. gazella*. He also compared community composition of dung beetles in pastures and in native forest fragments in El Salvador and Nicaragua and found that the communities in pastures were characterised by significantly reduced species richness in both regions (Fig. 20.7). Moreover, while the dung beetle

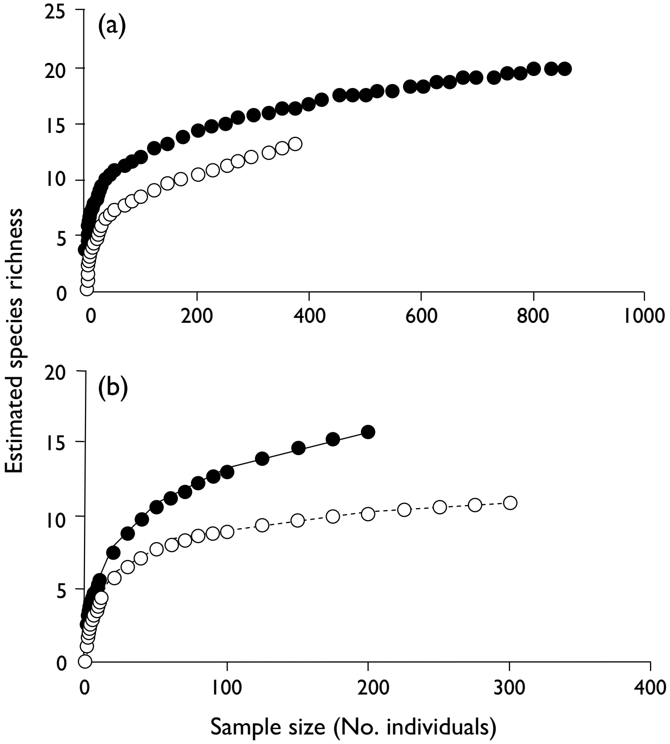

Fig. 20.7. Rarefraction curves for two different habitats in (a) El Salvador and (b) Nicaragua. Forest sites are represented by solid circles, pasture sites by open circles. (Adapted from Horgan 2007).

communities sampled in the forests differed strongly between El Salvador and Nicaragua, the composition and structure of the communities from cattle pastures were not only surprisingly species poor but also largely the same in both countries. Furthermore, the latter even resembled the communities from pastures in Mexico (Horgan 2007). This demonstrates that the conversion of original rain forest into pastures not only leads to severely reduced species richness, but also to homogenization of once regionally different dung beetle communities which represent another aspect of biodiversity loss.

Seeing that the principal cause of deforestation in Latin America is the clearing of native vegetation in order to create cattle pastures (Geist and Lambin 2002, Rudel and Roper 1997), the accompanying decline of the native dung beetle fauna and replacement by an impoverished synanthropogenic community (see also Horgan 2001, 2002) in this region takes on alarming dimensions. Horgan (2007) proposed that forest fragments of reasonable size be maintained in the pasture landscape. As long as these fragments are large enough to support diverse mammal and bird communities, native dung beetle diversity could possibly be preserved.

In tropical rainforest in Malaysian Borneo, Davis and Sutton (1998) caught significantly more arboreal dung beetles on the ground in logged forests and plantations than in primary forests, where this guild is strictly arboreal. It is unknown which effects to the ecosystem this change in vertical distribution may imply. Moreover, the post-logging plantations in Borneo have a much lower species richness (with a total absence of interior-forest specialists) and diversity of dung beetles than the original rain forest (Davis *et al.* 2000; Davis *et al.* 2001).

Rapid human-induced habitat transformation and recent land-use changes are also threatening the European dung beetle fauna (Martin-Piera 2001). Coastal dung beetle assemblages in the French Camargue have dramatically decreased in species richness, probably due to habitat loss in combination with insecticide use (Lobo *et al.* 2001).

But ironically, in some parts of Europe it seems to be the progressive reforestation of previously pastured areas that poses the highest threat to dung beetle communities (Barbero *et al.* 1999).

In Mediterranean Europe, many of the native dung beetle communities occur on pasturelands, where they are vital to maintaining pasture quality and livestock health, especially in low-intensity traditional grazing systems (Martin-Piera and Lobo 1995). Domestic livestock such as sheep and cattle are disappearing as more and more agricultural landscapes are highly mechanized, as monocultures are spreading, and as large areas of formerly grazed land are urbanized (Lobo 2001) or are being reverted to forests (Barbero *et al.* 1999; DiCocco 1988).

As a consequence, in northern Italy three *Gymnopleurus* species and at least one *Scarabaeus* species (all of which were common 100 years ago) have progressively decreased in numbers to virtual extinction (Barbero *et al.* 1999). A study by Carpaneto *et al.* (2005) documented the changes in a dung beetle assemblage as a result of a change in land use in Rome (Italy). The Urban Regional Park of Pineto, an area within the city limits of Rome, was intensely grazed by sheep until 1989. Then it was converted into a public recreational area and grazing was suspended entirely. With the disappearance of livestock, scats of domestic and feral dogs became the only food source for the dung beetle community in this area. Carpaneto *et al.* (2005) sampled the dung beetle assemblage 10 years after the conversion of the area into a recreational park and compared it to a dung beetle survey made for the same area before the conversion in land use. The result was that with the switch from sheep to dog dung, the total dung beetle species richness dropped from 19 to 9 species, with a seven-fold increase in total abundance but a decrease in diversity. This result is not too surprising seeing that Palaearctic dung beetles do not easily colonize carnivore dung (Barbero *et al.* 1999; Halffter and Matthews 1966; Martin-Piera and Lobo 1996).

In France, several species of dung beetles disappeared after 1950, probably also because of the decline of low-intensity pastoral systems (Lumaret 1990). Also in Finland, Biström *et al.* (1991) attributed the decline of several vulnerable dung beetle species to the changes in traditional husbandry.

Modern livestock farming in Europe is characterized by a massive use of anti-parasiticides and veterinary pharmaceuticals (Lumaret 1986; Lumaret *et al.* 1993). In Ireland, Hutton and Giller (2003) demonstrated that organic farms where no fertilizers or parasiticides were used, exhibited significantly greater dung beetle diversity, species richness, and biomass than intensive and rough grazing farms. The authors explained this further by the fact that organic farms usually consisted of patchy ecosystems characterized by a diversity of ungulate species which would increase dung beetle diversity and hence improve dung decomposition.

All the above mentioned factors are harmful to dung beetles. The abandoning of traditional herding management endangers the preservation of European grasslands and together with the mentioned factors leads to increasing loss of suitable habitat for dung beetles (Martin-Piera 2001). It comes as no surprise then that Verdu *et al.* (2000) proposed to reintroduce traditional grazing of livestock in Mediterranean ecosystems as a conservation management tool.

In an effort to identify priority areas for dung beetle conservation in Spain, Martin-Piera (2001) found the highest dung beetle species richness and phylogenetic diversity (Faith 1995) in the Guadarrama Mountains. Using a priority-area analysis with grid cells of 50 x 50 km, Martin-Piera (2001) suggested that with the protection of just six grid cells it would be possible to conserve the entire Iberian dung beetle fauna. However, he stressed that this priority area would not be sufficient, but rather represented the necessary nucleus of a potential network of nature reserves in which traditional herding management should be applied in order to secure the safe persistence of Iberian dung beetle populations (Araujo and Williams 2000; Martin-Piera 2001).

Jankielsohn *et al.* (2001) conducted a study in the north-western Free State Province of South Africa investigating the effect of habitat transformation from natural bushveld into cattle farms on dung beetle assemblages. To this end the authors compared dung beetle communities from two nature reserves and from two neighbouring cattle farms. Moreover, they also surveyed for differences between two different habitat types: grassveld and bushveld (savanna). They found that while larger dung beetles belonging to functional groups I and II (Doube 1990) preferred grassveld over bushveld, they also occurred in higher abundances in the natural habitats than in the disturbed habitats (Fig 20.8). Moreover, while biomass of the sampled dung beetles was higher in the grass-

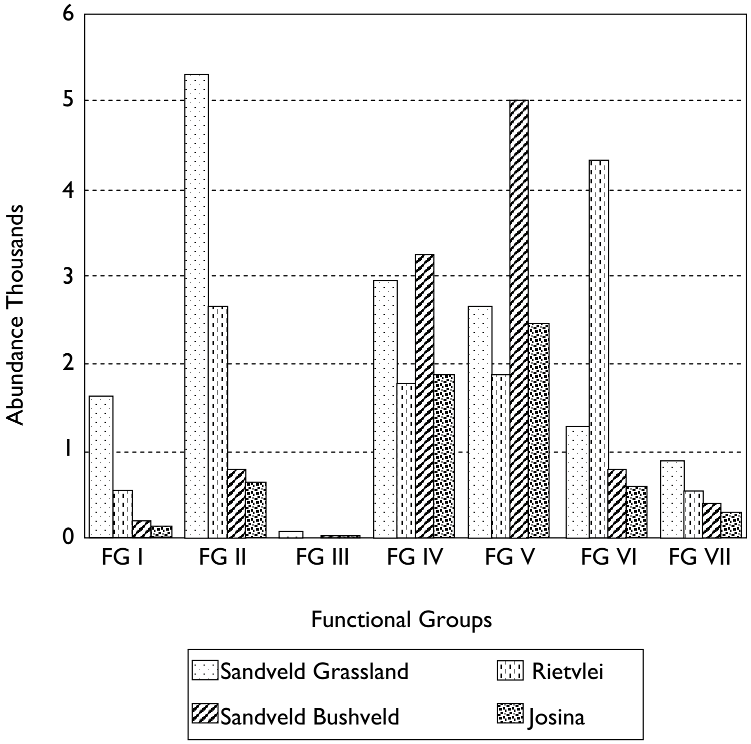

Fig. 20.8. Distribution of seven different functional groups of dung beetles recorded in four different habitats in South Africa: two natural habitats (Sandveld Grassveld and Sandveld Bushveld, both in the the Sandveld Nature Reserve) compared to two disturbed equivalent habitats (Rietvlei = a farmland grassland, and Josina = a farmland bushveld). (Adapted from Jankielsohn *et al.* 2001).

veld than in the bushveld, biomass was always clearly elevated in the natural habitats compared to the disturbed habitats (Fig. 20.9). As an explanation for their findings, Jankielsohn *et al.* (2001) proposed that trampling and overgrazing by cattle on the disturbed habitats had led to a change in the vegetational ground cover and thus made it more difficult for the larger dung beetle species to still be successful competitors.

Through the reduced height and density of the vegetation on cattle farms there will be shifts in the relative humidity and micro-environment, factors so important for dung beetles. More sensitive species (such as the larger species) will be affected more negatively and the structure of the dung beetle community will shift. This decline of larger dung beetle species will also reduce the rate of dung decomposition and therefore have cascading consequences for the entire ecosystem (Jankielsohn *et al.* 2001).

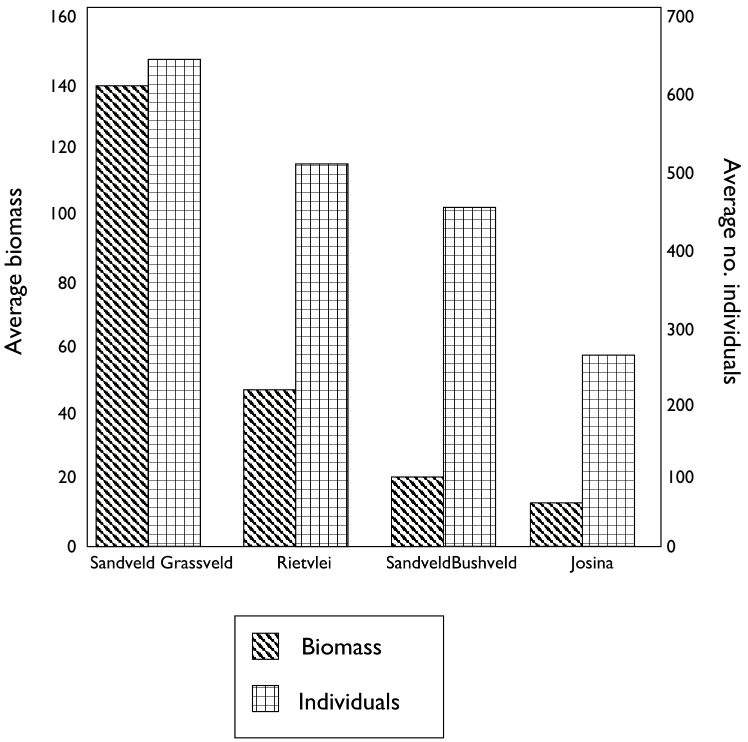

Fig. 20.9. Dung beetle abundance and biomass in four different South African habitats: two natural habitats (Sandveld Grassveld and Sandveld Bushveld, both in the Sandveld Nature Reserve) and two disturbed equivalent habitats (Rietvlei = a farmland grassland, and Josina = a farmland bushveld). Values based on a 2-year average (06/1996 – 06/1998). (Adapted from Jankielsohn *et al.* 2001).

Another study from South Africa (Botes *et al.* 2006) investigated and compared the impact of elephants (*Loxodonta africana*) and of humans on dung beetle assemblages in the Maputaland Centre of Endemism, an important centre of plant endemism and diversity in southern Africa. A special type of dry tropical forest, the Sand Forest, which occurs only in Mozambique and South Africa, is the most endangered habitat within the Maputaland Centre of Endemism (Matthews *et al.* 2001; van Rensburg *et al.* 2000; van Wyk 1996; van Wyk and Smith 2001). Sand Forest is a very old habitat type and harbours many endemic and rare species. Despite the relative dung beetle species poverty of the Sand Forest, it provides prime habitat for species endemic to the east coast of southern Africa such as *Proagoderus aciculatus* and an undescribed *Sisyphus* sp. and for shade specialists such as *Onthophagus lacustris*.

Rapid changes in land use threaten Sand Forest: local use of fuel wood, extensive commercial afforestation, and clearing for agriculture and housing (van Wyk and Smith 2001). Even within the conservation area of the Tembe Elephant Park (KwaZulu Natal, South Africa), the Sand Forest is threatened by over-utilization through elephants (Matthews *et al.* 2001; van Rensburg *et al.* 1999). It is of considerable conservation concern to preserve the remaining undisturbed Sand Forest patches and the associated fauna including the functionally important dung beetle fauna, especially since a post-disturbance recovery of this special and old habitat type has never been observed (van Rensburg *et al.* 1999). Instead, it had been warned that further disturbance by human clearing or elephant browsing would lead to an opening of the Sand Forest canopy and the associated dung beetle assemblages would change to resemble those of the Mixed Woodland assemblage (Botes *et al.* 2006). As a result of their survey, Botes *et al.* (2006) found lower dung beetle abundance and marked reduction in species richness in the human-disturbed Sand Forest than in the undisturbed equivalent. On the other hand, the elephant-disturbed Sand Forest revealed similar species richness to the undisturbed Sand Forest (and shared a higher number of species with it) but also to the interspersed patches of Mixed Woodland (Fig. 20.10). The authors emphasized that ongoing browsing pressure by elephants would eventually result in increased homogenization of the Sand Forest / Mixed Woodland assemblages and thus be equivalent to a loss in diversity (especially a loss of the shade specialists). Botes *et al.* (2006) attributed the human- and elephant-induced changes to the dung beetle assemblages to modifications in the quality and distribution of dung as well as to alterations in the habitat structure.

It has been discussed that in the face of continued habitat loss and fragmentation due to human exploitation, it will be important to consolidate and expand habitat fragments and restore degraded patches where possible (Young 2000). In this context, Davis *et al.* (2003) studied the changes in the

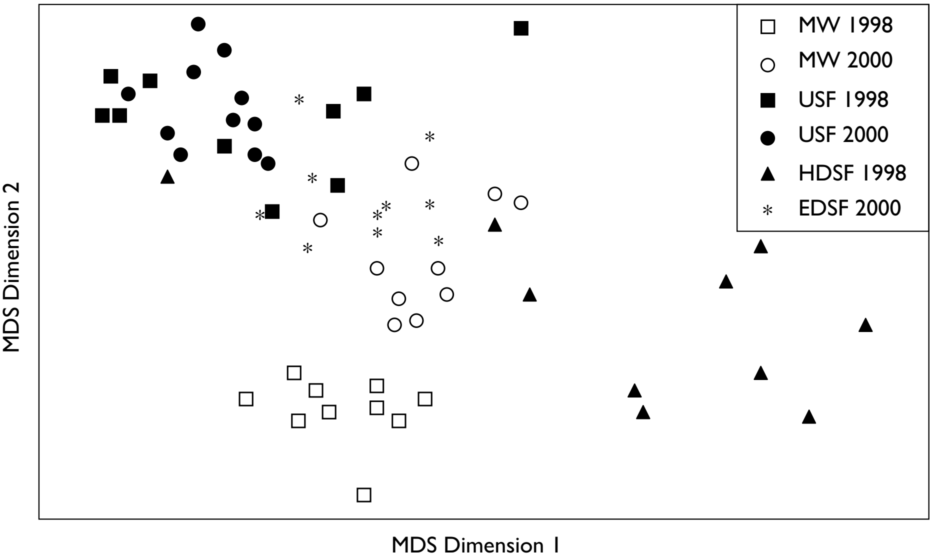

Fig. 20.10. Non-metric MDS ordination of dung beetle abundance and species richness in four different South African habitats (stress value 0.13). MW = Mixed Woodland, USF = undisturbed Sand Forest, HDSF = human-disturbed Sand Forest, EDSF = elephant-disturbed Sand Forest. (Adapted from Botes *et al.* 2006).

composition of the dung beetle fauna in post-mining dunes along the Indian Ocean coastline at the southern end of the Maputaland Centre of Endemism in South Africa. Since the late 1970s, titanium-bearing mineral sands have been dredge-mined in the coastal dunes around Richards Bay in Maputaland. Before the mining of an area commenced, the entire dune vegetation was cleared; after the mining had been concluded, one-third of the mined area was supposed to be rehabilitated with indigenous vegetation (van Aarde *et al.* 1996b). With the proceeding 14-year chronosequence of regeneration, the dune vegetation and associated fauna were characterized by a high species turnover and an increasing diversity and species richness and decreasing species-specific abundances (Ferreira and van Aarde 1997; Majer and de Kock 1992; van Aarde *et al.* 1996a,b; van Dyk 1997). But Mentis and Ellery (1998) cautioned that the full restoration of the dune forest would require many more years. Within this context, Davis at al. (2003) assessed progress towards full restoration of biota after 23 years post-mining succession using dung beetles as bio-indicators. The authors analyzed the following successional stages of the restoration of the dune forest: grassland, open *Acacia* shrubland thicket, and woodland dominated by *Acacia karroo*. They investigated the dung beetle assemblages across the chronosequence of restoration and evaluated whether these were converging toward assemblages in unmined natural forest. The results indicated a sequential trend towards a convergence of the composition of dung beetle species regarding the entire species complement, but especially in shade specialists (Fig. 20.11). However, species abundance only converged in the early chronosequence towards *Acacia* woodland (up to 12 years post-mining), and then diverged between the older *Acacia* woodland and unmined natural forest (Fig. 20.12). Since the distribution of dung beetles is generally closely linked to the physiognomy of the vegetation (Cambefort 1982; Davis 1996; Doube 1983), the similarity of the dung beetle fauna in the post-mining regenerating habitat and natural dune forest was tightly linked to the changes in vegetation and microclimate across the chronosequence (Davis *et al.* 2003). The authors concluded that a lasting convergence in the abundance of dung beetle species could only be attained once secondary natural forest replaces the *Acacia* woodland.

In Korea, there have also been reports about a general reduction in dung beetle diversity and abundance (Bang *et al.* 2001). These changes in dung beetle

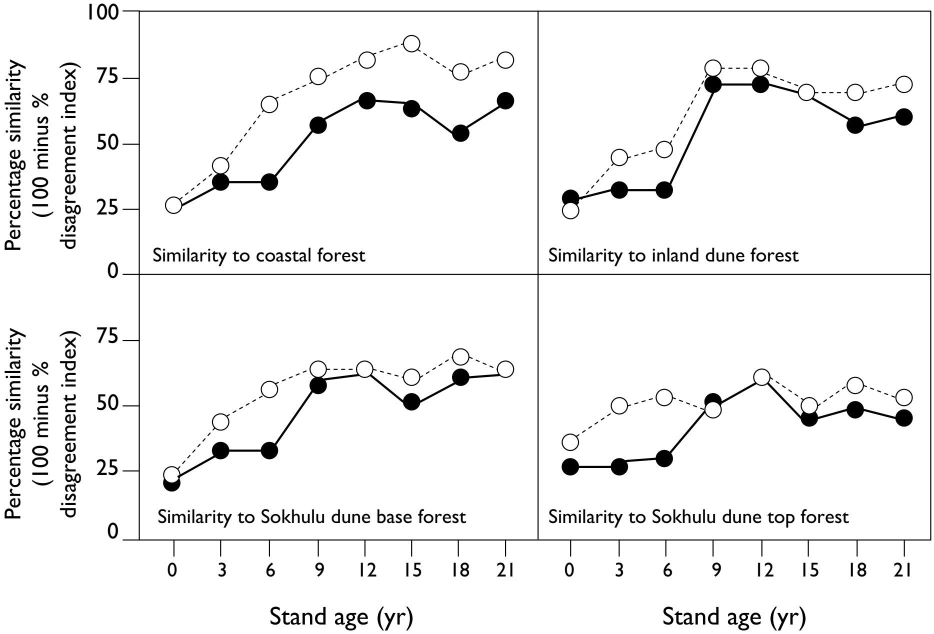

Fig. 20.11. Comparative temporal patterns of similarity of dung beetle composition between natural forest and regenerating stands of vegetation. Open circles = all dung beetle species, closed circles = shade specialists. (After Davis *et al.* 2002b).

