

**Sociobiology of the hypogaeic army ant
Dorylus (Dichthadia) laevigatus Fr. Smith**

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Stefanie M. Berghoff

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Mitglieder der Promotionskommission:

Vorsitzender: Dekan Prof. Dr. Rainer Hedrich

Gutachter: Prof. Dr. K. Eduard Linsenmair

Gutachter: Prof. Dr. Ulrich Maschwitz

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Doktorurkunde ausgehändigt am:

For my parents

The awe of army ants

“Even man, styled “*Lord* of creation,” bows to this more numerous foe; for let the Drivers enter one door and he quickly escapes at the other.” (Savage, 1849)

“I lost all sense of proportion, forgot my awkward human size, and with a new perspective became an equal of the ants, looking on, watching every passer-by with interest, straining with the bearers of the heavy loads, and breathing more easily when the last obstacle was overcome and home attained.” (Beebe, 1919)

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Summary

Originally renowned for their spectacular epigaeic raids with many thousands of participating workers, army ants have captured scientific attention for almost two centuries. They now belong to one of the best studied group of ants. However, although representing only a minority of specialized species, most of our knowledge about army ants was derived from the study of epigaeically active species. These epigaeic species evolved probably rather recently from hypogaeic ancestors. The majority of army ant species still leads a hypogaeic life and is almost completely unknown in its entire sociobiology. It thus remained speculative, whether the assumed 'general' characteristics of army ants represent an adaptation to epigaeic activity or apply also to the majority of hypogaeic species.

Based on the recent observation that the hypogaeic Asian army ant *Dorylus (Dichthadia) laevigatus* recruits predictably and in high numbers to palm oil baits, I developed different baiting containers, testing the suitability of the oil-baiting method to study hypogaeic (army) ants. Although *D. laevigatus* is scientifically known for almost 150 years, nothing was known about the sociobiology of this assumed rare species. Throughout my work, I could show *D. laevigatus* to be very common and abundant in a wide range of habitats in West-Malaysia and on Borneo. Investigating its foraging behavior, I revealed *D. laevigatus* to differ from epigaeically active species in several ways. Never demonstrated for any of the epigaeic species, *D. laevigatus* established stable trunk trail systems. Such a trail system contradicted the perception of army ant foraging, which was believed to be characterized by raids with constantly alternating trail directions. The trunk trail system further enabled a near omnipresence of *D. laevigatus* within its foraging area, which was also believed to be atypical for an army ant. Raids differed in structure and composition of participating workers from those of epigaeic species. Column raids were caste specific and bulky food sources could be exploited over long periods of time. The foraging system of *D. laevigatus* resembled in several ways that of e.g. leaf-cutter and harvester ants. I could thus demonstrate that the foraging behavior of epigaeic species can not be transferred without modifications to that of hypogaeic species. Likewise contrary to the assumptions, *D. laevigatus* had a wide food spectrum and showed only little effect on local arthropod communities, even falling itself prey to other ants. Strong aggressive behavior was observed only towards ant species with similar lifestyles. This enabled me to provide the first detailed documentation of interspecific fights between two sympatric *Dorylus* species.

Similar to foraging habits or ecological impact, nothing was known about colony size and composition, nesting habits, or worker polymorphism for *D. laevigatus* or any other hypogaeic *Dorylus* species prior to my work. By observing and eventually excavating a colony, I showed *D. laevigatus* to have a much smaller colony size and to lack the large sized workers of epigaeic *Dorylus* species. Similar to epigaeic Dorylinae, I showed *D. laevigatus* to have a non-phasic brood production, to emigrate rarely, and to alter its nest form along with habitat conditions.

Detailed morphological and geographical descriptions give an impression of the Asian *Dorylus* species and are expected to aid other researchers in the difficult species identification. The genetic analysis of a male collected at a light trap demonstrated its relation to *D. laevigatus*. Confirming the male and queen associations, *D. laevigatus* is now one of five *Dorylus* species (out of a total of 61), for which all castes are known.

