

Scarabaeid dung beetles are extraordinarily successful on a food resource that is patchy and ephemeral, but also rich: dung, especially from ruminants, contains substantial nitrogen (Hanski 1987). Although both larvae and adults feed on dung of mammalian herbivores, only larvae digest cellulose, with the help of bacteria in a hindgut fermentation chamber, and reingestion of faeces. This ensures maximum utilization of the strictly limited amount of food in the brood ball (Cambeport 1991). Larger particles in fresh dung are indigestible plant fragments, which may be macerated by larvae. By contrast, adults have filtering mouthparts that reject such coarse particles. Recently, latex balls of various diameters, manufactured for calibration of Coulter Counter[®] instruments, were mixed with the preferred dung of 15 species of adult Scarabaeinae (size range 0.05–7.4 g) to determine the maximum size of ingested particles (Fig. 2.10): the range was only 8–50 µm (Holter *et al.* 2002). These very small particles have higher nutritional value because their large surface area to volume ratios promote microbial activity. Fine particles (<20 µm) have a much lower C:N ratio than coarse particles (>100 µm) or bulk dung, and the value for fine particles resembles the C:N ratio for bacteria (P. Holter and C.H. Scholtz, unpublished). Thus,

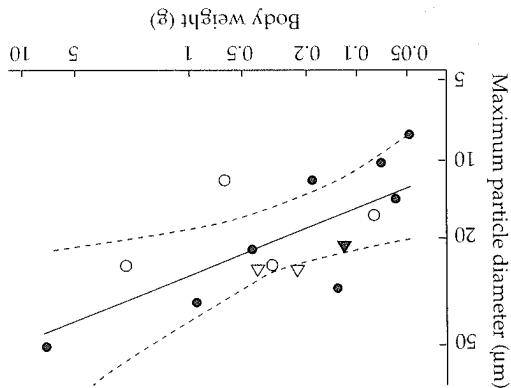


Figure 2.10 Maximum diameter of ingested particles as a function of body mass in 15 species of dung-feeding Scarabaeinae.

Note: Both scales are logarithmic. Empty symbols indicate species preferring rhino or elephant dung.

Source: Holter *et al.* (2002). *Ecological Entomology* 27, 169–176, Blackwell Publishing.

β-1,4-glucosidases, which hydrolyse cellobiose to glucose. Insects apparently lack an exoglucanase active against crystalline cellulose (Martin 1991), but their endoglucanases possess some exoglucanase activity and can be present in large quantities, as in *Panesthia cribrata* (Blattaria, Blaberidae), which feeds on rotting wood (Scrivenor and Slaytor 1994). An endogenous insect cellulase, endo-β-1,4-glucanase from the lower termite *Reticulitermes speratus* (Rhinotermitidae), was identified by Watanabe *et al.* (1998). It is secreted in the salivary glands, along with a β-glucosidase, and produces glucose from crystalline cellulose. Unhydrolysed cellulose is then fermented to acetate by hindgut protozoa, and this double action could account for the high efficiencies of cellulose digestion mentioned by Martin (1991).

The Macrotermitinae cultivate symbiotic fungi on combs constructed from undigested faeces, and consume fungus nodules and older comb. Besides enzymes, they acquire concentrated nitrogen, because fungi contain reduced quantities of structural carbohydrates (Mattson 1980). The fungus comb in newly founded termite colonies is inoculated with spores carried by alates or collected by foragers (Johnson *et al.* 1981). Genetic techniques have recently been applied to the evolutionary histories of fungus-farming in ants, termites, and beetles (see Mueller and Gerardo 2002). Fungiculture has evolved several times independently: multiple origins are evident in certain beetles such as cerambycid larvae, but only a single origin in each of ants and termites. This sophisticated form of cellulose digestion has enabled leaf-cutting ants and the Macrotermitinae to become dominant herbivores and detritivores in tropical ecosystems, and fungus-growing beetles are major forestry pests. The emphasis in the literature has been on cellulose digestion, but this is still in dispute where leaf-cutting ants and their symbiotic fungi together possess the enzymes necessary to degrade the xylan and laminarin of hemicellulose (D'Ettore *et al.* 2002). Workers of *Atta sexdens* obtain a large proportion of their nutritional needs from the extracellular degradation of starch and xylan by enzymes of fungal origin (Silva *et al.* 2003).

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