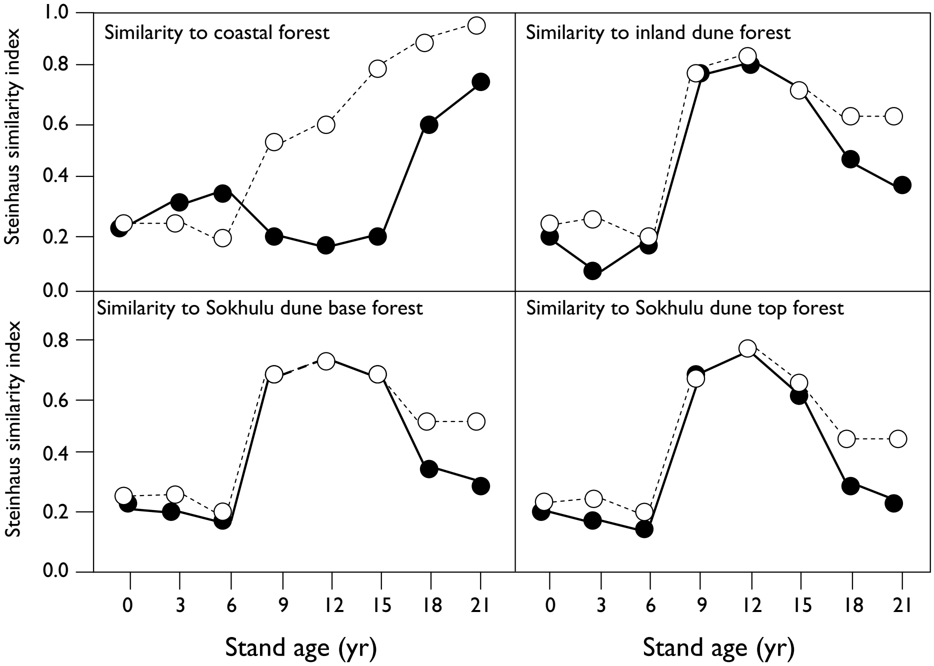

Fig. 20.12. Comparative temporal patterns of similarity of dung beetle composition between natural forest and regenerating stands of vegetation. Closed circles = all dung beetle species, open circles = species endemic to Maputaland and the South African east coast. (After Davis *et al.* 2003).

communities were attributed to changes in pasture and livestock management over the last 30 years; among these the widespread use of veterinary pharmaceuticals and insecticides (Bang *et al.* 2005).

20.2.2 Conservation value of secondary forest

Nichols *et al.* (2007) conducted a meta-analysis (based on 33 original studies) of the consequences of landscape change and fragmentation in tropical forests and the effects on dung beetles. They categorized several types of forest habitat modification along an approximate disturbance gradient: intact tropical forest, selectively logged forest, late and early secondary forest, agro-forestry, tree plantation, annually-cropped fields, cattle pasture, and clear-cuts. The dung beetle communities from the forest fragments were almost always characterized by reduced abundance, richness, and evenness compared to the communities from continuous intact forest (Fig. 20.13). Generally, dung beetle abundance declined with increasing habitat modification but was associated with a high variance. Dung beetle communities in heavily modified habitats were found to be species-poor with high rates of turn-over, dramatically changed abundances and smaller body-size (Nichols *et al.* 2007). In some included studies, dung beetle abundance increased as a consequence of severe habitat modification (e.g. cattle farms); in most of

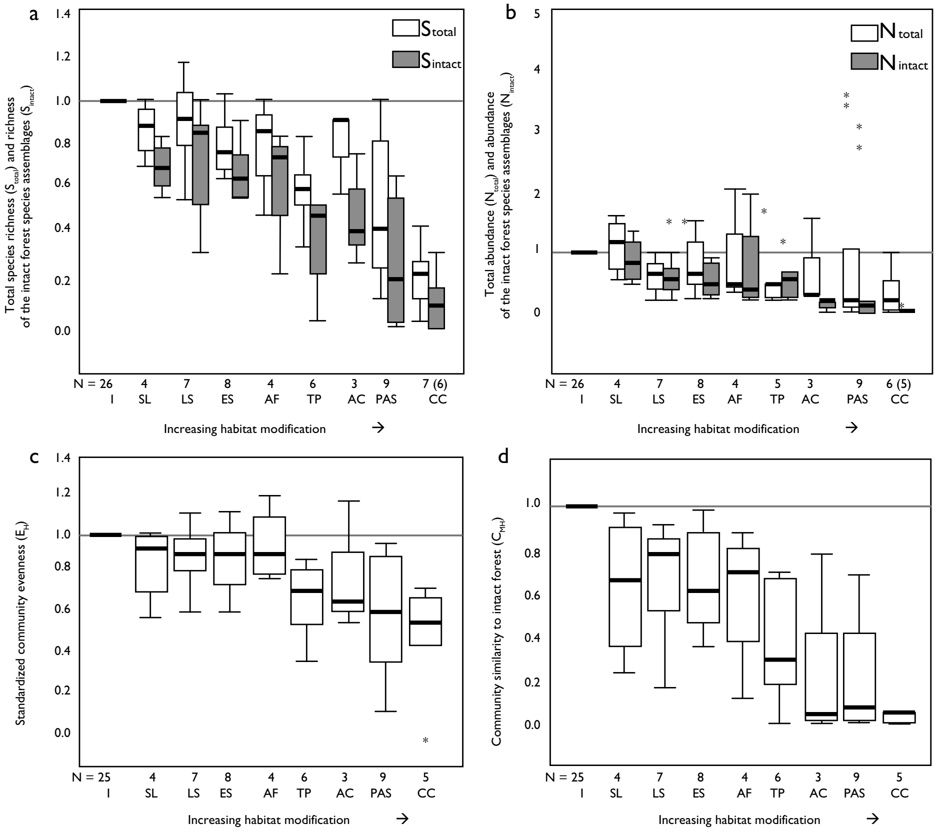

Fig. 20.13. Impact of habitat modification on standardized parameters in tropical forest dung beetle communities. S_{total} = total species richness, S_{intact} = proportion of species recorded in a given habitat that were also recorded in intact forest, N_{total} = total dung beetle abundance, N_{intact} = abundance of those dung beetle species that were also recorded in intact forest, E_H = Shannon evenness index, C_{MH} = Morisita Horn Index of community similarity, relative to intact forest. Habitat abbreviations are: selectively logged forest (SL), late secondary forest (LS), early secondary forest (ES), agroforests (AF), tree plantations (TP), annually cropped fields (AC), cattle pastures (PAS) and clear-cuts (CC). (Adapted from Nichols *et al.* 2007).

these cases Scarabaeinae communities were characterized by a hyper-abundance of a small number of small-bodied species belonging to the genera *Trichillum* (Scheffler 2005) and *Tiniocellus* (Davis and Philips 2005). Andresen (2003) and Larsen *et al.* (2005) have shown that these smaller species bury disproportionately less dung and secondarily disperse less and smaller plant seeds than large-bodied species; thus even a hyper-abundance of these small-bodied species is unlikely to translate into elevated functional capacity (Nichols *et al.* 2007).

Not surprisingly, total species richness was highest in intact forests and lowest in clear-cuts (averaging less than 25% of the species richness found in intact forests). However, in selectively logged forests and in secondary forests, their meta-analysis did not retrieve any significant differences in species richness compared to intact forests. They concluded that agriculture and clear-felling significantly reduced dung beetle diversity, while secondary forests (and other land uses maintaining high vegetation complexity and tree cover) harboured dung beetle communities with similar species richness to intact primary forests. In support of this, Quintero and Roslin (2005) suggested that dung beetle communities in Central Amazonia recovered rapidly after fragmentation (see Klein 1989) due to regrowth of secondary vegetation between forest fragments. This may suggest that secondary forests may have some conservation value (see also Dunn 2004b), which would be encouraging; seeing that secondary and plantation forests rapidly expand across the tropics (Wright 2005, FAO 2006a).

However, there is increasing concern about the continued loss of primary forest, because new evidence showed that re-forested areas such as secondary forest or plantation forest actually only provide low conservation benefits for dung beetles. While these habitats were formerly regarded as "conservation friendly", Gardener *et al.* (2008a) showed that they harbour exceptionally impoverished dung beetle communities suffering from depleted beetle abundances, reduced average body mass and local extinctions of especially larger bodied species. Gardener *et al.* (2008b) mentioned as possible explanations for the contrast to the results by Nichols *et al.* (2007) habitat differences between the studies. It has been noted before, that geographic location and landscape context influence the pool of available colonists and consequently modify the response of dung beetle communities to disturbances (Nichols *et al.* 2007). Escobar *et al.* (2007) also emphasized that the impact of human-induced habitat loss on dung beetle communities depends strongly on the geographical position, the biogeographic history, and the evolutionary restrictions (such as habitat specialization) of the species assemblage, and therefore, study results cannot be extrapolated or compared beyond their regional context.

Another reason for a too optimistic outcome of the meta-analysis by Nichols *et al.* (2007) could be that many of the relatively small number of studies analyzed were confounded by methodological problems and mostly failed to evaluate patterns of biomass as an important detail of dung beetle community response. Saint-Germain *et al.* (2007) showed that species abundance and biomass in arthropod community data are independent of each other; therefore ecological interpretations of analyses based on biomass or abundance data alone may result in conflicting results. It had been shown earlier that dung beetle biomass and abundance can respond very differently to habitat disturbances and that adverse effects of habitat modification are probably more clearly reflected by changes in biomass (Scheffler 2005; Vulinec 2002).

Gardener *et al.* (2008b) cautioned strongly against optimistically assuming that the loss of dung beetle species following primary forest degradation could be offset effectively by forest regeneration schemes. They emphasized the importance of protecting the remaining areas of primary forest.

There are further concerns that the existing conservation area networks are not sufficient to conserve dung beetle biodiversity (Nichols *et al.* 2008). Even in Costa Rica, a country with continued and strong conservation efforts, dung beetle records from La Selva Biological Station have shown that over the last 35 years community changes are characterized by an overall loss of dung beetle species, probably due to isolating effects of intensified agriculture in the region. While more than 23% of Costa Rica's land surface is protected as conservation area, this network of fragments comprises less than 13% of the areas with the highest dung beetle species richness and endemism in Costa Rica (Kohlmann *et al.* 2007).

20.2.3 Why hunting mammals is bad for dung beetles

Obviously, altered temperature, humidity, or soil characteristics as a consequence of habitat disturbance may directly impact on dung beetle species (Vulinec 2000). There are some irreversible forms of intensive land alterations in tropical areas, such as bulldozing (Buschbacher *et al.* 1992), which will also adversely affect dung beetles directly. Besides, there are indirect effects on dung beetles resulting from anthropogenic interference. Two synonyms often used are cascading effects or higher-order effects, referring to the steps of consequential effects cascading through larger communities causing unanticipated changes at lower and higher trophic levels (Koh *et al.* 2004; Letorneau *et al.* 2004; Redford 1992; Terborgh *et al.* 2006; Wright 2003).

After habitat destruction, hunting is considered the second greatest threat for numerous tropical mammals (Milner-Gulland and Bennett 2003; Redford 1992). In fact, Redford (1992) and Redford and Feisinger (2003) described "empty/half-empty forest" scenarios resulting from severe hunting pressures.

With proceeding fragmentation of tropical forests, hunters gain ever increasing access into formerly inaccessible areas. This situation is especially serious in Afrotropical forests where logging creates many new pathways into the bush and logging companies and their workers create a growing market for bushmeat. Large-bodied frugivorous primates and ungulates are preferentially hunted by rural hunters and already massive declines in abundance of large-bodied game species have been documented for forests in Africa (Fa *et al.* 2006), South-East Asia (Corlett 2007), and Amazonia (Peres 2000; Peres and Palacios 2007). The cascading effects of mammal hunting are known to be diverse (Wright 2003). Certainly, downstream effects of mammal declines on dung beetle communities are to be expected, seeing that these coprophagous taxa depend on mammal dung (Andresen and Laurance 2007).

Cambefort (1991c) detected a decline in overall dung beetle species richness (accompanied by an increase in abundance) along a gradient of large mammal persecution in tropical African savannas. Hanski and Cambefort (1991) recorded a dramatic effect of elephant hunting on west and southern African dung beetle communities. Some of the large-bodied species of the dung beetle genus *Heliocopris* are specialized on elephant dung. According to Cambefort (1982) they are rarely found in nature reserves where elephants were hunted to local extinction (for instance in parts of West Africa) but are still abundant in regions where historically high elephant numbers were retained (for instance in the Kruger National Park in South Africa).

Estrada *et al.* (1998) and Feer and Hingrat (2005) discovered a positive correlation between mammal abundance and species richness and abundance and species richness of dung beetles in continuous and fragmented forests in Mexico and in French Guiana, respectively. Numerous studies on forest fragmentation attribute a declining dung beetle fauna to a depauperate mammal community (Andresen 2003; Estrada *et al.* 1998; Estrada and Coates-Estrada 2002; Feer and Hingrat 2005; Klein 1989; Vulinec 2000).

In an investigation in the tropical rain forest in central Panama, Andresen and Laurant (2007) observed a decline in dung beetle abundances and diversities as well as altered community composition across a gradient of decreasing mammal abundance due to heavy hunting pressure (Fig 20.14). The changes in dung beetle communities were probably caused by alterations in availability and composition of mammal dung resources. Because of the functional importance of dung beetles for ecosystems, disassemblies of dung beetle communities will have serious negative consequences for the maintenance of key ecological processes. The impairment of these crucial ecosystem functions can thus precipitate an extinction cascade (Nichols *et al.* 2009). In a conceptual model, Nichols *et al.* (2009) illustrated the pathways along which overhunting of mammals in tropi-

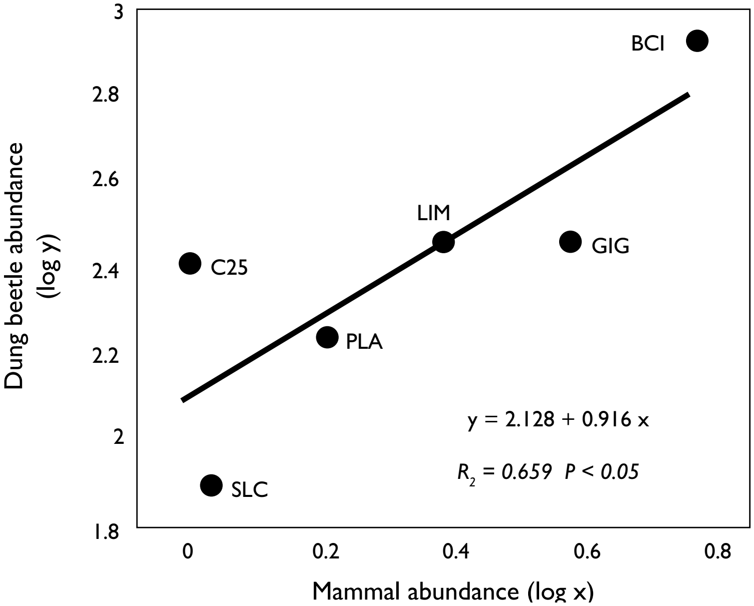

Fig. 20.14. Data from six rain forest sites in Panama, the relationship between mammal abundance and the log total dung beetle abundance is positive and significant. (After Andresen and Laurance 2007).

cal forests impairs coprophagous beetle communities and the associated ecosystem functions (Fig. 20.15). Overhunting leads to an altered composition of the mammal community, with decline and eventually extinction of large, frugivorous mammals. As a consequence, the dung profile available to coprophagous beetles changes, including dung diversity as well as dung availability effects. This, in turn, alters the composition of dung beetle communities (especially inducing a decline of large-bodied beetles and some feeding specialists) with direct functional consequences to the ecosystem. There will probably be a decrease in removal volume and rate of dung, a reduced rate of secondary seed dispersal with decreased buried seed size and shallower burial depth, thus impacting on the regeneration of the flora. Also bioturbation and nutrient recycling will be diminished, reducing the primary productivity of the entire system and making it more vulnerable to flooding and droughts. Through the reduced rate of waste removal in the system there will also be effects on parasite and pest fly suppression, which may be exacerbated by the fact that with lower dung beetle diversity and abundance fewer phoretic predatory mites will be transported to fresh dung deposits. Finally, with decreased dung beetle diversity and abundance there will also be an impact on those animals that prey on dung beetles.

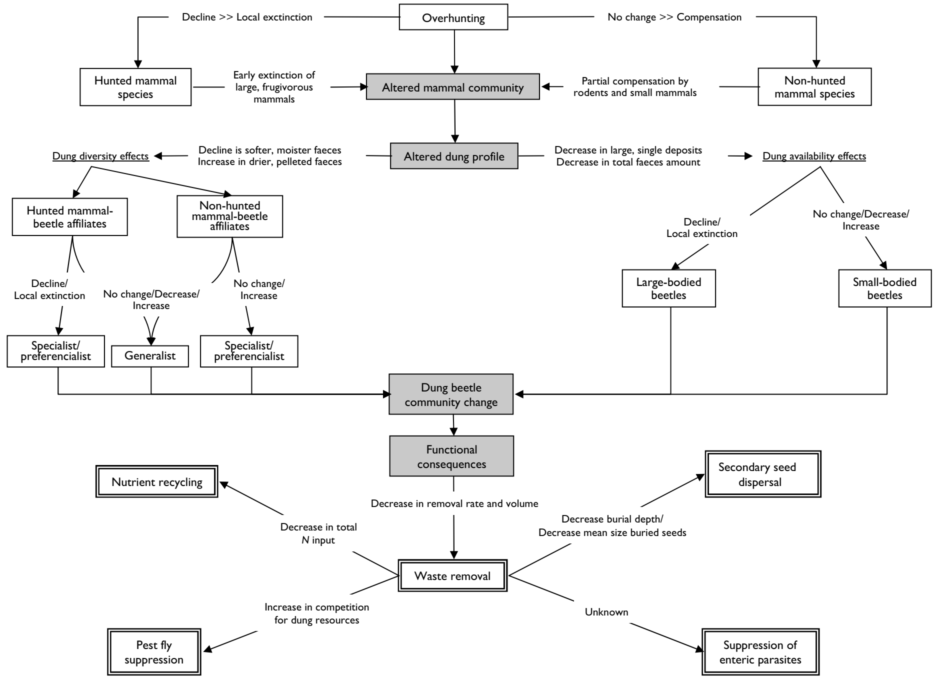

Fig. 20.15. Conceptual diagram showing the possible impact of overhunting mammals in tropical forests on dung beetles and dung beetle mediated ecological function. (Adapted from Nichols *et al.* 2009).

20.2.4 Scales of impact and conservation

While conservation is generally directed towards saving a global representation of the existing biodiversity within its natural context, it is also generally limited by a rather small pool of resources (Schwartz 1999). It is therefore critical to maximize the efficiency of protecting biological diversity. In this context of attempting to prioritize biological resources under threat, different scales for conservation have been discussed and emphasized by different scientists. These different scales reach from genes to species and habitats to landscapes. Schwartz (1999) coined two terms distinguishing "fine-filter" conservation (targeted at genes, populations, or single species) from "coarse-filter" conservation (directed at communities, ecosystems, or landscapes). He criticized the tendency in late 20th century conservation practice to focus on the "coarse-filter" approach basing management policies on ecosystems. Instead, Schwartz (1999) advocated an integrated approach accommodating "fine-filter" and "coarse-filter" conservation objectives at the same time.

And indeed, while the conservation of ecological functions and processes in entire ecosystems is the meaningful underlying goal of modern conservation efforts, it also holds true that even the loss of one or two species may have a severe impact on an ecosystem and even lead to its collapse (Larsen, in Stokstad 2004). This is valid for top carnivores as much as for large dung beetles species.

In Eastern Venezuela, where 4399 square kilometers of tropical forest have been flooded by a hydroelectric dam, ecosystem integrity in many of the small, newly arisen "islands" of tropical forest is compromised due to the loss of especially the larger dung beetle species – seed burial by dung beetles has declined and thus the diversity of the forest flora (and consequently also of the dependent forest fauna) will be reduced as well (Stokstad 2004).

Bowen (1999) defended the preservation of the process of life as the overall conservation objective. However, he admitted that certain species should be conserved as entities because of their phylogenetic distinctiveness, in an effort to maintain the bioheritage of this planet. This is a similar idea to the concept of "Phylogenetic Diversity" developed by Faith (1992). Moreover, Bowen (1999) acknowledged that those species that play a crucial role in the ecological processes, upon which a high number of other species depend, should be recognized as high conservation priorities; this notion is similar to Paine's (1969) concept of a "keystone species".

So while in practice the extent of biodiversity loss is often measured in terms of species extinction rates (Luck *et al.* 2003) or ecosystem deterioration rates, the importance of conserving the finest level of diversity – the level of genes – has gained more and more attention in recent years and is now acknowledged as a fundamental concern in conservation biology (Frankham 1995, 1996, 2003; Luck *et al.* 2003; Montgomery *et al.* 2000; O'Brien 1994). The genetic variation within a wildlife population is the raw material for evolutionary processes (Frankel and Soule 1981). It will confer greater resilience to the population allowing it to respond successfully to various environmental changes including diseases, parasites, pests, predators or competitors, greenhouse warming and the like. Therefore, the World Conservation Union (IUCN) also recognized genetic diversity as one of the three levels of biological diversity that require conservation (McNeely *et al.* 1990).