In cooperation with D. Kistner, I provide a morphological and taxonomical description of nine Coleopteran beetles associated with *D. laevigatus*. Behavioral observations indicated the degree of their integration into the colony. The taxonomic position of the beetles further indicated that *D. laevigatus* emigrated from Africa to Asia, and was accompanied by the majority of associated beetles. The diversity of *D. laevigatus* guests, which included a number of unidentified mites, was rather low compared to that of epigaeic species.

Overall, I demonstrated the developed baiting containers to effectively enable the study of hypogaeic ants. Collecting hypogaeic ants, I showed several species to be undersampled by other methods. Furthermore, the method enabled me to document a second hypogaeic *Dorylus* species on Borneo. A detailed description of this species' morphology, ecology, and interactions with *D. laevigatus* is provided.

My study indicated *D. laevigatus* to be an ecologically important species, able to influence soil structure and organisms of tropical regions in many ways. Relating the observed traits of *D. laevigatus* to epigaeicly active species, I conclude that our assumption of 'general' army ant behavior is erroneous in several aspects and needs to be changed.

The oil-baiting method finally provides a tool enabling the location and study of hypogaeic (army)ant species. This opens a broad field for future studies on this cryptic but nonetheless important group of ants.

Zusammenfassung

Ursprünglich durch ihre spektakulären Massenraubzüge bekannt geworden, werden Treiberameisen seit fast 200 Jahren wissenschaftlich untersucht und stellen nun eine der am besten untersuchten Ameisengruppen dar. Jedoch stützt sich unser Wissen über diese Tiere fast ausschließlich auf Daten, die durch die Erforschung der kleinen Gruppe oberirdisch fouragierender Arten gewonnen wurde. Nach dem bisherigen Kenntnisstand haben sich diese oberirdischen Arten erst vor evolutionär relativ kurzer Zeit aus unterirdischen Arten entwickelt. Die weitaus größere Zahl der Arten lebt auch heute noch unterirdisch und ist in ihrer Soziobiologie praktisch unbekannt. Es blieb daher bislang eher spekulativ, ob die als 'typisch' geltenden Treiberameisencharakteristika nur eine besondere Anpassung an ein oberirdisches Fouragieren darstellen, oder auch auf die unterirdische Mehrheit der Arten zutreffen.

Erst vor kurzem wurde die Entdeckung gemacht, dass die unterirdische asiatische Treiberameisenart *Dorylus (Dichthadia) laevigatus* voraussagbar und in großer Zahl an Palmöl-Köder rekrutiert. Basierend auf diesem Erkenntnis habe ich verschiedene Köderbehälter entworfen und die Eignung der Ködermethode für die Erforschung unterirdischer (Treiber)ameisen untersucht. Obwohl *D. laevigatus* seit fast 150 Jahren wissenschaftlich bekannt ist, war bis zu meiner Arbeit beinahe nichts über die Soziobiologie dieser als selten geltenden Art bekannt. Durch meine Arbeit konnte ich jedoch zeigen, dass *D. laevigatus* sehr häufig und verbreitet ist. Sie kommt in einer Vielzahl von Habitaten sowohl in West-Malaysia als auch auf Borneo vor. Durch die genauere Untersuchung des Fouragierverhaltens konnte ich zeigen, dass *D. laevigatus* von den bekannten, oberirdisch aktiven Arten in mehreren grundlegenden Merkmalen abweicht. So konnte ein fest etabliertes und lang genutztes Wegesystem wie das von *D. laevigatus* bisher nie für epigäische Arten gezeigt werden. Solch ein Wegesystem widerspricht dem bisherigen Bild des Lebensstyps Treiberameise, für den ständig wechselnde Wegrouten als charakteristisch angenommen wurden. Durch dieses Wegesystem wurde *D. laevigatus* nahezu omnipräsent in ihrem Fouragiergebiet. Weiterhin wichen Raubzüge in ihrer Struktur und Zusammensetzung der beteiligten Arbeiterinnen von denen oberirdischer Arten ab. Kolumnenraubzüge wurden vor allem von den kleinsten Arbeiterinnen durchgeführt und große Futtermengen konnten über längere Zeiträume hinweg genutzt werden. Das beobachtete Fouragierverhalten ähnelt daher zum Teil eher dem von Blattscheider- und Ernteameisen als dem von oberirdisch jagenden Treiberameisen. Damit erweist sich erstmalig, dass die bisher als treiberameisentypischen Fouragierstile nicht ohne Weiteres auf die unterirdischen Arten übertragen werden können. Ebenfalls entgegen den bisherigen Vermutungen hatte *D. laevigatus* ein weites Nahrungsspektrum und zeigte nur geringen Einfluss auf lokale Bodengemeinschaften. Zum Teil wurde sie selbst zur Beute. Stark aggressives Verhalten konnte ich vor allem gegenüber Arten mit ähnlicher Lebensweise beobachten. Dies erlaubte mir die erste detaillierte Dokumentation interspezifischer Kämpfe zwischen zwei sympatrischen *Dorylus* Arten.

