Introduction

Originally renowned for their spectacular raids, army ants have fascinated biologists for almost two centuries. They are defined by a combination of the three traits obligate group predation, nomadism and highly specialized ("dichtadiigyne") queens (Brady 2003, Gotwald 1982, Wilson 1958). The army ant life-style seems to have originated about 105 million years ago and the three army ant lineages Aenictinae, Dorylinae and Ecitoninae derive from a unique common ancestor (Brady 2003). Group predation allows the hunting of arthropods much larger than the ants themselves as well as of large colonies of other social insects. Nomadism (i.e. "relatively frequent migrations … accomplished in such an orderly fashion", Wilson 1958) may have evolved as a complement to group predation. As larger prey is more patchily distributed, colonies can locally deplete their food resources and may then be forced to move to new areas rich in prey (Wilson 1958). Dichtadiigyne queens have a worker-like thorax, permanently lack wings and have a greatly enlarged gaster filled with ovaries for enormous egg production. Colonies reproduce through fission like honeybees. In ants in general this is a rather unusual mode of reproduction but in army ants it is probably necessitated by the requirements of group predation. Colony fission directly creates colonies of sufficient size to efficiently hunt and retrieve prey.

The subfamily Dorylinae is constituted by the single genus *Dorylus* which is distributed from all over Africa through south Asia to south-east Asia. This genus represents a well-defined monophyletic group (Bolton 1990, Brady 2003) with six currently recognized subgenera (Bolton 1995). Members of the subgenera *Alaopone*, *Dichtadia*, *Dorylus* s.str., *Rhogmus* and *Typhlopone* all show a hypogaeic life-style, while in *Anomma* some species hunt in the leaf-litter (members of the *gerstäckeri* group, intermediate life-style) and others conduct massive swarm raids on the surface and up into the vegetation (the fierce and famous driver ants, epigaeic life-style). The *Dorylus* queens are the largest ants known (fig. 1). The worker caste displays a complex system of division of labour that is associated with mandible morphology (Gotwald 1978). *Dorylus* army ants are considered to be keystone predator species in many afrotropical habitats (Gotwald 1995). But despite enormous interest in these ants actually very little is known of their evolutionary history, their behavioural ecology and their life–history traits. One obvious explanation for the paucity of knowledge is the fact that most species live in the soil and are therefore hard to study (but see Berghoff et al. 2002a, 2002b). But more importantly at present neither a key to species nor a thorough revision, which examines which of all described forms represent real species, is available. Emery (1910) was the last one to

treat the genus as a whole taxonomically and since then numerous descriptions of species, subspecies, and varieties, mostly based on unassociated workers, queens or males, were added to the literature (Bolton 1995). This lack of a modern revision of the genus represents a huge impediment for the study of all aspects of the biology of this fascinating group. The phylogeny of the group is unclear and the status of the subgenera remains uncertain (Gotwald and Barr 1980, Barr and Gotwald 1982, Barr et al. 1985). *Dorylus laevigatus*, the only member of the subgenus *Dichtadia*, shows a number of more primitive characters (Wilson 1964) and is the sister species to all other *Dorylus* spp. (Brady 2003). Gotwald (1978) proposed that the extant *Dorylus* species derive from an ancestor with a completely hypogaeic life-style and that a few species adopted an epigaeic foraging style secondarily. He based this inference on the observation that workers are eyeless and have a reduced number of maxillary and labial segments in all species regardless of life-style.

Fig. 1 From top to bottom: Queen, male, large and small worker of the army ant *Dorylus* (*Anomma*) *molestus*.

In this thesis I present the results of three studies on the evolutionary and behavioural ecology of *Dorylus* species. In the first part, I examine the relationship between worker morphology and ecological niche. The worker caste of all *Dorylus* species studied so far is polymorphic (Emery 1901, Hollingsworth 1960, Raignier et al. 1974, Berghoff et al. 2002b). There is enormous size variation (e.g. the largest workers of *D. wilverthi* have a dry mass of up to 180 times as much as the smallest workers) and the differences in size are associated with differences in shape. While there are many studies that have described size-related differences in shape within single species, this work is the first to address the question of how the scaling relationships (i.e. allometries) of important functional traits have evolved and in particular which factors may have driven their evolution. In the second part, I analyse the food spectrum and food transport by the two epigaeic species *D. molestus* and *D. wilverthi* and thereby attempt to clarify the functional value of two traits that very probably represent adaptations to epigaeic foraging – long front and hind legs. The front and hind leg length allometries are relevant for food transport performance in *Dorylus* because prey is carried slung underneath the body so that leg length may represent a morphological constraint for efficient foraging. In the third part of the thesis, the spatial and temporal migration patterns of *D. molestus* are investigated with the objective to elucidate the role of intraspecific competition in this species. In order to ascertain large food intake and therefore colony growth army ant colonies should move at a frequency and in directions that will minimize re-exploitation of recently raided areas. When deciding to migrate they should then respond to the foraging activities of neighbouring colonies with which they compete for food resources between them.