20.2.5 The impact of habitat fragmentation and loss on genetic diversity

In general, habitat degradation will create new selection pressures that are often associated with increased extinction risk (Wilcove *et al.* 1998). Frequently, the fragmentation of a habitat will lead to a breaking up of a formerly larger population into a number of smaller, now isolated populations.

As a consequence of their reduced population size, these newly isolated populations have a smaller gene pool and therefore a more limited capability to respond adaptively to environmental pressures (Frankham 2003; Stockwell *et al*. 2003). Habitat fragmentation and loss can interrupt gene flow among newly separated sub-populations if the area of the dividing matrix is large enough to prevent exchange of migrants among the habitat fragments.

Especially in taxa with a low vagility (such as many dung beetle species) this can have serious consequences in terms of maintaining a healthy gene pool. Interrupted gene flow can reduce the effective genetic neighbourhood size as well as the genetic variability of progeny and thus lead to genetic drift (Didham *et al*. 1996) and the accumulation of deleterious mutations (Frankham 1995). A small population size as a result of habitat fragmentation may increase the number of matings between relatives and thus elevate the levels of inbreeding. Particularly in species that are obligately or predominantly ourcrossing this may even cause inbreeding depression (Alvarez-Buylla *et al*. 1996), which is characterized by reduced survivorship and reproduction success of the inbred individuals due to reduced heterozygosity and/or increased expression of recessive, deleterious alleles (Frankham 2003; Higgins and Lynch 2001; Tallmon *et al*. 2004). Inbreeding depression was identified as one of the chief concerns in the conservation and management of endangered species (Frankham *et al*. 2002; Hedrick and Kalinowski 2000). If a population remains small over a long period of time, deleterious alleles will accumulate and fitness will decline due to a progressive increase in this "genetic load". Eventually, this can lead to a "mutational meltdown" which in turn predisposes this population for entering an "extinction vortex" (Beebee and Rowe 2004; Frankham *et al*. 2002; Fig. 20.16).

In addition to a body of theoretical evidence for the detrimental effects of inbreeding, there is also mounting empirical evidence for various organism groups (Frankham 2003; Frankham *et al*. 2002). Crnokrak and Roff (1999) reviewed 157 data sets covering 34 different species for inbreeding depression in natural systems and found that in 90% of the cases inbred individuals showed inbreeding depression (see Table 20.5 for averaged inbreeding depression coef-

Table 20.5. Two measurements of inbreeding depression (with standard errors) for plants, poikilotherms and homeotherms. The measurements are the coefficient of inbreeding depression δ and the corrected coefficient of inbreeding depression *b*. Where $\delta = 1 - (X_I/X_0)$ with X_I = inbred trait value and X_0 = outbred trait value, and where $b_{X0} = \delta/F$ with F = inbreeding coefficient. (Adapted from Crnokrak and Roff 1999).

Species group	δ ± SE	b_{X_o} ± SE	n (δ), n (b_{X_o})
Plants	0.264 ± 0.032	0.552 ± 0.106	75, 34
Poikilotherms	0.197 ±0.028	0.661 ± 0.121	25, 23
Homeotherms	0.268 ± 0.041	0.818 ±0.472	63, 20

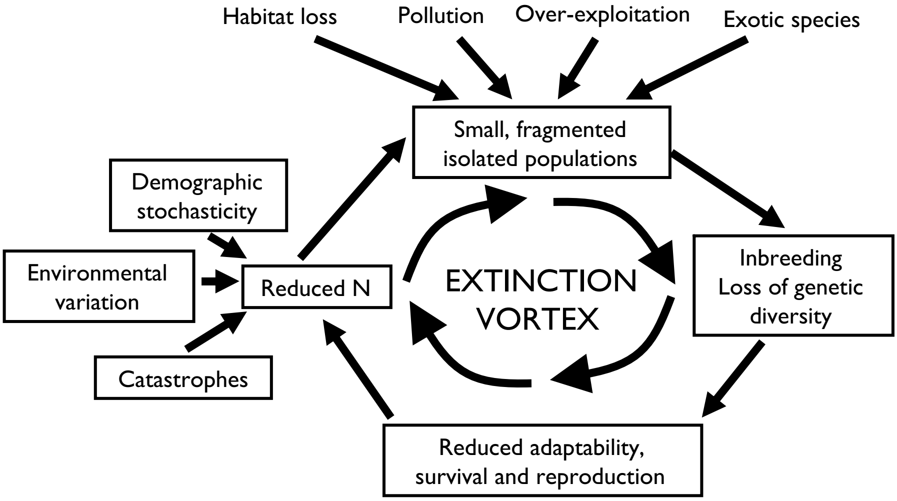

Fig. 20.16. Conceptualization of the extinction vortex illustrates how inbreeding reduces fitness and consequently leads to extinction by interacting with factors that reduce population size (N) and isolates small populations. (Adapted from Frankham *et al.* 2002).

ficients). They reported that particularly those wild populations that were small and isolated from immigration suffered from inbreeding effects and an elevated genetic load. Wright *et al.* (2008) demonstrated the reality of inbreeding depression and associated higher extinction rates in experiments with *Drosophila simulans*. Their results showed massive inbreeding depression especially with regard to life history traits such as female longevity and reproductive productivity (Fig. 20.17). Reed et al. (2003) evaluated the effect of the rate of inbreeding on the extinction risk in *Drosophila melanogaster* populations of different effective population sizes and found that smaller populations had an elevated extinction rate due to inbreeding in comparison to larger populations (Fig. 20.18). The authors explained that in larger populations the process of purging may slow the rate of extinction slightly, but it will not entirely eliminate the deleterious effects of inbreeding. Saccheri *et al.* (1998) showed that the extinction risk for butterfly populations in Finland was significantly linked to inbreeding. Within a metapopulation of the Glanville fritillary butterfly *Melitaea cinxia*, the extinction risk of local populations increased significantly with decreasing heterozygosity as retrieved with two different logistic regression models (Figure 20.19). The key fitness components negatively affected by inbreeding were egg-hatching rate, larval survival and adult longevity (Saccheri *et al.* 1998).

Besides close and persistent inbreeding and genetic drift, another problem that may arise from a small population size is the decline of genomic variation

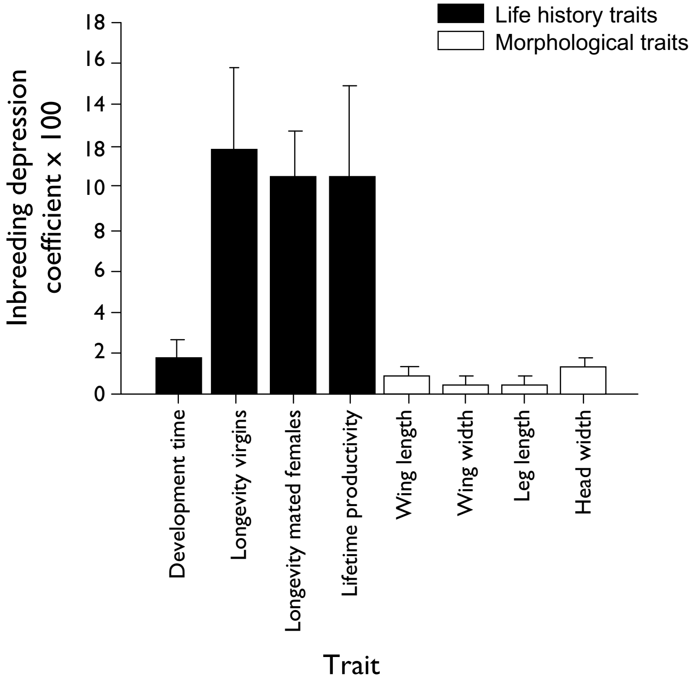

Fig. 20.17. Mean estimates (x 100 ± SE, across *Drosophila simulans* populations) of inbreeding depression coefficient for morphological and life history traits. (Adapted from Wright *et al.* 2008).

resulting from allelic loss (O'Brien 1994). Genetic variability is crucial for the long-term viability of a population, enabling it to respond adaptively to changing environmental conditions (Meffe and Carroll 1997). Habitat fragmentation has the potential to reduce genetic variation for neutral alleles as well as for traits related to fitness (Debinski and Holt 2000). Especially in small populations on small isolated habitat fragments the long-term stability is thus eroded. Isolation between fragments prevents the migration of individuals between these fragments. The consequent lack of gene flow leads to a decline in heterozygosity and therefore fitness. Just a few immigrants are thought to be sufficient to immediately impact positively upon the evolutionary trajectory of a population by increasing its fitness through the import of new alleles – this phenomenon is called "genetic rescue" (Tallmon *et al.* 2004). Reed and Frankham (2003) conducted a meta-analysis including 13 studies on invertebrates and observed a significant mean correlation between measures of genetic diversity and the fitness of a population. In a series of experiments with *Drosophila melanogaster*,

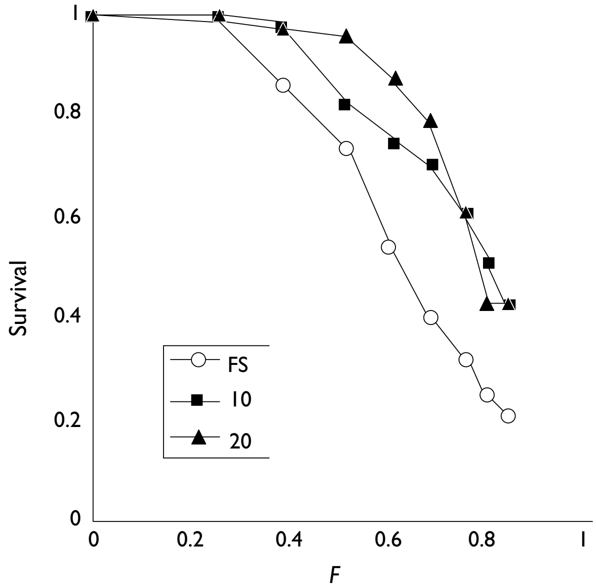

Fig. 20.18. Cumulative rate of extinction in *Drosophila melanogaster* populations plotted against the inbreeding coefficient (*F*). Data for three different treatments with the following effective population sizes: FS = 2.6 individuals, 10 = 10 individuals, 20 = 20 individuals. (Adapted from Reed *et al.* 2003).

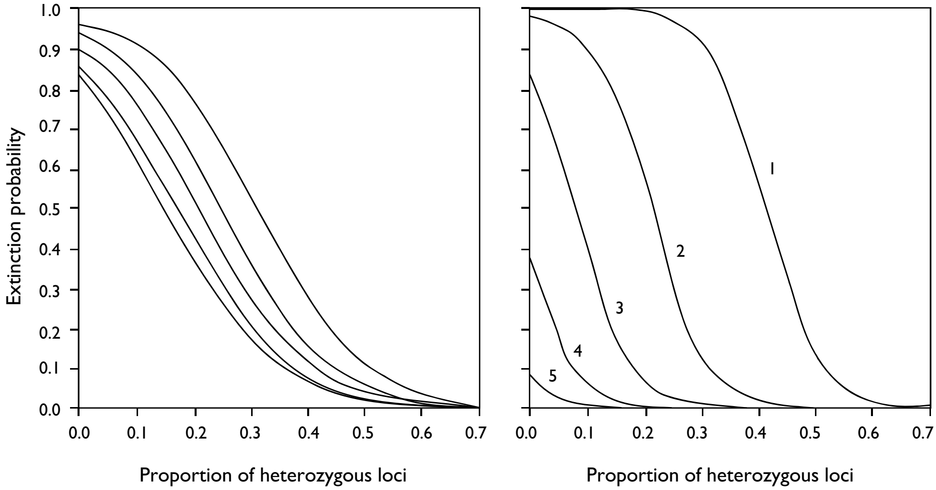

Fig. 20.19. Relationship of local exctinction risk and heterozygosity in populations of the Glanville fritillary (butterfly) as predicted by a global (left diagram) and a sample (right diagram) logistic regression model. Model predictions shown for local population sizes of 1-5 larval groups. (After Saccheri *et al.* 1998).

Montgomery *et al.* (2000) could prove that the originally theoretical conservation concerns about loss of genetic diversity due to a reduction of population size are indeed warranted, also for invertebrates. In their experiments they demonstrated that smaller *D. melanogaster* populations lost all forms of genetic diversity (including the important quantitative genetic variation for reproductive fitness) at a greater rate than larger populations (Table 20.6). Reed (2004) modelled the probability of extinction for a single population in a continuous habitat and for multiple populations that occupy isolated habitat fragments. He found that the probability of extinction was significantly lower in a single continuous population (Reed 2004).

Besides the genetic implications of a smaller population size it also has demographic implications, it leads to larger temporal fluctuations in population size and therefore an increased vulnerability to extinction (Reed and Hobbs 2004; Taylor and Woiwood 1980).

As mentioned above, the genetic effects of habitat fragmentation are particularly serious for species with a low vagility. Many arthropods, especially those without the capacity to fly, possess only moderate to low dispersal capabilities and are therefore expected to be majorly threatened by the breaking up of their habitat (Keller *et al.* 2004).

For the flightless carabid beetle *Abax parallellepipedus* it has been demonstrated by Mader (1984) in extensive field studies that even a narrow artificial barrier in the form of a 6-m-wide road had a strong isolating impact – only one of 742 recaptured individuals had managed to cross that road. Obviously, in invertebrates genetic approaches are much more reliable and elegant than mark-recapture experiments in order to assess the actual levels of gene flow (Keller *et al.* 2004). A study by Keller and Largiader (2003) revealed that the isolation due to roads was sufficiently strong to swiftly bring about significant genetic differentiation between isolated forest populations of the flightless ground beetle

Table 20.6. Correlations between various measures of genetic diversity and the logarithm of effective population size in *Drosophila melanogaster* populations maintained for 50 generations at effective population sizes (N_e) of 25 – 500. Probabilities based on one-tailed tests. (Adapted from Montgomery *et al.* 2000).

Measure of genetic diversity	**Correlation with log N_e**	**P**
Allozyme polymorphism	0.78	< 0.001
Allozyme allelelic richness	0.85	< 0.001
Allozyme heterozygosity	0.59	0.002
Number of inversions	0.44	0.017
Number of morphological variants	0.69	< 0.001

Carabus violaceus in Switzerland. Keller *et al.* (2004) reported on concordant results for *A. parallellepipedus* in the same study area, albeit the genetic differentiation (assessed via microsatellites) between isolated populations was less pronounced. The authors attributed this to the much higher population densities (as a surrogate for population sizes) in *A. parallellepipedus* and the inverse relationship between population size and genetic drift.

In a recent study on the endangered, flightless beetle species *Carabus variolosus*, Matern *et al.* (2009) investigated the variation at 16 allozyme loci of twelve German and French populations and found very low levels of genetic diversity but very high levels of differentiation between the isolated populations, indicative of the absence of gene flow even between geographically close populations. This semi-aquatic ground beetle species is strictly stenotopic and a specialist to a fragmented woodland habitat with small population sizes and very weak dispersal powers, not even dispersing between habitat fragments separated by a 3 km distance. The authors cautioned that further genetic erosion in this species

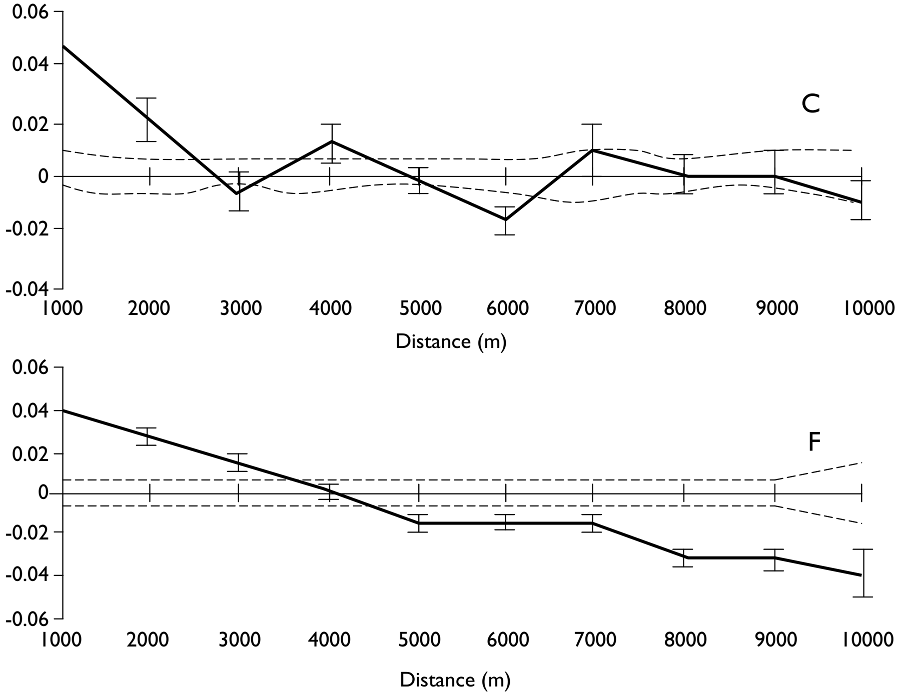

Fig. 20.20. Spatial autocorrelograms for the relatively immobile log-dwelling beetle species *Apasis puncticeps* in continuous (C) and fragmented (F) Australian forest. Solid black lines represent the autocorrelation coefficient (*r*), broken grey lines represent the upper and lower confidence interval. (After Schmuki *et al.* 2006).

might lead to extinction and demanded conservation of the remaining habitat and, where possible, even restoration of already disturbed habitat patches.

In an investigation on habitat fragmentation effects on Australian Tenebrionidae beetles, Schmuki *et al.* (2006) observed reduced mobility and gene flow in populations occurring in fragmented eucalypt forest compared to those in continuous eucalypt forest. The pine plantation matrix posed a barrier to gene flow for both species, *Apasis puncticeps* (Fig. 20.20) and *Adelium calosomoides* (Fig. 20.21). Earlier, Knutsen *et al.* (2000) discovered similar effects of forest fragmentation on a tenebrionid species in Norway. The population differentiation in forest fragments was elevated compared to continuous old forest, which the authors interpreted as a direct consequence of stronger genetic drift in conjunction with decreased dispersal rates resulting from habitat fragmentation and associated isolating effects.

Kryger and Scholtz (2008) reported on the effects of recent habitat fragmentation on a rare fruit chafer species with very low dispersal capabilities

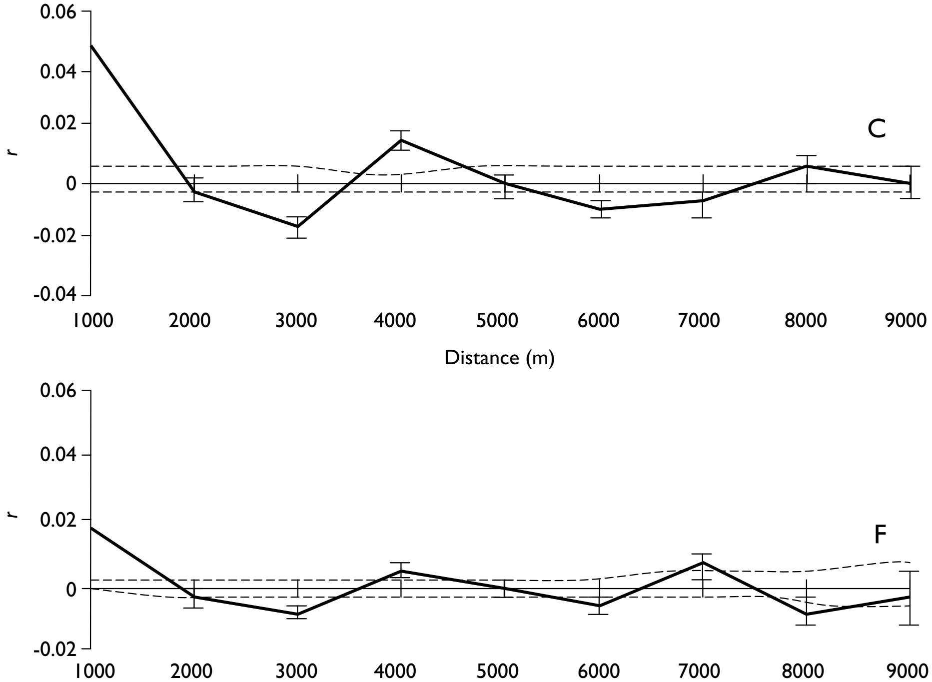

Fig. 20.21. Spatial autocorrelograms for the relatively immobile log-dwelling beetle species *Apasis calosomoides* in continuous (C) and fragmented (F) Australian forest. Solid black lines represent the autocorrelation coefficient (*r*), broken grey lines represent the upper and lower confidence interval. (After Schmuki *et al.* 2006).

[females are wingless] in South Africa, *Ichnestoma stobbiai*. This species, which belongs to an atypical and primitive genus in the Scarabaeidae subfamily Cetoniinae, is restricted to a few small habitat fragments of pristine grassland along the Transvaal Magaliesberg system; most confirmed localities occur in Gauteng Province. This province is one of the development hubs in South Africa; with the ever growing human population in the metropolitan areas of Pretoria and Johannesburg bringing about rapid and massive landscape fragmentation. Thus it is not surprising that four previously known local populations of *I. stobbiai* have already been the victim of progressive urbanization in the area. In a molecular genetic study, Kryger and Scholtz (2008) revealed that the species has undergone serious genetic erosion as a consequence of the recent fragmentation. Several of the remaining local populations suffer from extremely low levels of genetic diversity (Table 20.7) and due to the remnant populations being effectively isolated from each other there is no possibility for natural gene flow and genetic rescue. The severely reduced demographic and genetic connectivity could ultimately lead to the extinction of this highly specialized species.