Ähnlich den Fouragiergewohnheiten und des ökologischen Einflusses war bislang auch nichts über Koloniegroße, Nistgewohnheiten und Arbeiterinnen-Polymorphismus von *D. laevigatus* oder anderen unterirdischen *Dorylus* Arten bekannt. Nach der Beobachtung und Einsammlung eines Volkes konnte ich zeigen, dass eine *D. laevigatus* Kolonie bedeutend kleiner ist und ihr die großen Arbeiterinnen fehlen im Vergleich zu oberirdischen *Dorylus* Arten. Ähnlich den oberirdischen *Dorylinae* zeigte *D. laevigatus* eine nicht-phasische Brutproduktion, eher seltene Kolonienumzüge und eine mit dem Habitat variierende Nestform.

Detaillierte morphologische und geographische Beschreibungen geben einen Überblick über die asiatischen *Dorylus* Arten und sollen nachfolgenden Wissenschaftlern bei der schwierigen Artbestimmung unterstützen. Die genetische Analyse eines am Licht gefangenen Männchens

weist dies eindeutig *D. laevigatus* zu. Somit zählt *D. laevigatus* nun durch meine Arbeit zu einer von fünf *Dorylus* Arten (von insgesamt 61 Arten), von denen alle Kasten bekannt sind.

In Kooperation mit D. Kistner liefere ich eine morphologische und taxonomische Beschreibung von neun mit *D. laevigatus* assoziierten Käferarten. Verhaltensbeobachtungen geben Aufschluss über den Grad der Assoziation. Die taxonomische Position der Käfer lässt ferner darauf schließen, dass die Ameisen aus Afrika nach Asien emigrierten und der Großteil der assoziierten Käfer dieser Wanderung folgte. Die Diversität der Gäste, zu denen auch nichtidentifizierbare Milben zählen, ist gering im Vergleich zu der epigäischer Arten.

Die entwickelten Köderbehälter erwiesen sich als effektiv und gut geeignet für die Untersuchung unterirdischer Ameisen. Auf diese Weise konnte ich darlegen, dass unterirdische Arten in Studien mit anderen Sammelmethode oft unterrepräsentiert sind. Auch konnte ich mit Hilfe der Ködermethode eine zweite, auf Borneo bislang unbekannt, unterirdische *Dorylus* Art erstmalig nachweisen. Diese Art beschreibe ich genauer in ihrer Morphologie, Ökologie und Interaktionen mit *D. laevigatus*.

Meine Studie weist *D. laevigatus* als eine ökologisch wichtige Art aus, da sie in vielfacher Weise Bodenstruktur und Bodenorganismen tropischer Regionen beeinflussen kann. Im Vergleich mit den bekannten oberirdisch lebenden Arten komme ich zu dem Schluss, dass unser bisheriges Bild von 'typischen' Treiberameiseneigenschaften in verschiedener Hinsicht nicht zutrifft und geändert werden muss.

Die Ölköder-Methode bietet endlich eine Möglichkeit unterirdisch lebende (Treiber)ameisen aufzufinden und zu untersuchen. Dies eröffnet ein breites Feld für zukünftige Studien dieser versteckt lebenden aber nichtsdestotrotz wichtigen Ameisengruppe.

Chapter 1

Introduction

Representing a very striking life-form of tropical regions, army ants have captured scientific attention for almost two centuries. Renowned especially for the spectacular raids of some epigaeic species, army ants have been studied thoroughly in many aspects of their biology (Rettenmeyer, 1963; Schneirla, 1971; Gotwald, 1982; Gotwald, 1995). Some species were shown to represent local top predators of leaf litter arthropods and even of small vertebrates (Brosset, 1988; Roberts et al., 2000), and the recurrent disturbances their raids exert on litter communities were suggested to enhance arthropod diversity (Gotwald, 1995). Interacting in manifold ways with their environment, army ants are of high ecological importance. However, their behavior and significance was up to now analyzed by studying only the small minority of specialized and probably not very representative epigaeically foraging species (e.g. Gotwald, 1995). The majority of army ants leads a hypogaeic life and most of these species are virtually unknown in their entire biology. The little that is known about these species was based predominately on chance findings and occasional epigaeic appearances (Rettenmeyer, 1963; Rettenmeyer et al., 1980; Gotwald, 1982). Although numerous species were never recorded above the soil surface, hypogaeic army ants were generally assumed to conduct column raids, to be rather specialized predators, and otherwise to behave similar to epigaeic species (Gotwald, 1995). Many scientists are still unaware that the majority of army ant species leads this unknown hypogaeic life. Contradictory to our lack of knowledge, these species most likely represent an important factor in tropical ecosystems due to the following traits:

- 1) If they are similar proficient predators as epigaeic species, their feeding habits should have a strong impact on the fauna of the soil and leaf litter.
- 2) The digging activity of their assumed large colonies should play an important role in moving and aerating the soil and thus in the facilitation of nutrient cycling.
- 3) At least one species regularly feeds on plants, demonstrating the possibility to directly interact with plants and rendering it a serious agricultural pest (Roonwal, 1972).

Our ignorance of this important group of ants was predominately due to the difficulties in finding, following, and observing hypogaeic ants. Because of this, the definite importance of hypogaeic army ants remained to be demonstrated. Recently, it was observed that the hypogaeic army ant *Dorylus (Dichthadia) laevigatus* recruits predictably and in high numbers to palm oil baits in Malaysia (Weissflog et al., 2000). Finally provided with a potential tool, I conducted the first detailed study of a hypogaeic army ant. Although known to exist since 1857 (Smith, 1857), close to nothing was known about *D. laevigatus*. A major aim of my work was thus to investigate questions about the species' general biology. Taking pattern from the behavior of known epigaeic species, I sought to answer the following questions:

Occurrence and abundance

- In which habitats and up to which altitude does *D. laevigatus* occur in Malaysia?
- How common and abundant is *D. laevigatus* in Malaysia?

Foraging behavior

- Does *D. laevigatus* conduct raids? If so, what are the characteristics of these raids?
- Which prey objects are taken? Can a food specialization be detected?
- How are foraging trails distributed and used within an area?

Migrating behavior

Observations of entirely hypogaeic migrations are extremely difficult to conduct. Nevertheless, thought to be an important army ant characteristics, I attempted to find at least circumstantial evidence for the following questions:

- Do colonies migrate? If so, how often does a colony migrate to a new area?
- What can be made known about the implementation of migrations?

The colony

A nest of *D. laevigatus* has never been excavated and the believed associations of workers, queen, and males remained hypothetical. To change this situation, I attempted the excavation of a nest and thus to answer the following questions:

- How is the nest structured and where is it positioned within the foraging area?
- How large is a colony?
- Are the believed associations of the queen and males with *D. laevigatus* justified?
- Which developmental stages of brood are present in the nest?

In finding answers to these questions, a first comparison can be made between known epigaeicly and this first hypogaeicly foraging army ant species. These comparisons, which I conducted for each of the observed traits, will ultimately help to obtain a more comprehensive view of army ants in general.