Kryger *et al*. (2006a) mentioned that *Circellium bacchus*, a rare dung beetle endemic to South Africa has possibly undergone a range reduction due to human mediated habitat transformation. This flightless and ectothermic ball rolling species is a habitat specialist depending on densely vegetated, undisturbed thicket. *C. bacchus* is a large (almost up to 5 cm), charismatic roller with a high public profile in South Africa. It has therefore been used as a flagship species (New 1993) for the thicket habitat in the Cape Floristic Region by WWF South Africa. Currently, it is restricted to a few isolated habitat patches along the south coast of South Africa. The biggest (both area and specimen numbers)

Table 20.7. Sampled specimens per locality (*n*), number of haplotypes, haplotype diversity (*h*) and nucleotide diversity (π) for the remnant population of the beetle species *Ichnestoma stobbiai*. (Adapted from Kryger and Scholtz 2008).

Locality	***n***	**Number of haplotypes**	***h***	π
A	4	4	1	0.0102
B	9	2	0.222	0.0007
C	1	1	NA	NA
D	12	2	0.303	0.0005
E	12	3	0.439	0.0008
F	3	3	1	0.0055
G	4	1	0	0
H	9	1	0	0
I	3	2	0.667	0.0066

population occurs in the Addo Elephant National Park close to Port Elizabeth. The other remnant populations occur further to the west in much smaller habitat patches; all are isolated and separated from each other by a matrix of unfavourable agricultural land (Fig. 20.22). Under the absence of dispersal between the habitat islands, genetic depauperisation could be expected if the population sizes in the fragments are too small. This is indeed suspected for several of the small habitat patches in the west. Furthermore, it may be especially prone to extinction because of its relatively large body size, low dispersal capabilities, small geographical range and extremely low fecundity of only one offspring per female per year (Ewers and Didham 2006; Kryger *et al.* 2006a; Purvis *et al.* 2000; Tscharntke *et al.* 2002b).

Circellium bacchus has been placed in the tribe Canthonini (Cambefort 1978, Scholtz and Howden 1987a); however, this placement has resulted more from

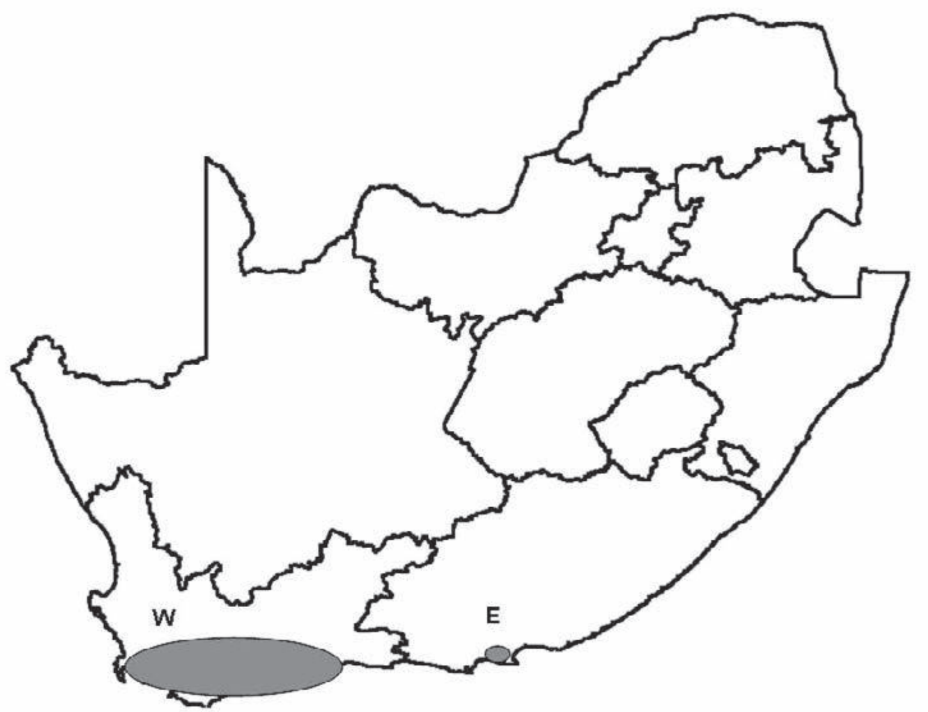

Fig. 20.22. Distribution of the two remnant populations of *Circellium bacchus* in South Africa. The biggest continuous population occurs in the Addo Elephant National Park (E). Several isolated smaller populations occur west of this area and are contained in the larger but severely fragmented western distribution area (W) of the species. (After Kryger *et al.* 2006a).

lack of a reasonable alternatives than from convincing evidence. As a matter of fact, we do not know the closest relative of *C. bacchus*, nor the correct phylogenetic placement of this monotypic genus within the phylogeny of Scarabaeinae. It is thought to be a relict from a formerly larger group of dung beetles, the only survivor and therefore carrying a large amount of Phylogenetic Diversity (Faith 1992, 1994). Samways (1994) also identified it as an intrinsically valuable species due to its unique genetic heritage. Since the species is rare and endangered and, moreover, a flagship species for a threatened habitat type in South Africa, there is a high interest in its conservation.

The identification of evolutionary lineages and conservation units is important for single-species conservation planning, in order to maintain the maximum genetic diversity as well as evolutionary history and potential of the species in question (Avise 1989; Brooks *et al.* 1992; Moritz 1994a, 1995). With this deliberation, a molecular genetic study was undertaken in order to elucidate the genetic structuring and diversity within *C. bacchus* (Kryger *et al.* in prep). The preliminary results of this study, based on mitochondrial COI sequences, indicated a deep phylogeographic structure dividing the species into two major assemblages (Fig. 20.23) that qualify as Evolutionarily Significant Units (ESUs) sensu Moritz (1994b) with highly independent evolutionary histories and potential. These should therefore be managed and protected as separate entities. Both lineages should be conserved, since the loss of distinct populations within species is also considered a severe loss of biodiversity (May 1990). Furthermore, applying the phylogenetic species concept (Nixon and Wheeler 1990), the identified lineages would even qualify as separate species, based on reciprocal monophyly in parsimony analysis.

Within one of these assemblages, there is concern about the isolation of the remnant small populations coupled with low population densities in these localities. It is not known for sure how far *C. bacchus* specimens can disperse. But seeing that they are wingless, ectothermic and prone to desiccation, they are unlikely to be more mobile than the tropical dung beetle species assessed by Peck and Forsyth (1982) that were able to transverse up to 1.0 km in 2 days. Assuming that *C. bacchus* survived as a metapopulation (as indicated by the genetic signal of historical fragmentation on various levels found by Kryger *et al* in prep.) it would have depended on sufficient dispersal among the patches of thicket habitat for the metapopulation to persist (Hanski *et al.* 1995; Hanski and Simberloff 1997). Currently, however, this important metapopulation dynamic seems to be interrupted. Because of the large areas of agriculturally transformed matrix separating the small habitat islands there are no dispersal opportunities (see Fig 20.22). With increasing patch isolation, metapopulation theory predicts a decline in the number of dispersers among habitat patches. The reasons for this

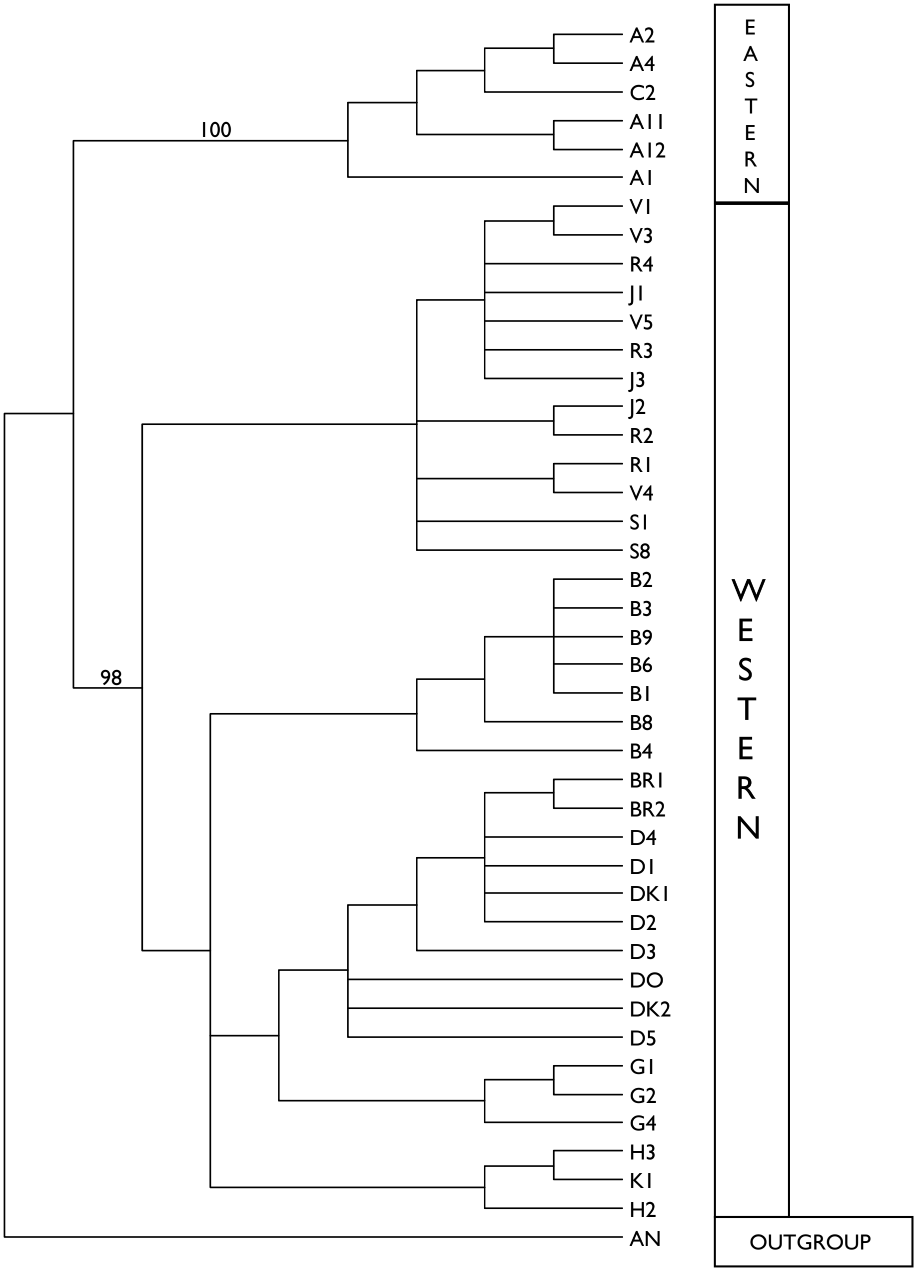

Fig. 20.23. Phylogenetic tree for *Circellium bacchus* specimens based on mitochondrial CO1 sequences. The reciprocal monophyly of the two separate assemblages (collected in eastern and western parts of the distribution area) is highly supported by bootstrap values. (Kryger *et al.* unpublished).

are increased mortality of individuals in the migration phase (Hanski *et al.* 1994) and a dilution effect associated with the spatial spread of individuals (Ims 1995). Especially those thicket patches with low *C. bacchus* population densities will run a high risk of extinction via population size fluctuations alone – without a chance for recolonization to compensate for this (Hanski *et al.* 1995). This would be the consequence of the disruption of demographic connectivity between these thicket habitat remnants. Furthermore, population viability is endangered in these small patches, because loss of genetic variability due to random genetic drift will be very severe and only gene flow from other habitat patches could provide "genetic rescue" (Brown and Kodrick-Brown 1977; Tallmon *et al.* 2004).

The southern African genus *Pachysoma* consists of 13 flightless species that are endemic to the arid west coast of southern Africa, covering the area from Cape Town in South Africa up to the Kuiseb River in Namibia (Harrison *et al.* 2003). The genus is characterized by highly unusual morphology as a result of their flightlessness (Harrison *et al.* 2003) (see Chapter 9.1.2). Moreover, their biology is also remarkable in that they drag their dry dung food forwards as opposed to the backwards rolling of wet dung by their relatives of the genus *Scarabaeus* (Scholtz *et al.* 2004). Given these special characteristics, this genus is significantly contributing to "feature diversity" *sensu* Faith (1992, 1995) within the Scarabaeini. This notion is further corroborated by the distinctness and long branches of the genus in molecular and total evidence phylogenetic trees of the tribe (Forgie *et al.* 2006) indicating a relatively large amount of "Phylogenetic Diversity" *sensu* Faith (1992, 1995). Based on this distinctness, the entire genus is thought to also hold high conservation value (for reasoning see Vane-Wright *et al.* 1991).

The distribution of one of the species, *P. gariepinum*, covers the central part of the distribution area of the genus, namely from the Buffels River in South Africa up to the Agub Mountains in Namibia (Sole *et al.* 2008). There are several isolated populations occurring in pockets of coastal sands in the Succulent Karoo Biome of South Africa and in the Namib Desert (Sole *et al.* 2008). The species has raised special conservation concerns due to its rareness combined with its commercial value to collectors. Aggravatingly, there is also increased human encroachment on the habitat of *P. gariepinum* in the form of mineral and diamond mining in Namibia and even more intensely in South Africa, as well as clearing of natural vegetation for farming in the Western Cape Province of South Africa (Sole *et al.* 2008). Molecular genetic analyses based on mitochondrial CO I sequences revealed three distinct assemblages within the species that coincide with three discrete geographic areas, two in South Africa and one larger area in Namibia (Fig. 20.24). All assemblages showed high amounts of genetic diversity as measured via haplotype diversity and nucleotide diversity

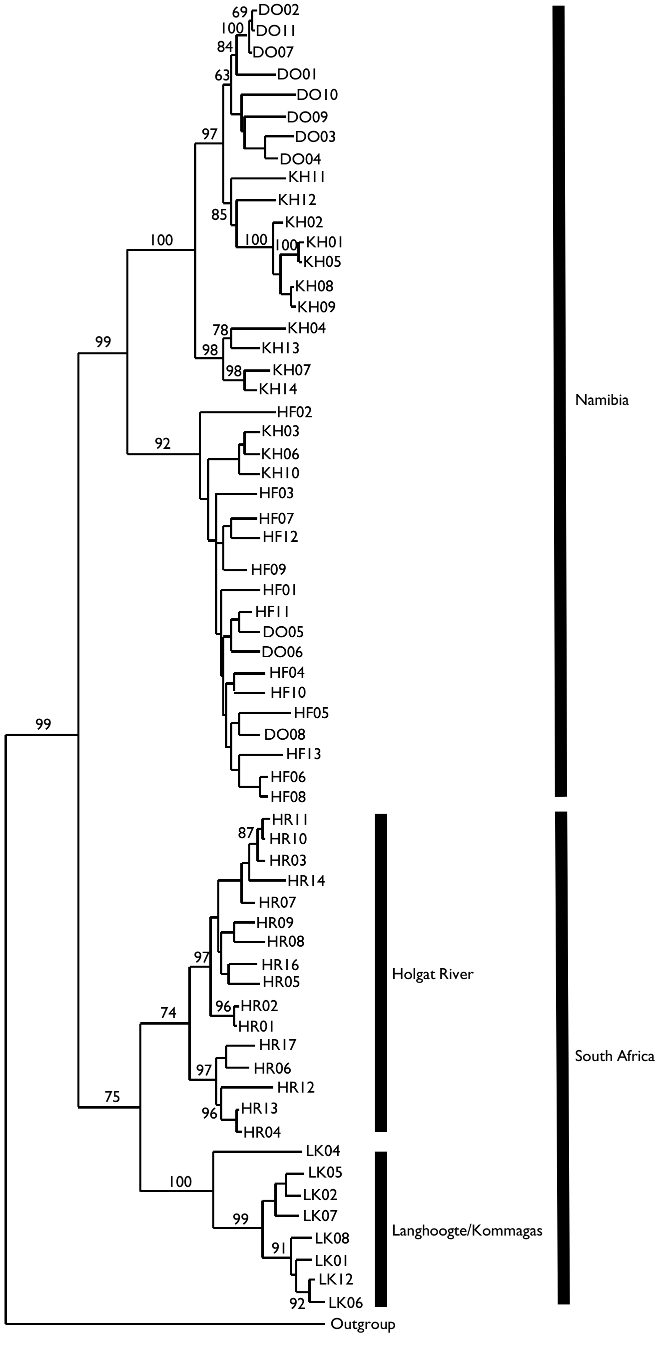

Fig. 20.24. Neighbour-joining tree of *Pachysoma gariepinum* mitochondrial CO1 haplotypes with Bayesian posterior probabilities. (After Sole *et al.* 2008).

(Table 20.8); thus the authors inferred that the fragmentation into three lineages must have occurred in the past over geological time (see also Moya *et al.* 2004 for supporting arguments). As potential geographic barriers for that past fragmentation the authors discussed the major rivers in the area. For a flightless dung beetle, major rivers may well pose an insurmountable barrier. Surprising for a species with very low vagility was the phylogenetic signal of apparent gene flow across the entire geographic area of the Namibian assemblage. However, Sole *et al.* (2008) explained that this may be the result of an almost panmictic situation (with the larger part of the distribution area of this lineage being undisturbed natural habitat with very little human interference) combined with passive dispersal of specimens with the windblown barchan dunes that shift up to 100 km per year. The three identified lineages are thought to reflect independent demographic histories and to have been isolated from each other for over one million years (Sole *et al.* 2008). The authors emphasized that the three monophyletic lineages should be managed as separate conservation units and future habitat loss should be avoided. It would be a significant loss to the intraspecific phylogenetic diversity if any of the assemblages would be lost (compare May 1990). This threat is particularly pronounced for the two South African populations due to the on-going human-induced habitat transformation and destructive farming practices in that area.

In this context, there are several dung beetle taxa that, like *Pachysoma*, have evolved in the arid areas along the West Coast of South Africa and Namibia. Among these are the species-poor genera *Dicranocara, Byrrhidium* and *Namakwanus* that are putatively placed in the tribe Canthonini (Deschodt *et al.* 2007). The members of these genera are also endemic to the narrow coastal strip between the Great Escarpment of southern Africa and the Atlantic Ocean. They have evolved in the context of the extreme conditions in the Fynbos, Succulent Karoo and Namib Desert Biomes in close association with rock hyraxes on

Table 20.8. Sampled specimens per locality (*n*), number of haplotypes, haplotype diversity (*h*) and nucleotide diversity (π) for the sampled populations of the beetle species *Pachysoma gariepinum*. (Adapted from Sole *et al.* 2008).

Locality	***n***	**Number of haplotypes**	***h***	π
Langhoogte/Kommagas	12	8	0.909	0.026
Holgat River	17	16	0.993	0.023
Hohenfels	13	13	1.00	0.022
Dabernas/Obib Dunes	11	11	1.00	0.038
Klingharts Mountains	14	14	1.00	0.042
Overall	67	62	0.997	0.057

whose dung pellets they depend for food (Deschodt *et al.* 2007). Their exact phylogenetic placement is as yet uncertain, but it is evident that they are systematically unique, mostly flightless and they probably carry a large amount of phylogenetic diversity. They, too, are threatened by increasing habitat deterioration brought about by humans. Even in conservation areas such as the Richtersveld Transfronteir Park in southern Africa, the deterioration of the habitat that these exceptional organisms are adapted to and depend upon is seemingly unstoppable. Besides scientific arguments, it would be a great shame for our species to lose these fascinating components of biodiversity before we even had a chance to study and understand them.

While natural fragmentation over geological time is an important driver of speciation through vicariance, human-mediated habitat fragmentation acts much faster and usually leads to extinction events rather than speciation events. However, there may be exceptions to the rule. Orsini *et al.* (2007) and Wirta *et al.* (2008) undertook molecular genetic studies on dung beetles in Madagascar. Their results suggested that the Madagascar-endemic subtribe Helictopleurina of the Oniticellini, may have co-evolved in association with lemurs, because the main radiation of the tribe happened concurrently with the main radiation of lemurs. As a consequence, these beetles were adapted to lemur dung as a food resource. When analyzing resource use in the Helictopleurina, Wirta *et al.* (2008) found that four species were specialists of cattle dung, which is very different to lemur dung. With the absence of native ungulates and with cattle having been introduced to Madagascar by humans only 1500 years ago, this resource shift was interpreted by the authors as recent. Along with the shift in food resource, four atypical *Helictopleurus* species (*H. neoamplicollis*, *H. quadripunctatus*, *H. sinuatocornis*, and *H. marsyas*) also had to shift from their original closed forest habitat to the open habitat where cattle graze. Since much of Madagascar's area has been deforested by humans, the shift in resource use and habitat has allowed three of these species to expand their range and they now occur all across Madagascar with a significantly larger (and ever increasing) geographical range than the 41 forest-dwelling species. In the case of *H. marsyas* the authors even alluded that this shift may have triggered a speciation event. This species is morphologically and genetically very similar to *H. nicollei* and may exemplify the process of incipient speciation (Wirta *et al.* 2008). Unfortunately, such swift "anthropogenic speciations" are extremely rare and certainly occur at a much lower rate than the very abundant and even swifter "anthropogenic extinctions". This also holds true for the situation of Helictopleurina in Madagascar – with cattle having been present for only 1500 years (which probably equates to thousands of beetle generations), the different texture, size and fiber content of cattle dung compared to lemur dung and also the drastic differences in humidity and temperatures of the open grazing habitat as opposed to the original closed forest habitat still make such radical shifts in resource and habitat use highly unlikely (Wirta *et al*. 2008). The dung beetle species that managed to do this were possibly preadapted to dry habitats and cattle-like dung.