The observations on the general biology of *D. laevigatus* will provide a first hint to its ecological importance. To gain a more detailed insight into its role in tropical ecosystems, the interactions of *D. laevigatus* with other organisms are of interest. Therefore, I focused part of my study on the investigation of the interactions between *D. laevigatus* and sympatric mass raiding species, its predators, and its prey species. Furthermore, since an army ant colony itself often hosts numerous associated species and thus enriches the local diversity, the guest community of a colony was investigated in detail. The following questions were treated:

Army ant interactions

- How do neighboring *D. laevigatus* colonies interact?
- Which other mass raiding species occur sympatrically with *D. laevigatus*?
- How do different army ant species interact?

Interactions with other organisms

- How does *D. laevigatus* interact with the soil and leaf litter fauna?
- Which organisms can be observed to prey on *D. laevigatus*?
- Which arthropods are associated with the colony? How do these interact with the colony and how close is their integration?

To further enhance the study of *D. laevigatus* and to develop the method into a standardized tool useful to other researchers, I aspired the following aims:

- The enhancement of the oil-baiting method to be able to study different behavioral aspects of *D. laevigatus*.
- To test the suitability of the study method for the investigation of other hypogaeic ant species.

Within the scope of answering the proposed questions, I developed and employed a variety of methods (Chapters 3 and 4). The potential use of the main method as a supplement for studies of other hypogaeicly foraging ant species is discussed in Chapter 8. To answer questions about *D. laevigatus*' general biology, I analyzed the species' occurrence (Chapters 6 and 8), abundance (Chapter 4), foraging system (Chapters 4 and 6), prey choice (Chapters 4, 5, and 6), and colony structure (Chapter 5). Interactions with a sympatric *Dorylus* species are

described in Chapter 6 and with other ant species in Chapter 7. The influence of *D. laevigatus* on the soil and leaf litter fauna was investigated (Chapter 7). Arthropods preying on *D. laevigatus* are described in Chapters 7 and 9, and Coleoptera associated with a colony are discussed in Chapter 9.

Chapter 2

Army ants – a life history strategy

As one of the first naturalists, Reverend T.S. Savage reported on the habits of "driver" ants of West Africa (Savage, 1847). He noted on the appellation "driver", from which the German *Treiberameise* was derived: "[The ant] not only travels and visits, in common with other species of ants, but it also *drives* every thing before it capable of muscular motion, so formidable is it from its numbers and bite; in respect to the last fact it stands unique in its habits, and, in distinction from other species of this country, may well take for its vulgar name that of *Driver*." (Savage, 1847).

Driver ants were shortly afterwards recognized to belong to the genus *Dorylus* (Savage, 1849). Due to their comparable lifestyles, "driver ants", "legionary ant" (mainly relating to ants of the genus *Eciton*), and ants of the genera *Aenictus*, *Cheliomyrmex*, *Labidus*, *Neivamyrmex*, and *Nomamyrmex* were referred to collectively as "true army ants" (Gotwald, 1995). Besides these "true" or "classical" army ants, belonging to the subfamilies Dorylinae, Ecitoninae, and Aenictinae, several Ponerinae species in the genera *Leptogenys*, *Megaponera*, *Onychomyrmex*, *Simopelta*, and *Termitopone* (Gotwald, 1982) and probably species of the Leptanillinae (Wilson, 1958) exhibit army ant lifestyles as well. Characterizing army ants is a unique combination of mass raiding and frequent migrations (Gotwald, 1995). In the following, I will discuss the characteristics of the classical army ant species first, followed by an analysis of how species of other subfamilies relate to them.

Foraging habits

Army ants are well-known for their impressive raids, conducted simultaneously by many thousands of workers. Foraging activity can generally be divided into three phases: search, overwhelming, and retrieval of prey. The collective implementation of raiding activity and prey retrieval classifies army ant foraging as "group raids" (Wilson, 1958). Linked to varying forms of food search and the associated recruitment to located prey, the term "group raid" has been used inconsistently in the literature. In army ants, all three foraging phases are conducted collectively. Chemical trails laid by a mass of workers without distinct leaders are the primary source of orientation during a raid. By definition, the ants display "mass recruitment" (Chadap and Rettenmeyer, 1975). To describe the foraging-communication of army ants unequivocally, Witte (2001) proposed to use the term "mass raids", which he defined as follows: "All phases of the raid, including the search, overwhelming, and retrieval of prey, are conducted collectively by a mass of foragers." The collective swarming out during a raid prior to the first prey contact is characteristic for mass raiding ant species. In the following, I will keep to this definition and term the raids of army ants mass raids.

Mass raids can assume either the form of a column or a swarm (Fig. 2.1, Schneirla, 1933, 1934), although gradations between the two forms are known (Rettenmeyer, 1963). Column raids are believed to be the more primitive form of mass raids (Rettenmeyer, 1963). Because of this and the restraints of a subterranean habitat, hypogaecic species, and thus the majority of army ants, were believed to raid predominately in columns. During such a raid, workers move out from the nest in an extending column (Fig. 2.1). The terminal group of this occasionally branching column is formed by a mass of advancing workers. In the search of food, these workers spread over the ground, yet only rarely extending the terminal groups for more than a few decimeters in diameter. Contrary, the terminal group of a swarm raid can surpass 15 m in diameter (Schneirla, 1971). Just as in column raids, the swarm's terminal group is constantly connected to the nest via an extending base column (Fig. 2.1). Workers of the terminal group advance a few centimeters onto new terrain before they retreat and are replaced by on-following nest-mates. In this way, no specific worker class or subcaste forms the advancing

group. Most army ant species conduct daily raids. Generally, army ants avoid to reuse old foraging trails, preventing to recrop a recently raided area (Franks, 1982a). *Eciton burchelli* was even shown to regularly space and rotate successive raids around its bivouac site, minimizing the foraging overlap (Franks and Fletcher, 1983). For a more detailed description of swarm and column raids see (Rettenmeyer, 1963; Schneirla, 1971; Gotwald, 1982).

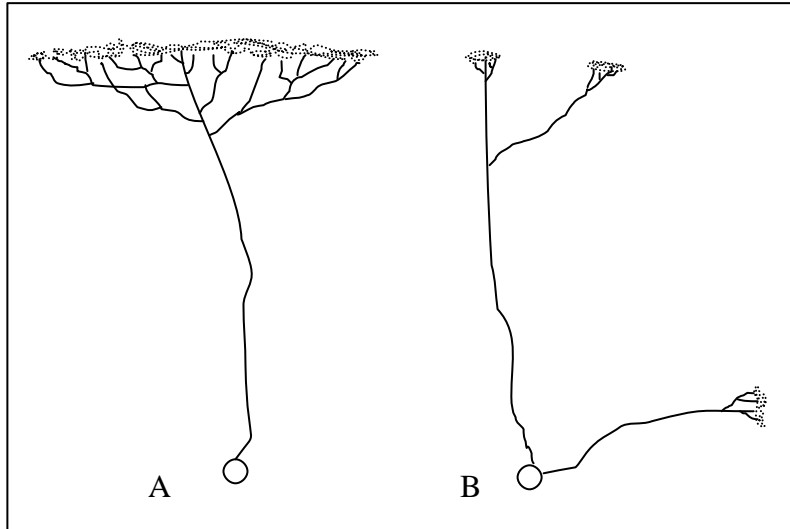


Figure 2.1. Army ant raiding forms: A. Swarm raid, B. Column raid.