CHAPTER 21

DUNG BEETLES AS BIO-INDICATORS

21.1 THE NEED FOR INVERTEBRATE BIO-INDICATORS

Virtually every ecosystem on earth is dominated by invertebrates, be that in terms of species richness, faunal biomass or critical ecological functions (Spector 2006). Many invertebrate taxa are characterized by a hyper-diversity in terms of species richness but also in terms of ecological niches that they occupy (Spector 2006). For this reason it is not feasible to monitor all invertebrate taxa or to undertake comprehensive surveys of all invertebrate species at any given scale (Miller and Coddington 2004 cited in Spector 2006). Unfortunately, decisions in conservation planning and management strategies are usually based on just such data on species distributions (Cowling *et al*. 2003; Myers *et al*. 2000; Ricketts *et al*. 2005). The selection of areas as conservation priorities is usually rooted in data on species richness and endemism (Margules and Pressey 2000; Pressey *et al*. 2003). Such data is simply missing for many invertebrate groups and thus it is not surprising that still today most conservation relevant decisions are grounded on data from plants and a few vertebrate groups such as birds or mammals, while entirely ignoring a disproportionately large and functionally important component of biodiversity – insects (Black *et al*. 2001; Myers 2003; Stein *et al*. 2002). This situation is highly inadequate, especially since it has been shown that vertebrate assemblages or vascular plants are poor surrogates for invertebrate diversity (Moritz *et al*. 2001; Oliver *et al*. 1998).

Limited by temporal and financial constraints, conservation practitioners in general have an increasing interest in using focal taxa as information surrogates for broader patterns of biodiversity (Spector 2006). Also, or rather especially in the case of invertebrates, this call for a focal taxon has been repeated frequently, with the hope that this would open the door to include invertebrates more strongly in conservation research and action (Andersen 1999; Caro and O'Doherty 1999; Halffter and Favila 1993; Favila and Halffter 1997; Kremen 1992; Kremen *et al*. 1993).

21.2 NECESSARY TRAITS OF INVERTEBRATE BIO-INDICATORS

Several authors have suggested lists of traits that the ideal invertebrate focal taxon should possess (Halffter and Favila 1993; Kremen 1992; Lambeck 1997; McGeoch 1998; Noss 1999; Pearson 1994). Most commonly these lists entail that the group should be widespread and abundant, with a well resolved taxonomy, functionally important and sensitive to disturbances to the community.

Various invertebrate groups have been suggested as focal taxa (Hill 1996; Niemela *et al*. 1996; Didham *et al*. 1996, 1998). However, most of the suggested groups failed to be supported by a clearly resolved taxonomy, quantitative sampling protocols or convincing research results. Spector (2006) identified a general lack of coordinated expert effort as the reason for this and continued to bring forth convincing arguments why in the case of dung beetles both conditions are fulfilled: the coordinated expert effort (organized through the Scrab-Net collaborative network of scientists working on dung beetles) as well as the suitability of the group.

Before Spector (2006), numerous other scientists had proposed or already used dung beetles as indicator taxa for biodiversity inventory and monitoring. Among these were Davis *et al*. 2001; Davis *et al*. 1999c, 2004; Favila and Halffter 1997; Feer 1999; Halffter and Favila 1993; Jankielsohn *et al*. 2001; Lobo *et al*. 2001; McGeoch 1998; Newmark and Senzota 2004; Roslin and Koivunen 2001; van Rensburg *et al*. 1999.

Halffter and Favila (1993) proposed using dung beetles as indicators for evaluating and monitoring the effects of anthropogenic disturbance to tropical forests. With reference to Kremen (1992), Halffter and Favila (1993) summarized the following characteristics as crucial for a focal group:

1) The group should represent a well defined and rich guild that is important to ecosystem structure and function.
2) The selected guild should respond sensitively and along a gradient to changes and disturbances in the system.
3) It should be easy and standardizable to catch the organisms making up the guild so that it is possible to compare data from different geographic locations.
4) The collected data should allow determination of the composition and structure of the guild and its interactions with the entire community, so that it is possible to extrapolate from the indicator group to the community as a whole.
5) The group should have a well established taxonomy and clearly defined species delineations.

6) The group should be resilient to the sampling of individuals for monitoring purposes so that it will not be compromised in its persistence by the use as a focal group.
7) The group should be a direct measure of the intact community as well as of any reduction in biodiversity in the community.

21.3 HOW DUNG BEETLES MEET THE CRITERIA FOR BIO-INDICATORS

Dung beetles fulfil all these requirements. They are a very diverse and abundant group with a wide global distribution (Nichols *et al*. 2007). Thus their application as biodiversity surrogates allows researchers to evaluate and compare human impact on ecosystems around the globe. They exhibit a large variety of behavioural and morphological traits and fulfill well investigated ecological roles (Hanski and Cambefort 1991). They are key providers of several important ecosystem services (Horgan 2005; Nichols *et al*. 2008). Their alpha taxonomy is reasonably well resolved (Philips *et al*. 2004b), and they are easily and cost-effectively sampled using standardized, simple trapping methods (Gardener *et al*. 2008a; Larsen and Forsyth 2005). They display swift and differentiated responses to anthropogenic as well as natural disturbances to the ecosystem (Horgan 2005; Spector and Ayzama 2003). They are particularly vulnerable to habitat changes such as deforestation or shifts in the mammal faunal elements and are thought to be useful indicators of ecosystem health because of this sensitivity (Halffter *et al*. 1992; Klein 1989). Their primary association with mammals also makes them indicators of mammalian abundance, and possibly, also diversity (Estrada *et al*. 1999; Vulinec 2000).

So dung beetles have repeatedly been identified as an ideal focal group for biodiversity monitoring and inventory, because they fulfill all the requirements of a useful bioindicator in different contexts and at different levels. Spector (2006) published the most recent and detailed summary of the reasons for this.

A very important first reason is the ease of the sampling procedure, which therefore can be standardized and applied very broadly, also by laymen. In comparison to other invertebrates, dung beetles can be sampled more rapidly and quantitatively with simple, inexpensive baited pitfall traps (see Fig. 21.1, also Halffter and Favila 1993). In this way, it is possible even for non-specialists to swiftly (typically within days) acquire quantitative assessments of abundance, structure and composition of dung beetle assemblages (Spector 2006). Furthermore, the low cost and ease of the sampling method allows for continuous and long term monitoring programs (Halffter and Favila 1993).

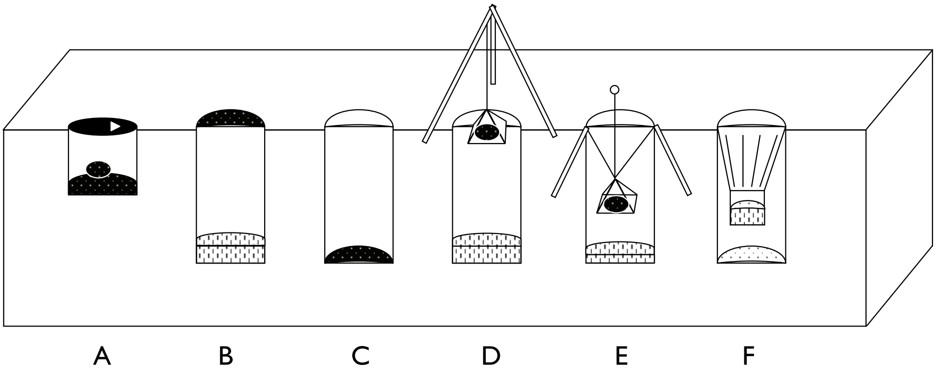

Fig. 21.1. Types of commonly used traps for collecting coprophagous beetles. Bait is represented by the black areas. (After Lobo *et al.* 1988)

Larsen and Forsyth (2005) suggested spacing traps at 50 m distance from each other along linear transects in order to gain optimal collecting efficiency. So far, unfortunately, there is not yet a standardized, quantitative sampling procedure accepted by all dung beetle researchers worldwide (Spector 2006). This would be a large step towards a methodological consistency so direly needed for regional and global comparisons.

A second crucial point is that the taxonomy of dung beetles is well established (Halffter and Favila 1993; Spector 2006). There is even the ScarabNet Global Taxon Database available online (at www.scarabnet.org) listing over 5700 valid dung beetle species organized in 225 genera. However, at local scales, species richness lies only up to around 75 species in tropical zones and therefore it is realistically feasible to train personnel to reliably identify local assemblages. The field of dung beetle taxonomy is still very active, with approximately 60 specialists globally currently active. However, it will be important that these specialists find ways and means to translate their expert know-how into easy-to-use field keys and identification tools such as reference collections (see also Halffter and Favila 1993).

A third reason making dung beetles useful as a focal group is their wide geographic distribution with multi-species communities present at most localities (Spector 2006) - from a few sympatric species in local communities of the temperate zones (Hanski 1989) to over 75 species in tropical habitat assemblages (Escobar 2004). Moreover, most genera are restricted to a single biogeographic region with high levels of local species endemism (Halffter *et al.* 1995).

As a fourth factor, Spector (2006) elaborated on the graded response of dung beetles to environmental change. It has been shown in a meta-analysis including 26 individual studies on dung beetle community response to tropical forest fragmentation that dung beetle species richness, abundance and biomass declined step by step along a modification gradient from intact forest to clear-cut degraded areas (Nichols *et al.* 2007).

Furthermore, Horgan (2005) documented shifts in nesting behaviour, average body size and diel activity as a consequence of habitat disturbances. There is a large body of literature reporting the multiple and graded impacts on dung beetles of various veterinary parasiticides used on livestock (see Floate *et al.* 2005 for a review). So it is safe to say that dung beetles clearly reflect anthropogenic changes in a sensitive but differentiated response.

As a fifth argument in favour of dung beetles as bio-indicators, Spector (2006) stressed the combination of their well-known natural history and their ecological and economic importance. The feeding and nesting behaviours of dung beetles are well documented and their natural histories are very often well understood (Halffter and Edmonds 1982; Halffter and Matthews 1966; Hanski and Cambefort 1991). As shown above in the chapter on ecosystem services, dung beetles contribute to a suite of essential ecosystem functions such as waste removal, nutrient cycling, soil conditioning and aeration, suppression of pest and parasite populations and secondary seed dispersal (see Nichols *et al.* 2008 for a review). They could therefore reasonably be regarded as a keystone group.

Finally, the sixth feature qualifying dung beetles as ideal bio-indicators is that their geographic patterns of species richness and endemism are closely correlated with those of other taxa in the same region (Spector 2006). Moritz *et al.* (2001) and Oliver *et al.* (1998) showed that dung beetles (in combination with vascular plants) probably are the optimal surrogates for total biodiversity and hence for conservation area selection. Their small range sizes and habitat specialization may account for that (Moritz *et al.* 2001). Additionally, dung beetle biomass is supposed to be dependent on and therefore indicative of mammalian biomass (Halffter and Matthews 1966) and hence dung beetle communities react swiftly and sensitively to any changes in the associated mammalian communities. Dung beetle assemblages restructure and lose species in response to declines in the abundance or richness of sympatric mammal communities (Andresen 2003; Cambefort 1991; Carpaneto *et al.* 2005; Estrada *et al.* 1998; Feer and Hingrat 2005; Hanski and Cambefort 1991).

Halffter and Favila (1993) gave detailed guidelines for which parameters should be analyzed when using dung beetles as indicators for biodiversity. In an initial step, the diversity of the guild should be investigated. Firstly, species richness should be assessed; secondly, diversity and equitability indices (e.g. Shannon index, Simpson index, Hill index). In a consecutive step, the structure of the guild should be documented. This involves species abundance, trophic diversity (generalists, strict coprophages, necrophages or saprophages), diversity in temporal activity (diurnal, nocturnal, crepuscular species; but also seasonal and annual activity patterns), and finally spatial segregation.

While Halffter and Favila (1993) particularly recommended dung beetles as bio-indicators for use in tropical rainforest, they speculated that they should also be useful indicators in open tropical habitats and savannas. This view has certainly been supported by Davis *et al*. (2004) who summarized the usefulness of dung beetles as indicators of biodiversity, habitat transformation, and pesticide use in agro-ecosystems in South Africa.

Because dung beetles satisfy all of the criteria of an ideal bioindicator for investigating impacts of anthropogenic disturbances to ecosystems, numerous ecological and biodiversity conservation studies have already used them in many regions of the world. Dung beetles have been used as indicators of environmental change in forest ecosystems of Borneo (Davis *et al*. 2001) and restored Andean landscapes in Colombia (Medina *et al*. 2002). Newmark and Senzota (2003) monitored biodiversity in the Usambara Mountains in Tanzania over a 10-year period and found forest interior dung beetles to be ecological indicators with a high statistical power.

In South Africa they were successfully used as indicators for habitat transformation in pastoral systems at different scales (summarized in Davis *et al*. 2004).

In the regions of the earth with a warmer, moister climate (>15 °C mean annual temperature and >250 mm annual rainfall) dung beetles are an integral part of livestock pasture ecosystems; therefore they are ideal indicators in this context (Davis and Scholtz 2001; Davis *et al*. 2002; Halffter 1991). Davis (1993) investigated the extensive transformation of South African winter rainfall shrublands into arable lands and pastures and found that transformed habitats did not retain the characteristic winter rainfall dung beetle assemblages but rather showed a mix of species with taxa from the adjacent summer rainfall areas. In the [eastern] South African provinces of KwaZulu-Natal and Mpumalanga, Davis *et al*. (1999b) could indicate the transformation of natural grassland into highly improved pastures by a decline in dung beetle species richness with a shift in community structure and by significant decreases in species diversity and abundance, respectively. While the differences between dung beetle communities from natural and transformed forest habitats are generally more pronounced (due to the more drastic alterations in microclimatic and physiognomic conditions), the differences between dung beetle assemblages from natural and disturbed wood-, shrub- and grasslands are still high enough to use them as bio-indicators of habitat transformation (Davis *et al*. 2004). In fact, they are even utilized in South Africa as a tool to characterize natural pasture systems and market certified "natural meat" (Davis *et al*. 2004).

In South Africa, Australia, Canada, Europe and South America, dung beetles are used for bio-assaying the environmental toxicity of antiparasitic drugs used in livestock farming.

CHAPTER 22

CONSERVATION OF DUNG BEETLES AND MODERN PARASITE MANAGEMENT

The previous chapters illustrated how important dung beetles are in many different ecosystems, how they are threatened by habitat loss and why they are such a good surrogate taxon to monitor biodiversity and habitat condition. With mankind's shift from a nomadic hunter and gatherer society towards a sedentary agricultural society, its negative impact on natural habitats sharply intensified along with its growing psychological distance from nature. Today we are witnessing how some of mankind's agricultural habits and practices pose a major threat to the balanced functioning of the natural life-sustaining systems on this planet as summarized in "Livestock's Long Shadow" (Steinfeld *et al*. 2006). The FAO (2006a,b) has recently documented that livestock production contributes majorly to our most pressing environmental problems, including pollution and degradation of land as well as loss of biodiversity. Not only do vast areas of primary forest still get cleared for expansion of grazing land, even livestock production on natural rangeland usually reduces biodiversity in this area. Besides the anthropogenic elimination of most predators and of any wild herbivores that may possibly compete for grazing with the livestock, very often pesticide use on livestock may pose a serious hazard to biodiversity as well.

22.1 PARASITICIDES IN THE LIVESTOCK INDUSTRY, AND THEIR NON-TARGET EFFECTS

In commercial livestock farming today, it is common practice to control external and internal parasites using chemical compounds with insecticidal, acaricidal, or anthelmintic properties. To some extent most of these agents and /or their metabolites are voided in the faeces of the treated animals (Strong and Wall 1990). Via this route the residues enter the pasture environment and may have deleterious effects on beneficial non-target organisms utilizing the dung, for instance dung beetles (for reviews see Floate *et al.* 2005 and McKellar 1997). Some residues can persist in the dung of animals for months after treatment/deposition and thus adversely affect pasture ecology over an extended period of time (Floate *et al.* 2005).

Anderson (1966) was among the first to raise concerns about potential adverse effects of faecal residues on pasture biodiversity. Ten years later, Blume *et al.* (1976) documented that certain anthelmintics (dichlorvos and phenothiazene) that were used as feed additives for livestock inhibited the survival of dung beetles and disrupted the important process of dung degradation. Moreover, phenothiazene reduced the content of clover in the pastures and led to a decline in nitrification rates (Southcott 1980). In the 1970s and 1980s a whole range of new antiparasitic products were developed with high potency at low dosage rates (Miller 1987). Most prominent among these were the avermectins, the synthetic pyrethroids, and the insect growth regulators (Wardhaugh 2005; also see below for further details). Along with the novel product range, new methods of drug administration (such as ear-tags, injectables, sustained-release devices, pour-on formulations) were developed during that time period and seemed to make antiparasitic therapy easier and more effective (Wardhaugh 2005). However, Lumaret (1986) and Wall and Strong (1987) suspected early on that this revolution in parasite management may negatively impact upon the beneficial dung fauna. Since the 1980s a large body or research results has accumulated to validate these initial concerns about the effects of veterinary pharmaceuticals in the environment (e.g. Floate 2006, 2007; Floate *et al.* 2005; Lumaret and Errouissi 2002; McKellar 1997; Strong and Wall 1990; Wardhaugh 2005; Wardhaugh and Beckman 1996/97; Wardhaugh and Ridsdill-Smith 1998). So far there have been many studies investigating the environmental impact of macrocyclic lactones, especially ivermectin. For many of the other veterinary pharmaceuticals frequently used today, there is frustratingly little information on their ecotoxicological effects on non-target organisms utilizing the faeces (Wardhaugh 2005).

22.2 DIFFERENT TYPES OF PARASITICIDES

Depending on the target organism, parasiticides can be divided into anthelmintics, ectocides, and endectocides. Those drugs used against internal parasites such as gastrointestinal nematodes or lungworms are called anthelmintics. Parasiticides that provide control of external parasites such as ticks, mites, lice and biting flies are labeled ectocides and are generally administered during summer. Finally, endectocides are applied against external and internal parasites simultaneously, the treatment usually occurs in spring with a possible consecutive treatment later in the season (Floate *et al.* 2005). With the advent of broad-spectrum antiparasitic agents, the risk of ecotoxicological effects on non-target organisms has increased further (McKellar 1997).

Antiparasiticides are usually grouped according to the chemical substance class of their active ingredients: such classes with action against arthropods are organophosphates, macrocyclic lactones, synthetic pyrethroids, insect growth regulators; classes with anthelmintic action include the benzimidazoles, the imidazothiazoles, the macrocyclic lactones, the salicylanilides, and the tetrahydropyrimidines (see Wardhaugh 2005 and Floate *et al.* 2005).

Some active ingredients are on the market in different formulations: oral formulations are presented as an oral paste or liquid drench; injectables are given as subcutaneous injections; pour-on formulations are applied topically onto the skin of the animal to be treated and are then absorbed through the skin (transcutaneously); ear-tags are made up of a plastic matrix that is impregnated with the active ingredient which is then slowly released onto the animal; sustained-release devices consisting of a reservoir with the active ingredient which attaches to the rumen of the animal and slowly releases small doses of the active ingredient over a prolonged period of time after it has been applied orally (Floate *et al.* 2005). The drug formulation influences the pattern and the period over which residues and/or metabolites of the active ingredient are excreted by the treated animal. For oral formulations there is a sharp, short peak of residue concentration in the excrement, this period usually covers a few days. For injectable and topical pour-on formulations, the peak residue concentration in the excrement is found 2 to 7 days after the application; this is followed by 4 to 6 weeks when the concentration slowly tails off. The concentration of drug residues originating from sustained release formulations may only peak several weeks after the administration of the device, with measurable traces still found for periods of over 140 days post-treatment (Errouissi *et al.* 2001; Strong *et al.* 1996).

To some extent, all antiparasitic drugs are metabolized by the treated animal in the gastrointestinal tract or after absorption via the hepatic metabolism (Boxall *et al.* 2004; McKellar 1997) and it seems that there are no large inter-specific differences in compound metabolism between the different livestock species (Floate *et al.* 2005). Generally ivermectin is metabolized to a moderate extent; while closantel, cypermethrin, deltamethrin, diazinon, fenbendazole, levamisole, and morantel are examples of extensively metabolized active ingredients. But even metabolites can retain pesticidal activity, sometimes to the same degree as the parent compound (for instance in the case of doramectin, see Floate *et al.* 2005). The route of excretion was shown to be determined by the chemical class that a parasiticide belongs to, but it seems to be largely independent of the formulation (Wardhaugh 2005). Synthetic pyrethroids are excreted in urine and faeces, but in cattle mainly via faeces. The organophosphate diazinon and the imidazothiazole levamisole together with their highly polar metabolites are eliminated mainly with urine, but to a small extent also in faeces. The opposite holds true for macrocyclic lactones, which are mainly excreted in faeces (Floate *et al.* 2005).

Table 22.1 gives a summarized overview of the most frequently used veterinary antiparasitic drugs grouped according to the targeted organisms and the chemical substance class, with information on the major excretion route.

22.3 PARASITICIDE PERSISTENCE IN THE ENVIRONMENT

Experiments on the persistence of ivermectin in faeces from sub- or transcutaneously treated cattle on pastures under Danish and Tanzanian weather conditions showed no measurable degradation over a 45-day period (Sommer *et al.* 1992). Furthermore, photodegradation was found to have a minimal effect on the persistence of ivermectin in dung pats (Sommer and Steffansen 1993). Leaching by rain is also minimal for ivermectin, because it binds tightly to the organic matter in the dung and the soil (Halley *et al.* 1989). In soil or soil/manure mixtures, ivermectin has a half-life of 14-56 days (Halley *et al.* 1993); in soil the reported half-life of eprinomectin was 64 days and of doramectin 61-79 days (see Floate *et al.* 2005 and reference therein); the half-life of moxidectin in soil was determined to be 60 days (see Floate *et al.* 2005 and reference therein).

In a study on the persistence of organophosphates in dung, Miller and Pickens (1973) found that while residues of coumaphos stayed stable throughout the 28-day exposure, residues of ruelene decreased significantly.

The persistence of synthetic pyrethroids in soil is relatively moderate, because they readily hydrolyze into cis- and trans-isomers with half-lives of 2-4 weeks for cypermethrin and 21-25 days under aerobic conditions and 31-36 days under anaerobic conditions for deltamethrin (Roberts and Hutson 1999).

Not much is known about the degradation of benzimidazoles or levamisole, but McKellar (1997) suggested that they probably do not degrade readily in dung.

22.4 DELETERIOUS EFFECTS OF THE DIFFERENT TYPES OF PARASITICIDES ON DUNG BEETLES

McKellar (1997) summarized that the deleterious non-target effects of any antiparasiticide will be determined by the toxicity of the active incredient and its metabolites, the amount and period of active agent and/or metabolite excretion, and the stability of the ecotoxic residue in the environment. For pyrethroids there is evidence that the delivery route of the drug may influence the excretion route as well as the negative impact on the non-target dung fauna (Wardhaugh 2005). Several authors observed that the insecticidal effects of synthetic pyrethroid pour-on formulations were greater than those of spray/dip formulations, which in turn had a more severe impact than ear-tags (Bianchin *et al.* 1992; Kryger *et al.* 2005, 2007). This could be explained by differential absorption of the active ingredients depending on the formulation, and Vale *et al.* (1999) reported that the faecal concentration of deltamethrin was 10-fold higher in cattle treated with a pour-on formulation than in cattle treated with a spray-on preparation.

There are two major approaches used in the assessment of ecotoxicological effects of antiparasitic drugs on dung beetles – laboratory based bioassays and field based studies. In the first approach either dung spiked with the parasiticide in question or dung collected from livestock previously treated with the parasiticide is fed to dung beetles in lab colonies. Then parameters such as adult survival, brood production, brood survival, development time, emergence of the new beetle generation, sex ratios, body weight and size in the new generation are documented and compared to those values derived from set-ups using untreated control dung for beetle food. In the field-based approach, the dung beetle communities from pastures with treated livestock are compared to those from pastures with untreated livestock in terms of species richness and diversity, evenness and dominance, characteristic and distinguishing species. While laboratory based bioassays are more sensitive in registering any adverse effects and are easier and cheaper to conduct, field studies have the advantage of testing the ecotoxicological impact of veterinary pharmaceuticals on an entire community of dung beetles under natural conditions. In laboratory bioassays, it is important to remember that results retrieved on one dung beetle species are not automatically valid for other species. In field studies, results from one specific pasture system cannot be taken as generally valid for all grazing systems. The environmental impact of antiparasitic drugs depends on the specific habitat and cannot be extrapolated to other habitats with totally different dung beetle communities and climatic and edaphic conditions.

22.4.1 Non-target effects of anthelmintics

According to Wardhaugh (2005) many of the veterinary pharmaceuticals used for control of internal parasites are excreted mainly via the urine (see Table 22.1) and therefore are unlikely to have a significant non-target effect on coprophagous organisms. For albendazole there are data supporting this idea (Ward-

Table 22.1. Major veterinary pharmaceuticals for parasite control on livestock, their main target organism and excretion route. (Adapted from Wardhaugh 2005 and Floate *et al.* 2005).

Group / Class / Active Ingredient	Target Organism	Excretion Route
1. Anthelminthics		
Benzimidazoles		
Albendazole	Liver fluke, lung-, round-, tapeworms	Urine
Fenbendazole	Lung-, round-, tapeworms	Faeces
Mebendazole	Flukes, lung-, round-, tapeworms	Faeces
Oxfendazole	Lung-, round-, tapeworms	Faeces
Triclabendazole	Liver Fluke	Faeces
Imidazothiazoles		
Levamisole	Lung-and roundworms	Urine
Salicylanilides et al.		
Closantel	Flukes, lung-, round-, tapeworms	Faeces
Nitroxynil	Flukes, roundworms	Urine
Tetrahydropyrimidines		
Morantel citrate	Barbers pole worm, brown stomach worm	Faeces
2. Ectocides		
Organophosphates		
Diazinon	Blow flies, keds, lice, ticks	Urine
Chlorfenvinphos	Blow flies, lice, ticks	Urine
Insect Growth Regulators		
Cyromazine	Blow flies	Urine
Dicyclanil	Blow flies	uncertain
Diflubenzuron	Blow flies, lice	Faeces
Fluazuron	Ticks	Faeces
Synthetic Pyrethroids		
Cyhalothrin	Itch mite, keds, lice	Faeces
Cypermethrin	Biting flies, blow fly, lice, scab, ticks	Faeces
Deltamethrin	Biting-, blow-, head fly, keds, lice, ticks	Faeces
Flumethrin	Ticks	Faeces
3. Endectocides		
Macrocyclic Lactones		
Abamectin	Lice, lungworms, mites, nematodes, warbles	Faeces
Doramectin	Gastrointest. worms, lice, lungworms, mites	Faeces
Eprinomectin	Lice, lung- and roundworms, mites, warbles	Faeces
Ivermectin	Lice, lung- and roundworms, mites, warbles	Faeces
Moxidectin	Gastrointestinal worms, lungworms	Faeces

haugh *et al.* 2001a). Levamisole belongs to the class of imidazothiazoles and is used as an anthelmintic mainly against roundworms and lungworms (Table 22.1). It acts as a cholinergic antagonist, more specifically it acts at nicotinic neuromuscular receptors in nematodes (McKellar 1997).

Triclabendazole is an anthelmintic against liver fluke belonging to the benzimidazoles. These antiparasitic agents bind to nematode tubulin and also inhibit fungal growth. The latter action could negatively affect the dung fauna that depends on fungi; especially since triclabendazole is mostly excreted in the faeces and is thought to resist degradation in the dung (McKellar 1997). However, faecal residues or metabolites of benzimidazole are not thought to be harmful to invertebrates in the dung pats (Lumaret and Errouissi, 2002). Blume *et al.* (1976) and Ridsdill-Smith (1988) published supporting data for the harmlessness of levamisole for the invertebrate dung fauna. And a recent whole-season field study in South Africa failed to observe any adverse effects of a combined levamisole/triclabendazole treatment in cattle on the grassveld dung beetle fauna (Kryger *et al.* submitted). Even morantel, fenbendazole and mebendazole, despite being excreted mainly via the faeces of the treated livestock, appear to be harmless to dung dwelling and feeding organisms (McKellar 1997; Strong *et al.* 1996; Lumaret 1986, respectively). Insecticidal activity has only been reported for oxfendazole applied on sheep and goats, where 65-80% of the dose is excreted in the faeces. Wardhaugh *et al.* (1993) found adverse effects of the oxfendazole residues on larvae of the bush fly (*M. vetustissima*) but no effect on earthworms or dung beetles. For some commonly used anthelmintics there is no available information on any non-target toxicity; these include closantel, netobimin, nitroxynil, and pyrantel (Floate *et al.* 2005). In the case of closantel such ecotoxicological effects on dung beetles are possible, since it is poorly metabolized and up to 80% of the dose is eliminated unaltered in the faeces (Wardhaugh 2005).

22.4.2 Non-target effects of ectocides

22.4.2.1 Organophosphates

Studies from the 1970s and 1980s showed that some of the then widely used organophosphates (coumaphos, dichlorvos, ruelene) were very effective against fly larvae in livestock faeces, but they were also harmful to dung beetles (for instance the species *Onthophagus gazella*) (Blume *et al.* 1976; Lumaret 1986; Miller and Pickens 1973). Unfortunately, there are no data available on organophosphates currently in use. Since organophosphates, when applied topically or parenterally, are generally rapidly metabolized and excreted predominantly in urine, Wardhaugh (2005) and Floate *et al.* (2005) suggested that they are not likely to majorly impact on coprophagous beetles. However, the same authors also cautioned that further studies on the more frequently used organophosphate compounds should be undertaken, because of their importance in the control of myasis flies and lice.

22.4.2.2 Insect growth regulators

Insect growth regulators are chemical agents that disrupt the life cycle of insects in various ways (mostly by inhibiting chitin synthesis in larval stages of the target organisms) and thus can be used as tools in parasite control. Not much is known about the environmental risk of these pesticides (Floate *et al.* 2005). It has been shown that triflumuron and methoprene act against larvae of coprophagous Diptera (Fincher 1991; Miller 1982; Miller *et al.* 1979). Diflubenzuron is an insect growth regulator that is used on cattle and sheep against lice, but it also acts against various coprophagous Diptera (see Table 22.1). The faeces of animals treated with a diflubenzuron bolus were lethal to fly larvae (*H. irritans*) for up to 21 weeks and lethal to the larvae of two species of dung beetles (*O. gazella* and *Sisyphus rubrus*) for seven weeks (Fincher 1991). Wardhaugh (2005) mentioned that a dust formulation of diflubenzuron is also toxic to Diptera larvae. Fluazuron (benzoylphenyl urea) is a systemic chitin esterase inhibitor with relatively poor insecticidal properties but a high toxicity against ticks, especially the blue tick (*Rhipicephalus* (*Boophilus*) *decoloratus*, Bull *et al.* 1996). Maree and Casey (1993) recorded the development of resistance in South African *R. decoloratus* to DDT, organophosphates, carbamates, synthetic pyrethroids and toxaphene. Since there is no widespread resistance in natural pest populations against benzoylphenyl urea chitin-synthesis-inhibitors, they have gained considerable popularity (Wilson and Cain 1997) and fluazuron is therefore widely used in tick-control, especially in Australia and South Africa (Wardhaugh 2005; Kryger *et al.* 2005, 2007 respectively). As a consequence, and because this tickicide is mainly excreted via the faeces, there were concerns about adverse non-target effects of fluazuron on coprophaguous beetles (Wardhaugh 2005).

In laboratory-based bioassays it has been found that exposure to fluazuron leads to reduced brood production in *O. gazella*, and *O. taurus* but had no detrimental effect on brood production or egg to adult development in the dung beetle species *Euoniticellus intermedius* (Fisara, 1994, 1995a,b, 1996a,b). The differences between the two *Onthophagus* species and *E. intermedius* may be explained by the fact that various species of beetles have different tolerance thresholds to residues of antiparasitic drugs, it is well established that the action of benzoylphenyl urea compounds is highly selective (Wardhaugh *et al.* 1998). In two field trials, Kryger *et al.* (2005 and submitted) found no indication for any ecotoxicologial impact of fluazuron treatment of cattle on dung beetle communities. Furthermore, a laboratory-based bioassay detected no indication of any lethal or sub-lethal effects of fluazuron on the dung beetle species *O. gazella* (Kryger *et al.* 2007; Tables 22.2, 22.3, 22.4). This differed from the results generated by Fisara (1994, 1996b) on the same dung beetle species. These conflicting findings may be the result of differing genetic strains of *O. gazella* or varying laboratory conditions or a combination of those (compare Krüger and Scholtz 1997). As stated in Forbes and Forbes (1994), the results of single species laboratory tests depend on various biotic (e.g. genetic) and abiotic factors (e.g. temperature, humidity, dung-pH and -moisture; see also Edwards 1991; Cook *et al.* 1995; Wardhaugh *et al.* 2001b).

Table 22.2. Percentage corrected mortality calculated following Abbott (1925) and mean number of adult F1 *Onthophagus gazella* (per pair) surviving seven to 14 days of exposure to dung from cattle treated with a fluazuron pour-on and to control dung. All comparisons between treatment and control group were statistically non-significant (Mann-Whitney U Test), n = number of F1 beetle pairs. (Adapted from Kryger *et al.* 2007).

Week1 Control			**Fluazuron**			**Week2 Control**		**Fluazuron**		
day	**n**	**x̄, ± SD**	**n**	**x̄, ± SD**	**% mort**	**n**	**x̄, ± SD**	**n**	**x̄, ± SD**	**% mort**
1	10	1.90 ± 0.10	10	2.00 ± 0.00	-5.26	10	1.80 ± 0.13	10	1.90 ± 0.10	-5.56
2	10	1.70 ± 0.15	10	2.00 ± 0.00	-17.65	10	1.60 ± 0.16	10	1.80 ± 0.13	-12.50
3	10	1.90 ± 0.10	10	2.00 ± 0.00	-5.26	10	1.90 ± 0.10	10	1.80 ± 0.13	5.26
5	10	1.90 ± 0.10	10	2.00 ± 0.00	-5.26	10	1.70 ± 0.21	10	1.50 ± 0.22	11.77
7	10	1.90 ± 0.10	10	2.00 ± 0.00	-5.26	10	1.80 ± 0.13	10	1.80 ± 0.13	0.00
14	10	2.00 ± 0.00	10	2.00 ± 0.00	0.00	10	1.90 ± 0.10	10	2.00 ± 0.00	-5.26
21	10	2.00 ± 0.00	10	2.00 ± 0.00	0.00	10	2.00 ± 0.00	10	1.90 ± 0.10	5.00
28	10	1.90 ± 0.10	10	2.00 ± 0.00	-5.26	10	1.90 ± 0.10	10	1.90 ± 0.10	0.00

Table 22.3. Mean number of F2 brood balls formed per parental F1 *Onthophagus gazella* pair in the second experimental week with dung from cattle treated with fluazuron pour-on and with control dung. * = P<0.05; Mann-Whitney U Test, n = number of parental F1 beetle pairs. (Adapted from Kryger *et al*. 2007).

	Control		**Fluazuron**	
day	**n**	**x̄, ± SD**	**n**	**x̄, ± SD**
1	10	22.90 ± 5.82	10	31.20 ± 8.18
2	10	19.50 ± 5.83	10	19.70 ± 5.82
3	10	17.40 ± 4.47 *	10	34.90 ± 6.10
5	10	13.30 ± 5.11	10	8.80 ± 4.03
7	10	20.40 ± 3.40	10	19.20 ± 5.05
14	10	42.70 ± 3.20	10	42.80 ± 4.59
21	10	10.30 ± 5.25	10	22.90 ± 5.36
28	10	19.50 ± 5.63	10	18.80 ± 5.54

Table 22.4. Mean number of adult F2 *Onthophagus gazella* emerged from brood balls (per F1 parental pair) formed with dung from cattle treated with fluazuron pour-on and with control dung. * = P<0.05; Mann-Whitney U Test, n = number of parental F1 beetle pairs. (Adapted from Kryger *et al*. 2007).

	Week1 Control		**Fluazuron**		**Week2 Control**		**Fluazuron**	
day	**n**	**x̄, ± SD**	**n**	**x̄, ± SD**	**n**	**x̄, ± SD**	**n**	**x̄, ± SD**
1	5	15.00 ± 6.24	2	9.50 ± 4.50	8	20.50 ± 3.67	10	22.60 ± 6.56
2	3	30.33 ± 15.56	3	12.66 ± 7.86	8	11.13 ± 3.50	8	9.50 ± 2.17
3	7	21.43 ± 3.64	5	15.00 ± 4.04	9	11.22 ± 3.24	9	20.00 ± 2.53
5	5	7.80 ± 2.75	0	0.00 ± 0.00	6	4.00 ± 1.84	6	11.33 ± 5.02
7	9	11.44 ± 2.59	8	13.75 ± 4.45	10	8.40 ± 2.25	9	10.44 ± 2.52
14	7	8.00 ± 3.83	8	3.37 ± 0.96	10	8.50 ± 1.62	10	5.70 ± 2.20
21	5	7.00 ± 2.10	5	12.00 ± 4.11	5	11.20 ± 5.11	9	13.11 ± 3.36
28	7	6.29 ± 2.69	7	6.14 ± 2.50	7	6.14 ± 2.18 *	7	1. 43 ± 0.57

22.4.2.3 Synthetic pyrethroids

Synthetic pyrethroids, derivatives of natural pyrethrins, are synthetic axonic poisons that work by keeping the sodium channels in the neural membranes of insects open, thus preventing the nerves from de-exciting, and paralyzing the insect. They are extremely active against insects and mites, but show low toxicity for birds and mammals (Wardhaugh and Beckmann, 1996/97). Therefore, synthetic pyrethroids were initially regarded as environmentally friendly alternatives in parasite management. However, several studies from various countries indicated that dung from cattle treated with various synthetic pyrethroids can be extremely toxic to beneficial dung beetles and dung-breeding flies. The toxicity was observed for periods of two weeks or more after the treatment with cypermethrin, deltamethrin or cyhalothrin. Among these studies were Bianchin *et al.* (1992, 1997, 1998) from Brazil, Krüger *et al.* (1999) and Vale *et al.* (1999) from southern Africa, Sommer *et al.* (2001) from Denmark, and Wardhaugh *et al.* (1998) from Australia.

As mentioned above, it is suspected that the formulation, and consequently the mode of application, plays a major role in the toxic impact of pyrethroids. This could explain the following contradictory results: In a laboratory bioassay Krüger *et al.* (1999) found 80-100% mortality among dung beetles of the species *E. intermedius* exposed to dung from cattle treated with a cypermethrin pour-on formulation for up to seven days post-treatment (Tables 22.5, 22.6). In another laboratory bioassay, Kryger *et al.* (2006b) could not discover any evidence for increased mortality or reduced fertility / fecundity among beetles of the same species feeding on dung from cattle treated with a cypermethrin spray-on formulation (Tables 22.7, 22.8). Bang *et al.* (2007), however, found lethal and sub-lethal toxic effects of a cypermethrin / chlorpyrifos spray-on in the dung beetle species *Copris tripartitus*. In a field study conducted by Kryger *et al.* (submitted) no adverse effects of cypermethrin spray-on treatment of cattle could be detected in South African dung beetles communities.

For flumethrin the non-target action against dung beetles remains controversial: initially there were reports by Bianchin *et al.* (1997) that flumethrin residues were lethal to adult dung beetles for up to 18 days after the drug applica-

Table 22.5. Mean number of adult F1 *Euoniticellus intermedius* surviving seven days of exposure to dung from cattle previously treated with a cypermethrin pour-on and to control dung. ** = P<0.01 and *** = P<0.001; Mann-Whitney U test. (Adapted from Krüger *et al.* 1999).

	Control		**Cypermethrin pour-on**	
Day after treatment	**n**	**$\bar{x}$, ± SE**	**n**	**$\bar{x}$, ± SE**
1	5	1.8 ± 0.20	5	1.6 ± 0.25
2	10	1.8 ± 0.13	10	0
3	5	2.0 ± 0.00	5	0.4 ± 0.25**
5	5	1.6 ± 0.25	5	0
7	10	1.9 ± 0.10	10	0.1 ± 0.10***
14	10	1.9 ± 0.10	10	2.0 ± 0.00
21	10	1.9 ± 0.10	10	1.9 ± 0.10
28	10	1.9 ± 0.10	10	1.9 ± 0.10

Table 22.6. Mean number of F2 brood balls formed by *Euoniticellus intermedius* F1 adults with dung from control cattle and from cypermethrin pour-on treated cattle, * = $P<0.05$ and ** = $P<0.01$; a = sample size too small for statistical analysis; Mann-Whitney U Test. (Adapted from Krüger *et al.* 1999).

	Week1Control		**Cypermethrin pour-on**		**Week2 Control**		**Cypermethrin pour-on**	
Day after treatment	**n**	**$\bar{x}$, ± SE**	**n**	**$\bar{x}$, ± SE**	**n**	**$\bar{x}$, ± SE**	**n**	**$\bar{x}$, ± SE**
1	5	13.00 ± 3.5	5	7.0 ± 3.1	4	16.8 ± 2.2	3	17.3 ± 0.7^{a}
2	10	7.3 ± 1.3	10	0	8	10.5 ± 3.4	-	-
3	5	15.2 ± 2.6	5	0.8 ± 0.8**	5	9.4 ± 1.9	-	-
5	5	1.2 ± 1.2	5	0	3	9.7 ± 3.9	-	-
7	10	3.8 ± 1.1	10	0	9	9.3 ± 1.3	-	-
14	10	7.9 ± 1.9	10	5.1 ± 4.0	9	9.3 ± 1.5	10	10.1 ± 1.3
21	9	6.2 ± 1.5	9	1.3 ± 0.5*	9	9.8 ± 1.6	9	7.0 ± 1.4
28	10	5.6 ± 1.2	10	5.9 ± 1.3	9	9.0 ± 1.9	9	10. 9 ± 1.5

Table 22.7. Mean number of adult F1 *Euoniticellus intermedius* (per pair) surviving seven and 14 days of exposure to control dung and to dung from cattle previously treated with a cypermethrin spray; n = number of beetle pairs, m = median, 25-75% = interquartile range. (Adapted from Kryger *et al.* 2006b).

	Week1 Control		**Cypermethrin spray**		**Week2 Control**		**Cypermethrin spray**	
Day after treatment	**n**	**m / 25-75%s**	**n**	**m / 25-75%s**	**n**	**m / 25-75%s**	**n**	**m / 25-75%s**
1	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2
2	10	2 / 2 -2	10	2 / 2 -2	10	2 / 2 -2	10	2 / 2 -2
3	10	2 / 2-2	10	2 / 2-2	10	2 / 1-2	10	2 / 2-2
5	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2
7	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2
14	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2
21	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2
28	10	2 / 2-2	10	2 / 2-2	10	2 / 2-2	10	2 / 1-2

tion. Krüger *et al.* (1998) confirmed this in an investigation of dung colonization and degradation in South Africa. However, Krüger *et al.* (1999), using the same application method and dosage rate as Bianchin *et al.* (1997), could not confirm any adverse effects of flumethrin residues on *E. intermedius* (Tables 22.9, 22.10)

Table 22.8. Mean number of F2 brood balls formed by *Euoniticellus intermedius* F1 adults with dung from control cattle and from cattle treated with a cypermethrin spray; n = number of beetle pairs, m = median, 25-75% = interquartile range. (Adapted from Kryger *et al.* 2006b).

	Week1 Control		**Cypermethrin spray**		**Week2 Control**		**Cypermethrin spray**	
Day after treatment	**n**	**m / 25-75%s**	**n**	**m / 25-75%s**	**n**	**m / 25-75%s**	**n**	**m / 25-75%s**
1	10	11 / 4-28	10	10.5 / 8 - 14	10	13 / 10 - 22	10	11.5 / 7 - 16
2	10	15 / 13 - 17	10	15 / 11 -18	10	13.5 / 10 - 19	10	11.5 / 5 - 22
3	10	21 / 8 - 22	10	14 / 10 - 22	10	17 / 14 - 27	10	19.5 / 15 - 22
5	9	13 / 5 - 21	10	14 / 11 - 19	9	7 / 4 - 9	10	17.5 / 14 - 19
7	9	14 / 12 - 18	10	19 / 15 - 22	9	9 / 6 - 16	10	14.5 / 12 - 19
14	10	13.5 / 8 - 16	10	12 / 3 -14	10	15.5 / 13 - 18	10	17 / 10 - 21
21	10	9 / 4 - 17	10	6 / 0 - 13	10	12 / 11 - 13	9	10 / 6 - 11
28	10	7.5 / 5 - 19	10	11 / 5 -16	10	11 / 4 - 17	9	9 / 7 - 16

Table 22.9. Mean number of adult F1 *Euoniticellus intermedius* surviving seven days of exposure to dung from cattle previously treated with a flumethrin pour-on and to control dung, no significant differences using Mann-Whitney U test. (Adapted from Krüger *et al.* 1999).

	Control		**Flumethrin pour-on**	
Day after treatment	**n**	**x̄, ± SE**	**n**	**x̄, ± SE**
1	7	2.0 ± 0.00	7	1.9 ± 0.14
2	10	1.9 ± 0.10	10	1.7 ± 0.15
3	10	1.8 ± 0.13	10	1.8 ± 0.13
5	5	1.8 ± 0.20	5	1.8 ± 0.20
7	9	1.9 ± 0.11	9	1.8 ± 0.15
14	4	1.8 ± 0.25	4	2.0 ± 0.00
21	5	1.8 ± 0.20	5	2.0 ± 0.00
28	5	2.0 ± 0.00	5	2.0 ± 0.00

while they found significant toxic effects of cypermethrin in the same study (see above, and Tables 22.7, 22.8) (the experimental set-up was well suited to detect any adverse effects). Differences in results among studies may be due to different laboratory assay test organisms (*O. gazella* in the case of Bianchin *et al.* 1997 versus *E. intermedius* in the case of Krüger *et al.* 1999).

Alternatively, the treated cattle in Bianchin *et al.*'s (1997) study may have been allowed to auto- or allo-groom which could have dramatically increased

Table 22.10. Mean number of F2 brood balls formed by *Euoniticellus intermedius* F1 adults with dung from control cattle and from flumethrin pour-on treated cattle. * = $P<0.05$, a = sample size too small for statistical analysis; Mann-Whitney U Test. (Adapted from Krüger *et al.* 1999).

	Week1 Control		**Flumethrin pour-on**		**Week2 Control**		**Flumethrin pour-on**	
Day after treatment	**n**	**$\bar{x}$, ± SE**	**n**	**$\bar{x}$, ± SE**	**n**	**$\bar{x}$, ± SE**	**n**	**$\bar{x}$, ± SE**
1	7	12.4 ± 3.0	6	7.0 ± 1.6	7	13.4 ± 1.8	6	8.2 ± 2.6
2	10	13.9 ± 1.2	8	12.6 ± 1.2	8	11.9 ± 1.2	8	13.4 ± 1.8
3	9	15.1 ± 1.4	10	12.3 ± 2.8	9	17.2 ± 1.4	10	16.4 ± 0.9
5	5	10.6 ± 1.6	4	8.0 ± 1.7	4	12.8 ± 3.3	4	11.5 ± 1.6
7	8	12.5 ± 1.1	10	7.1 ±1.3*	8	10.5 ± 1.0	7	6.6 ± 1.8
14	4	14.5 ± 3.3	4	8.0 ± 2.1	2	5.0 ± 1.0	4	10.8 ± 1.3[a]
21	5	16.8 ± 2.4	5	13.2 ± 1.9	5	12.6 ± 2.5	5	11.0 ± 2.2
28	5	3.0 ± 2.3	5	5.6 ± 0.9	5	5.8 ± 2.9	5	4.8 ± 1.9

the systemic uptake and hence the dose of the parasiticide (see Laffont *et al.* 2001 for grooming effects in this context). In support of the low or even absent toxicity of flumethrin on dung dwelling organisms, Sommer *et al.* (2001) found no negative impact of faecal flumethrin residues on laval survival in the common dung fly *Neomyia cornicina* (Muscidae), while in the same study residues of cyfluthrin, cypermethrin, and deltamethrin were found to exert a lethal impact for up to two weeks after treatment.

22.4.3 Non-target effects of endectocides

Endectocides consist of various macrocyclic lactones belonging to the avermectins and milbemycins. Macrocyclic lactones, especially ivermectin, are commonly used because of their broad range of activity against gastro-intestinal nematodes and lungworms (anthelmintic) as well as arthropod endo- and ectoparasites (hence the term endectocide) while possessing only low vertebrate toxicity (Benz *et al.*, 1989; Pulliam and Preston, 1989; Strong and Wall, 1990; Wardhaugh and Beckmann, 1996/97). These substances affect nematodes and arthropods by activating glutamate-gated chloride channels, and in arthropods, also GABA-activated chloride channels (Arena *et al.* 1995; Cully *et al.* 1994; Duce and Scott 1985). The mode of action of endectocides is not specific to any parasitic nematode or arthropod groups and therefore they carry the potential of significant ecotoxicological effects on non-target organisms (McKellar 1997).

Many tests have been conducted on the environmental toxicity of the widely used avermectins (e.g. Boxall *et al.* 2007; Dadour *et al.* 1999; Diao *et al.* 2007; Floate 1998, 2006, 2007; Floate *et al.* 2005; Hempel *et al.* 2006; Iglesias *et al.* 2006; Kolar *et al.* 2008; Krüger and Scholtz 1997, 1998a,b; Lumaret *et al.* 2007; McCracken and Foster 1993; Ridsdill-Smith *et al.* 1993, 1996; Sommer *et al.* 1993; Strong and Wall 1994; Strong *et al.* 1993; Wardhaugh and Rodriguez-Menendez 1988).

Strong (1993) reported lethal action of the avermectins against adult and larval insects as well as sub-lethal effects on growth, moulting, metamorphosis and reproduction. In general, endectocides show the strongest action against flies and beetles (McKellar 1997). This includes the non-parasitic fly groups - Muscoidea, Sepsidae, Sphaeroceridae, and many Cyclorrapha and/or their larvae (Madsen *et al.* 1990; Schaper and Liebisch 1991; Wardhaugh and Rodriguez-Menendez 1988). There are many reports on adverse effects of endectocides on dung beetles. Sommer and Overgaard Nielsen (1992) and Sommer *et al.* (1993) showed in laboratory bioassays that subcutaneous injections of avermectin/ivermectin to heifers can negatively impact on the larvae of *Diastellopalpus quinquedens* and *O. gazella*. Roncalli (1989) found the same for *O. binodis*, Ridsdill-Smith (1993) for *O. ferox*, and Krüger and Scholtz (1997) for *E. intermedius* and *Onitis alexis*. Furthermore, it was observed that ivermectin is lethal to adults and reduces adult emergence in *E. intermedius* (Fincher 1992; Krüger and Scholtz 1997).

Field studies in South Africa discovered a reduction in species diversity and an increase in species dominance in dung beetle communities as a consequence of ivermection treatment of cattle under drought conditions (Krüger and Scholtz 1998a) but not under high-rainfall conditions (Krüger and Scholtz 1998b). A follow-up field study by Kryger *et al.* (2005) at the same study site (two South African cattle farms under extensive farming management) confirmed the absence of any observable adverse effects of ivermectin treatment of cattle on the local dung beetle communities: species richness and diversity were unaffected in the treated communities and the ecological similarity of the treated and control communities remained high throughout the trial (Fig. 22.1). This follow-up study was carried out in a year with above average rainfall.

Summarizing the results of many field studies and laboratory assays on the non-target effects of macrocyclic lactones, Floate *et al.* (2005) suggested that these endectocides can be ranked along a gradient of decreasing toxicity to coprophagous insects with abamectin being the most toxic, followed by doramectin and ivermectin, followed by eprinomectin. Residues of abamectin have been shown to be drastically more harmful to dung beetle larvae than ivermectin residues (Roncalli 1989). Laboratory assays comparing the toxicity

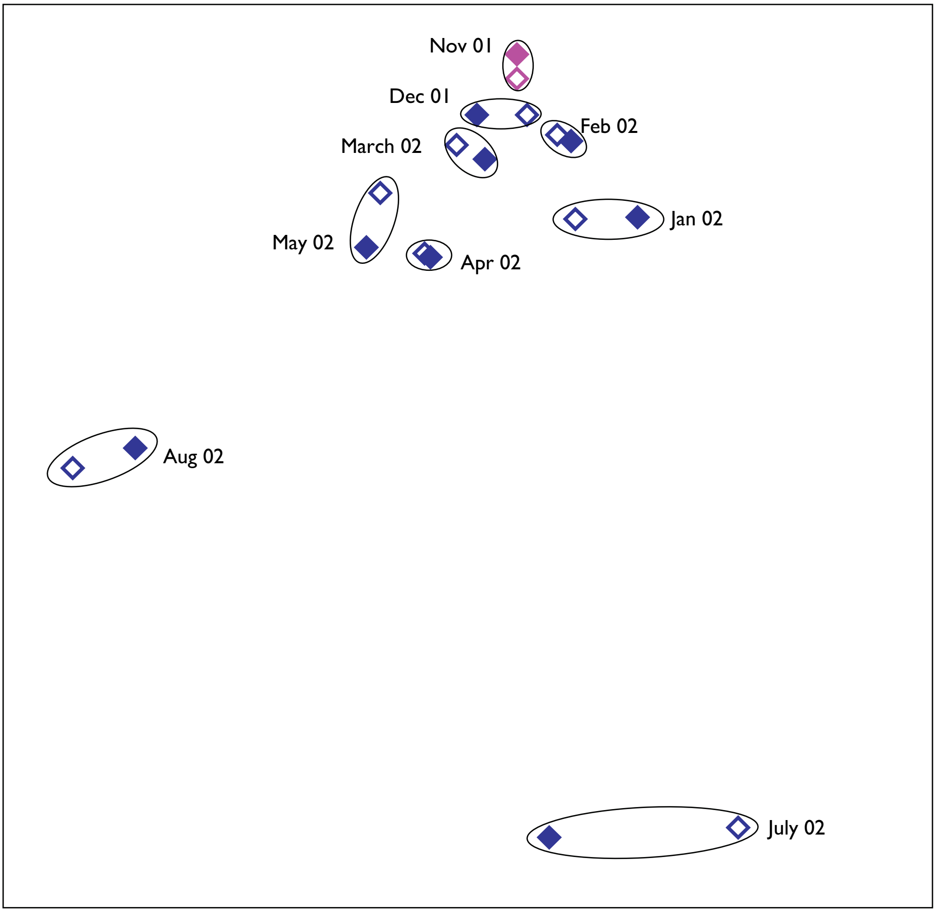

Fig. 22.1. Two-dimensional, non-metric scaling ordination of the relative, fourth-root transformed species abundance data of pooled samples collected on nine different dates on South African farms; open diamonds = dung beetle communities on control paddocks with untreated cattle, closed diamonds = dung beetle communities on paddocks with fluazuron-ivermectin treated cattle. The dung beetle communities sampled in November 01 represent the pre-treatment situation. (After Kryger *et al.* 2005).

of abamectin and doramectin to adults and larvae of the dung beetle species *Onthophagus binodis* found that the adverse effects of doramectin were confined to dung voided during the first six days after drug application, whereas abamectin residues were toxic up to 42 days post-treatment (Dadour *et al.* 2000).

The milbemycin moxidectin is thought to be significantly less toxic to dung-dwelling arthropods than any of the avermectins (Floate *et al.* 2005). An estimate by Doherty *et al*. (1994) stated that moxidectin was 64 times less toxic to larvae of Diptera and Coleoptera than abamectin. Most other studies on moxidectin supported the hypothesis that this milbemycin does not negatively impact upon the beneficial dung fauna when used according to the manufacturer's recommendations (Fincher and Wang 1992; Floate *et al*. 2001; Strong and Wall 1004; Wardhaugh *et al*. 1996, 2001b). However, Hempel *et al*. (2006) compared the toxicity of four veterinary parasiticides on larvae of *Aphodius constans* and found that the toxicity of moxidectin is only five times weaker than that of ivermectin.

CHAPTER 23
MITIGATION OPTIONS

The conservation of dung beetles and their various habitats is imperative to the integrity of many different ecosystems and should therefore be made a focus of attention. Unfortunately, conservation efforts still focus on vertebrates and models of conservation management underestimate the large differences in life-history traits of vertebrates and invertebrates (Tscharntke 1992) – thereby not doing justice to the needs of the latter. This disparity needs to be addressed. Furthermore, the public, and especially decision makers, need to be better informed and thus empowered to make the right choices and develop the necessary policies. Informed consumers will also be better equipped to use their power and exert pressure by adapting their buying behaviour.

23.1 MITIGATING ADVERSE EFFECTS OF CHEMICAL PARASITE MANAGEMENT

There is a growing global awareness of the importance of dung beetles for the sustainability of agro-ecosystems. In recent years this issue has also received the attention of regulatory agencies (see Floate *et al.* 2005; Hempel *et al.* 2006). The International Cooperation on Harmonization of Technical Requirements for Registration of Veterinary Medicinal Products (VICH) has produced a guidance paper that makes it a requirement for new veterinary pharmaceuticals in Japan, Australia, the European Union, Canada, and the US to be tested for their non-target effects on dung flies and beetles. In order to work out standardized test protocols for toxicity testing on dung beetles, the expert working group DOTTS (Dung Organism Toxicity Testing Standardization) was formed in 2001 and is now recognized as officially affiliated with the Society for Environmental Toxicology and Chemistry (SETAC). This working group has successfully developed a standardized test protocol for the beetle species *Aphodius constans* (Hempel *et al.* 2006; Römbke *et al.* 2006) and is aiming to validate this test according to the Test Guideline Program of the Organisation for Economic Co-operation and Development (OECD).

In this context, it would be necessary that each new antiparasitic product gets tested for its toxicity, because even if products contain the same active ingredients the various formulations may have totally different carrier substances or additives as well as different administration routes, and therefore, potentially different ecotoxicological effects (compare Floate *et al.* 2005). If field studies are to be a part of this standardized testing, it would also be important to undertake such field trials for the various bioregions and habitats where the veterinary pharmaceutical is supposed to be used, because it is not possible to directly extrapolate results from one habitat to others.

Besides regulatory measures, further mitigation possibilities lie in the education and empowerment of livestock farmers. This will have to include general recommendations with regards to the environmental safety of the various antiparasitic products, the dosage and the timing of treatment. Overdosing of antiparasitic drugs will often lead to more serious ecotoxicological effects. As also highlighted by Wardhaugh (2005), a general recommendation to livestock producers is to treat livestock at times that are least likely to affect the dung degrading fauna (e.g. not at the peak of seasonal dung beetle activity; see also Ridsdill-Smith *et al.* 1993; Wardhaugh and Beckmann 1996/97) and as infrequently as possible (this also helps slowing down any resistance developments). In South Africa, the Scarab Research Group at the University of Pretoria has registered a three-graded "dung beetle friendliness" trademark that informs livestock farmers about the non-target toxicological effects of parasiticides on dung beetles. Only products that have been shown to be harmless to dung beetles in field studies as well as in laboratory assays are awarded the three-star trademark. In a further attempt to spread vital information on the topic of parasite management and dung beetles, the Scarab Research Group has developed a website under www.dungbeetlesforafrica.org .

23.2 MITIGATING GENERAL THREATS TO DUNG BEETLES AND BIODIVERSITY

According to the FAO (2006b), the livestock sector is generally driven by various, sometimes conflicting policy objectives and thus it is difficult for decision makers to equally address economic, social and environmental issues. This is probably also true for many other relevant sectors with regards to dung beetle conservation.

However, as we have clearly illustrated for the example of dung beetles, that ecological and economic dimensions are intrinsically interwoven. Only an ecologically intact system can provide us with the services that directly translate into economic benefits, and on which we ultimately depend for our long-term survival. And yet this is very rarely understood or acknowledged. Logging companies, fast food companies and rural subsistence farmers alike are motivated by short-term goals such as maximized profit or their bare survival, respectively. While more information and education may enhance the willingness of some to adapt more sustainable ways (FAO 2006b), commercial and political pressure by consumers may be a much more efficient tool to influence decision makers to act more intelligently, responsibly and in an environmentally friendly manner.

In "Living beyond our means" Reid *et al.* (2005b) listed a few mitigation suggestions that are available to us in order to reduce the further degradation of ecosystems. The first among these steps is to bring about a change in the economic background to decision-making by taking into account the value of all ecosystem services and by rewarding landowners (and livestock farmers) for applying sustainable management practices that protect these ecosystem services.

A second step concerns an improvement of policy and ecosystem management planning by integrating the decision-making processes of different departments and international institutions. With regard to the conservation of dung beetles, the above mentioned standardization of toxicity testing by the VICH is certainly a step into the right direction.

Influencing individual behaviour by providing public education on the value of, and the threats to, ecosystems and their services is another mitigation tool mentioned by Reid *et al.* (2005b). In this context it is also effective to establish reliable certification systems that give consumers the choice to selectively buy sustainably produced goods. In many countries this has already begun. In South Africa there is one striking example extending this principle to dung beetles, the marketing of "Certified Natural Meat" which is based on an assessment of the health of the local dung beetle communities on the pastures where the livestock graze.

Lastly, Reid *et al.* (2005b) recommended that we invest in science and technology that enables us to increase food production with minimal harmful trade-offs and that we restore degraded ecosystems.

CHAPTER 24
CONCLUDING REMARKS

> *"Everyone in the world depends on nature and ecosystem services to provide the conditions for a decent, healthy, and secure life."*
>
> (Reid *et al*. 2005b, *Living beyond our means: Natural assets and human well-being*, p 3)

Mankind in its soaring success as a species surviving and thriving even under great difficulties has alienated itself dangerously from its natural origins and currently "survives" in an illusion of isolation and separateness. The superiority complex that arose with the notion of "man as the crown of creation" led to a lifestyle of relentless and remorseless exploitation of nature driven by insatiable human greed. So long has this dogma of man as the far removed and untouchable semi-god persisted in, and spread through, our societies that by today, many especially urban people, have totally disconnected their awareness from their intrinsic dependence on nature. This deep deterioration of the relationship between human society and the natural world has been called "uncultural" by Halffter (2005). This author further stressed, that it is not sufficient to gather scientific knowledge if we really want to succeed in preserving biological diversity. We need to develop a culture of biodiversity conservation, where our motivation to accept and implement conservation measures and policies is fuelled by ethical and aesthetic values as much as by scientific insight. Halffter (2005) suggested we make a conscious effort to educate our people to appreciate nature and to understand our place within the natural environment. We need to look at ourselves critically and objectively and re-adjust our cultural perspective; we need to get our priorities right.

Looking at oneself critically and objectively in all honesty demands a certain degree of maturity as well as humility; qualities that are not particularly cultivated in our civilization that values the shortsighted impulsiveness of youth over the wisdom of age and the egomania of self-infatuated "go-getters" over the reflective empathy of the "Albert Schweitzers", the aggressive extrovert male principle over the caring introvert female, our faculty of reason ("logos") over our faculty of feeling ("pathos").

But it is high time that we do look at ourselves critically and evaluate objectively how functional our current culture (or lack thereof) really is. It is high time that we finally wake up from our dream of being separate from nature, of being superior to nature, of being able to dramatically disturb natural systems with indifference and even hostility while presuming that we ourselves are totally immune to the consequences of this abuse. This delusion has slowly but surely turned into a nightmare as our self-centred activities have had many centuries to gather destructive momentum and to do enough accumulative damage to the system that we, too, in reality are a part of and depend upon - nature.

While we may have distanced ourselves emotionally and psychologically from nature, objectively and existentially we still rely completely on the services it delivers (Reid *et al.* 2005b). The ecosystem services provided by intact natural systems contribute to our well-being on many different levels. Reid *et al.* (2005b) summarized that these services support the following constituents of our well-being: basic good life, security, health, good social relations, and freedom of choice and action.

As stated in the Millenium Ecosystem Assessment (Reid *et al.* 2005a), it is our challenge to reverse the degradation of ecosystems while at the same time meeting increasing demands for their services. We are currently indeed "living beyond our means" (Reid *et al.* 2005b) and if we are to survive this crisis we need to address this challenge as a matter of urgency. It will involve significant changes in policies and practices of how we interact with the natural system. We need to stop abusing nature and instead become stewards of nature. We need to reinstate balance in our global ecosystem, in our relationship with nature, and with ourselves.

There is hope, since there is a growing global awareness of threats to the environment and as a result a rising demand for environmental services (FAO 2006b). And after all, the history of our species has demonstrated before that we are sometimes indeed capable of operating at a level more advanced than that of a laboratory colony of bacteria that is mindlessly growing exponentially and relentlessly over-utilizing its resources in the petri-dish until the inevitable fatal collapse. Among the First Nations of North America, it was a wide-spread custom to consider the consequences of one's actions for the next seven generations to come – and only if these extrapolated consequences were deemed to be positive was an action deemed to be justified. So we are gifted with the intelligence to anticipate the long-term consequences of our actions; and we are also gifted with a sense of morality, a wish to do what is right. There have been times in our history when these were stronger than our greed.

> "…, *we shall progressively lose our humanness even on Earth if we continue to pour filth into the atmosphere; to befoul soil, lakes, and rivers; to disfigure landscapes with junkpiles; to destroy wild plants and animals that do not contribute to monetary values; and thus transform the globe into an environment alien to our evolutionary past. The quality of human life is inextricably interwoven with the kinds and variety of stimuli man receives from the Earth and the life if harbours, because human nature is shaped biologically and mentally by external nature.*"
>
> (Dubos 1972, *A God Within*, p 38)

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INDEX

Appendix A.
World genera of dung beetles

Genera	Tribe	Region
Acanthonitis Janssens 1937	Onitini	Afrotropical
Agamopus Bates 1887	Canthonini	Neotropical
Aleiantus Olsoufieff	Canthonini	Madagascar
Aliuscanthoniola Deschodt & Scholtz 2008	Canthonini	Afrotropical
Allogymnopleurus Janssens 1940	Gymnopleurini	Afrotropical, Oriental, Palaearctic (Arabia)
Allonitis Janssens 1936	Onitini	Afrotropical
Alloscelus Boucomont 1923	Onthophagini	Afrotropical
Amietina Cambefort 1981	Onthophagini	Afrotropical
Amphistomus Lansberge 1874	Canthonini	Australasian, Oriental (Moluccas)
Anachalcos Hope 1837	Canthonini	Afrotropical
Anisocanthon Martinez & Perreira 1956	Canthonini	Neotropical
Anoctus Sharp 1875	Onthophagini	Oriental
Anomiopsoides Blackwelder 1944	Eucraniini	Neotropical
Anomiopus Westwood 1842	Dichotomiini	Neotropical, Caribbean
Anonthobium Paulian 1984	Canthonini	New Caledonia
Anonychonitis Janssens 1950	Onitini	Afrotropical
Anoplodrepanus Simonis 1981	Oniticellini	Caribbean
Aphengium Harold 1868	Dichotomiini	Neotropical
Aphengoecus Peringuey 1901	Canthonini	Afrotropical
Apotolamprus Olsoufieff 1947	Canthonini	Madagascar
Aptenocanthon Matthews 1974	Canthonini	Australasian
Aptychonitis Janssens 1937	Onitini	Afrotropical
Arachnodes Westwood 1842	Canthonini	Madagascar
Ateuchus Weber 1801	Dichotomiini	Neotropical, Nearctic, Caribbean
Attavicinus Philips & Bell 2008	Oniticellini	Neotropical

Genera	Tribe	Region
Aulacopris White 1859	Canthonini	Australasian
Baloghonthobium Paulian 1986	Canthonini	New Caledonia
Bdelyropsis Pereira, Vulcano & Martinez 1960	Dichotomiini	Neotropical
Bdelyrus Harold 1869	Dichotomiini	Neotropical
Besourenga Vaz de Mello 2008	Dichotomiini	Neotropical
Bohepilissus Paulian 1975	Canthonini	Afrotropical
Bolbites Harold 1868	Phanaeini	Neotropical
Boletoscapter Matthews 1974	Canthonini	Australasian
Bradypodidium Vaz de Mello 2008	Dichotomiini	Neotropical
Bubas Mulsant 1842	Onitini	Palaearctic
Byrrhidium Harold 1869	Canthonini	Afrotropical
Caccobius Thomson 1859	Onthophagini	Afrotropical, Oriental, Palaearctic
Caeconthobium Paulian 1984	Canthonini	New Caledonia
Cambefortantus Paulian 1886	Canthonini	Madagascar
Cambefortius Branco 1989	Onthophagini	Afrotropical
Canthidium Erichson 1847	Dichotomiini	Neotropical, Nearctic
Canthochilum Chapin 1934	Canthonini	Caribbean
Canthodimorpha Davis, Scholtz, Harrison 1999	Canthonini	Afrotropical
Canthon Hoffmansegg 1817	Canthonini	Neotropical, Nearctic, Caribbean
Canthonella Chapin 1930	Canthonini	Neotropical, Caribbean
Canthonidia Paulian 1939	Canthonini	Neotropical
Canthonosoma MacLeay 1871	Canthonini	Australasian
Canthotrypes Paulian 1939	Canthonini	Neotropical
Cassolus Sharp 1875	Onthophagini	Oriental
Catharsius Hope 1837	Coprini	Afrotropical, Oriental, Palaearctic
Cephalodesmius Westwood 1841	Canthonini	Australasian
Chalcocopris Burmeister 1846	Dichotomiini	Neotropical
Cheironitis van Lansberge 1875	Onitini	Afrotropical, Oriental, Palaearctic
Circellium Latreille 1825	Canthonini	Afrotropical
Cleptocaccobius Cambefort 1984	Onthophagini	Afrotropical, Oriental, Palaearctic
Copridaspidus Boucomont 1920	Coprini	Afrotropical
Copris Muller 1764	Coprini	Afrotropical, Oriental, Palaearctic, Nearctic, Neotropical

Genera	Tribe	Region
Coproecus Reiche 1841	Canthonini	Australasian
Coprophanaeus Olsoufieff 1924	Phanaeini	Neotropical, Nearctic
Coptodactyla Burmeister 1846	Coprini	Australasian
Coptorhina Hope 1830	Dichotomiini	Afrotropical
Cryptocanthon Balthasar 1942	Canthonini	Neotropical
Cyobius Sharp 1875	Onthophagini	Oriental
Cyptochirus Lesne 1900	Onticellini	Afrotropical
Degallieridium Vaz de Mello 2008	Dichotomiini	Neotropical
Delopleurus Erichson 1847	Dichotomiini	Afrotropical, Oriental
Deltepilissus Pereira 1949	Canthonini	Neotropical
Deltochilum Eschscholtz 1822	Canthonini	Neotropical, Nearctic
Deltorrhinum Harold 1867	Canthonini	Neotropical
Demarziella Balthasar 1961	Dichotomiini	Australasian
Dendropaemon Perty 1830	Phanaeini	Neotropical
Diabroctis Gistel 1857	Phanaeini	Neotropical
Diastellopalpus van Lansberge 1886	Onthophagini	Afrotropical
Dichotomius Hope 1838	Dichotomiini	Neotropical, Nearctic
Dicranocara Frolov & Scholtz 2003	Canthonini	Afrotropical
Digitonthophagus Balthasar 1959	Onthophagini	Afrotropical, Oriental, Palaearctic
Diorygopyx Matthews 1974	Canthonini	Australasian
Disphysema Harold 1873	Onthophagini	Oriental
Dorbignyolus Branco 1989	Onthophagini	Afrotropical
Drepanocerus Kirby 1828	Oniticellini	Afrotropical, Oriental, Palaearctic
Drepanoplatynus Boucomont 1921	Oniticellini	Afrotropical
Dwesasilvasedis Deschodt & Scholtz 2008	Canthonini	Afrotropical
Endroedyolus Scholtz & Howden 1987	Canthonini	Afrotropical
Ennearabdus van Lansberge 1874	Eucraniini	Neotropical
Epactoides Olsoufieff 1947	Canthonini	Madagascar
Epilissus Reiche 1841	Canthonini	Madagascar
Epirinus Reiche 1841	Canthonini	Afrotropical
Eucranium Brulle 1834	Eucraniini	Neotropical
Eudinopus Burmeister 1840	Canthonini	Neotropical
Euoniticellus Janssens 1953	Oniticellini	Afrotropical, Oriental, Palaearctic, Caribbean
Euonthophagus Balthasar 1959	Onthophagini	Afrotropical, Palaearctic
Eurysternus Dalman 1824	Eurysternini	Neotropical
Eusaproecius Branco 1989	Onthophagini	Afrotropical

Genera	Tribe	Region
Eutrichillum Martinez 1969	Dichotomiini	Neotropical
Falsignambia Paulian 1987	Canthonini	New Caledonia
Feeridium Vaz de Mello 2008	Dichotomiini	Neotropical
Frankenbergerius Balthasar 1938	Dichotomiini	Afrotropical
Garreta Janssens 1940	Gymnopleurini	Afrotropical, Oriental
Genieridium Vaz de Mello 2008	Dichotomiini	Neotropical
Gilletellus Janssens 1937	Onitini	Afrotropical
Glyphoderus Westwood 1838	Eucraniini	Neotropical
Gromphas Brulle 1834	Phanaeini	Neotropical
Gymnopleurus Illiger 1803	Gymnopleurini	Afrotropical, Oriental, Palaearctic
Gyronotus van Lansberge 1874	Canthonini	Afrotropical
Hammondantus Cambefort 1978	Canthonini	Afrotropical
Hansreia Halffter & Martinez 1977	Canthonini	Neotropical
Haroldius Boucomont 1914	Onthophagini	Afrotropical, Oriental
Helictopleurus d'Orbigny 1915	Oniticellini	Madagascar
Heliocopris Hope 1837	Dichotomiini	Afrotropical, Oriental, Palaearctic (Arabia)
Heteroclitopus Peringuey 1901	Onthophagini	Afrotropical
Heteronitis Gillet 1911	Onitini	Afrotropical
Heterosyphus Paulian 1975	Oniticellini	Madagascar
Holocanthon Martinez & Pereira 1956	Canthonini	Neotropical
Holocephalus Hope 1838	Dichotomiini	Neotropical
Homalotarsus Janssens 1932	Phanaeini	Neotropical
Hyalonthophagus Palestrini 1988	Onthophagini	Afrotropical
Hypocanthidium Balthasar 1938	Dichotomiini	Neotropical
Ignambia Heller 1916	Canthonini	New Caledonia
Isocopris Pereira & Martinez 1960	Dichotomiini	Neotropical
Janssensantus Paulian 1976	Canthonini	Afrotropical
Janssensellus Cambefort 1975	Onitini	Afrotropical
Kolbeellus Jacobson 1906	Onitini	Afrotropical
Krikkenius Branco 1991	Onthophagini	Afrotropical
Labroma Sharp 1873	Canthonini	Australasian
Larhodius Balthasar 1963	Canthonini	Oriental
Leotrichillum Vaz de Mello 2008	Dichotomiini	Neotropical
Lepanus Balthasar 1966	Canthonini	Australasian
Liatongus Reitter 1892	Oniticellini	Afrotropical, Oriental, Palaearctic (east), Nearctic
Litocopris Waterhouse 1891	Coprini	Afrotropical

Genera	**Tribe**	**Region**
Lophodonitis Janssens 1938	Onitini	Afrotropical
Macroderes Westwood 1942	Dichotomiini	Afrotropical
Macropanelus Ochi, Kon & Araya 1998	Canthonini	Oriental
Madaphacosoma Paulian 1975	Canthonini	Afrotropical, Madagascar
Malagoniella Martinez 1961	Canthonini	Neotropical, Nearctic
Martinezidium Vaz de Mello 2008	Dichotomiini	Neotropical
Megalonitis Janssens 1937	Onitini	Afrotropical
Megaponerophilus Janssens 1949	Onthophagini	Afrotropical
Megatharsis Waterhouse 1891	Phanaeini	Neotropical
Megathopa Eschscholtz 1822	Canthonini	Neotropical
Megathoposoma Balthasar 1939	Canthonini	Neotropical
Melanocanthon Halffter 1958	Canthonini	Nearctic
Mentophilus Laporte de Castelnau 1840	Canthonini	Australasian
Metacatharsius Paulian 1939	Coprini	Afrotropical, Palaearctic (Saharo-Sindian)
Milichus Peringuey 1901	Onthophagini	Afrotropical
Mimonthophagus Balthasar 1963	Onthophagini	Afrotropical
Monoplistes van Lansberge 1874	Canthonini	Australasian
Namakwanus Scholtz & Howden 1987	Canthonini	Afrotropical
Nanos Westwood 1837	Canthonini	Madagascar
Nebulasilvius Deschodt and Scholtz 2008	Canthonini	Afrotropical
Neonitis Peringuey 1901	Onitini	Afrotropical
Neosaproecius Branco 1990	Onthophagini	Afrotropical
Neosisyphus Muller 1942	Sisyphini	Afrotropical, Oriental
Nesosisyphus Vinson 1946	Sisyphini	Mauritius
Nesovinsonia Martinez & Pereira 1959	Canthonini	Mauritius
Nunoidium Vaz de Mello 2008	Dichotomiini	Neotropical
Ochicanthon Vaz-De-Mello 2003	Canthonini	Oriental
Odontoloma Boheman 1857	Canthonini	Afrotropical
Oficanthon Paulian 1985	Canthonini	Australasian
Oniticellus Lep. Aud. Serville 1825	Oniticellini	Afrotropical, Oriental
Onitis Fabricius 1798	Onitini	Afrotropical, Oriental, Palaearctic, Australasian (New Guinea)
Onoreidium Vaz de Mello 2008	Dichotomiini	Neotropical
Ontherus Erichson 1847	Dichotomiini	Neotropical, Caribbean (Trinidad)

Genera	Tribe	Region
Onthobium Reiche 1860	Canthonini	New Caledonia
Onthophagus Latreille 1802	Onthophagini	Afrotropical, Madagascar, Oriental, Palaearctic, Neotropical, Nearctic, Caribbean, Australasian
Onychothecus Boucomont 1912	Dichotomiini	Oriental
Oruscatus Bates 1870	Phanaeini	Neotropical
Outenikwanus Scholtz & Howden 1987	Canthonini	Afrotropical
Oxysternon Laporte de Castelnau 1840	Phanaeini	Neotropical
Pachylomera Hope 1849	Scarabaeini	Afrotropical
Pachysoma MacLeay 1821	Scarabaeini	Afrotropical
Panelus Lewis 1895	Canthonini	Afrotropical, Oriental, Palaearctic
Paracanthon Balthasar 1938	Canthonini	Neotropical
Parachorius Harold 1873	Dichotomiini	Oriental
Paracryptocanthon Howden & Cook 2002	Canthonini	Neotropical
Paragymnopleurus Shipp 1897	Gymnopleurini	Oriental, Palaearctic (East)
Paroniticellus Balthasar 1963	Canthonini	Australasian
Paraphacosomoides Balthasar 1966	Dichotomiini	Afrotropical, Oriental
Paraphytus Harold 1877	Oniticellini	Palaearctic
Paronthobium Paulian 1984	Canthonini	New Caledonia
Parvuhowdenius Deschodt & Scholtz 2008	Canthonini	Afrotropical
Peckolus Scholtz & Howden 1987	Canthonini	Afrotropical
Pedaria Laporte de Castelnau 1832	Dichotomiini	Afrotropical
Pedaridium Harold 1868	Dichotomiini	Neotropical
Penalus Paulian 1985	Canthonini	Australasian
Peyrierasantus Paulian 1976	Canthonini	Madagascar
Phacosomoides Martinez & Pereira 1959	Canthonini	Madagascar
Phaedotrogus Balthasar 1985	Canthonini	Oriental
Phalops Erichson 1848	Onthophagini	Afrotropical, Oriental, Palaearctic (Arabia, Afghanistan)
Phanaeus MacLeay 1819	Phanaeini	Neotropical, Nearctic
Pinacopodius Branco 1991	Onthophagini	Afrotropical
Pinacotarsus Harold 1875	Onthophagini	Afrotropical
Platyonitis Janssens 1942	Onitini	Afrotropical
Pleuronitis van Lansberge 1875	Onitini	Afrotropical

Genera	Tribe	Region
Proagoderus van Lansberge 1883	Onthophagini	Afrotropical, Oriental, Palaeaearctic (Arabia)
Pseudarachnodes Lebis 1953	Canthonini	Madagascar
Pseudignambia Paulian & Pluot-Sigwalt 1984	Canthonini	Australasian
Pseudocanthon Bates 1887	Canthonini	Neotropical, Nearctic, Caribbean
Pseudochironitis Ferreira 1977	Onitini	Afrotropical
Pseudocopris Ferreira 1960	Coprini	Afrotropical
Pseudonthobium Paulian 1984	Canthonini	New Caledonia
Pseudopedaria Felsche 1904	Coprini	Afrotropical
Pseudosaproecius Balthasar 1941	Onthophagini	Afrotropical
Pseuduroxys Balthasar 1938	Dichotomiini	Neotropical
Pteronyx van Lansberge 1874	Dichotomiini	Neotropical
Pycnopanelus Arrow 1931	Canthonini	Afrotropical, Oriental
Saphobiamorpha Brookes 1944	Canthonini	New Zealand
Saphobius Sharp 1873	Canthonini	New Zealand
Sarophorus Erichson 1847	Dichotomiini	Afrotropical
Sauvagesinella Paulian 1934	Canthonini	Australasian
Scaptocnemis Peringuey 1901	Oniticellini	Afrotropical
Scarabaeus Linnaeus 1758	Scarabaeini	Afrotropical, Madagascar, Oriental, Palaearctic
Scatimus Erichson 1847	Dichotomiini	Neotropical
Scatonomus Erichson 1835	Dichotomiini	Neotropical
Scatrichus Genier & Kohlmann 2003	Dichotomiini	Neotropical
Scybalocanthon Martinez 1948	Canthonini	Neotropical
Scybalophagus Martinez 1953	Canthonini	Neotropical
Sikorantus Paulian 1976	Canthonini	Malagasy
Silvinha Vaz de Mello 2008	Dichotomiini	Neotropical
Sinapisoma Boucomont 1928	Canthonini	Neotropical
Sinodrepanus Simonis 1985	Onticellini (D)	Oriental
Sisyphus Latreille 1807	Sisyphini	Afrotropical, Oriental, Palaearctic, Neotropical
Stiptocnemis Branco 1989	Onthophagini	Afrotropical
Stiptopodius Harold 1871	Onthophagini	Afrotropical
Stiptotarsus Branco 1989	Onthophagini	Afrotropical
Strandius Balthasar 1935	Onthophagini	Oriental, Palaearctic (east)
Streblopus van Lansberge 1874	Canthonini	Neotropical

Genera	Tribe	Region
Sukelus Branco 1992	Onthophagini	Afrotropical
Sulcophanaeus Olsoufieff 1924	Phanaeini	Neotropical, Caribbean
Sylvicanthon Halffter & Martinez 1977	Canthonini	Neotropical
Synapsis Bates 1868	Coprini	Oriental, Palaearctic
Tanzanolus Scholtz & Howden 1987	Canthonini	Afrotropical
Temnoplectron Westwood 1841	Canthonini	Australasian
Tesserodon Hope 1837	Canthonini	Australasian
Tesserodoniella Vaz de Mello & Halffter 2006	Canthonini	Neotropical
Tetraechma Blanchard 1843	Canthonini	Neotropical
Tetramereia Klages 1907	Phanaeini	Neotropical
Thyregis Blackburn 1904	Coprini	Australasian
Tiniocellus Peringuey 1901	Oniticellini	Afrotropical, Oriental
Tomogonus d'Orbigny 1904	Onthophagini	Afrotropical
Tragiscus Klug 1855	Oniticellini	Afrotropical
Trichillidum Vaz de Mello 2008	Dichotomiini	Neotropical
Trichillum Harold 1868	Dichotomiini	Neotropical
Tropidonitis Janssens 1937	Onitini	Afrotropical
Uroxys Westwood 1842	Dichotomiini	Neotropical, Caribbean
Vulcanocanthon Pereira & Martinez 1960	Canthonini	Neotropical
Walterantus Cambefort 1977	Onthophagini	Afrotropical
Xenocanthon Martinez 1952	Canthonini	Neotropical
Xinidium Harold 1869	Dichotomiini	Afrotropical
Yvescambefortius Ochi & Kon 1996	Oniticellini	Oriental
Zonocopris Arrow 1932	Canthonini	Neotropical

Just described not used in analyses		
Eodrepanus Barbero, Palestrini & Roggero 2009	Oniticellini	Afrotropical, Oriental, Palaearctic (fossil)