Prey

Mass raids enable army ants to include brood of other social insects and large arthropods into their diet - prey not normally accessible to solitary foragers (Wilson, 1958). Swarm raiding species flush and potentially capture a wide variety of possible prey, including diverse arthropods, annelids, gastropods, isopods, and even small vertebrates (Gotwald, 1995). Column raiding species efficiently raid colonies of other social insects (Rettenmeyer, 1963; Mirenda et al., 1980). Because of this, the majority of column raiding species are assumed to be specialized myrmecophagous or termitophagous predators, and swarm raiding species to have rather generalized diets (Gotwald, 1982). However, to some extent swarm raiding species include the brood of social insects into their diet, and some column raiding species prey on "almost any invertebrate that the ants can find and overcome" (Schneirla and Reyes, 1966). The prey spectrum of a species can also vary between geographical sites and habitats (Gotwald, 1974b; Mirenda et al., 1980; Rosciszewski and Maschwitz, 1994).

Mass raids of some epigeally foraging species were shown to have a strong impact on local arthropod communities (Franks, 1982b). Influencing community composition and prey densities (Franks and Bossert, 1983), army ants can represent the top predators of leaf litter arthropods and even of small vertebrates (e.g. Brosset, 1988; Roberts et al., 2000). The repeated disturbances army ant raids exert on litter communities can possibly prevent the establishment of climax communities. In this way, army ants could enhance arthropod diversity (Gotwald, 1995).

Migrating behavior

The second most important army ant trait is believed to be the habit of periodically migrating to new nesting sites (Gotwald, 1995). Most ant species are able to change their nesting site if environmental conditions become unfavorable (Smallwood, 1982). However, for army ants, migrations and mass raids were believed to be closely linked (Wilson, 1958). Mass raids could have evolved initially as a coadaptation to specialized feeding on large arthropods and

social insects. To allow more efficient exploitation of this relatively widely dispersed food source, nomadism was theoretically developed either concurrently with mass raids, or added shortly afterwards (Wilson, 1958).

A few army ants (e.g. epigaeic *Aenictus*, *Eciton*, and *Neivamyrmex* species) were shown to emigrate regularly in functional cycles of alternating nomadic and stary phases (Schneirla, 1958, 1963). In these phasic species, the onset and length of the phases were closely linked to brood developmental factors (Schneirla, 1957). At the beginning of the nomadic phase, callow workers just emerged and young larvae have hatched from eggs. During this phase, the colony conducts extensive raids and on average one emigration each day. The gaster of the queen remains contracted and no eggs are laid. With the pupation of the larvae, the colony establishes a more permanent bivouac, entering the stary phase. Raiding activity is reduced and the queen lays a large amount of eggs (e.g. Schneirla, 1971). Contrary to these phasic species, all Dorylinae and probably most hypogaeic species, are believed to have emigration patterns without regularly alternating nomadic and stary phases (Raignier and Van Boven, 1955; Gotwald, 1995). In these non-phasic species, several weeks to months may elapse between two successive emigrations (Raignier et al., 1974). Other species may emigrate even less often (Gotwald, 1982).

Nesting habits

Epigaeic army ants construct remarkable nests by clinging to each other. Such tight masses of clustering workers, the bivouacs, contain the queen, brood, and guests (Schneirla, 1971). A bivouac is by definition a temporary nest fitted into its momentary environment and is rather a "state of the colony more than a particular place" (Schneirla, 1971). Internal bivouac conditions can be altered via positional shifts of the workers (Franks, 1989). Apart from army ants, bivouacs are only known from migrating herdsmen, i.e. *Dolichoderus* species (Maschwitz and Hänel, 1985).

Challenging Schneirla's (1971) bivouac definition, the majority of army ant species nests hypogaeicly (Gotwald, 1982), allowing the allocation of a specific site to the nest. Within such soil nests, the brood may be distributed onto specific chambers, which would contradict the conception of a tight worker cluster. Nevertheless, epigaeic as well as hypogaeic army ant nests are referred to equivalently as bivouacs.

Castes within the colony

Workers

Worker morphology varies greatly between army ant genera. Except for *Aenictus*, all species are at least moderately polymorphic (Gotwald, 1995). Statistically, *Eciton burchelli* showed a quadrimodal worker size distribution (Franks, 1985), while workers of other species could be arranged in a continuous series from smallest to largest (Hollingsworth, 1960). However, even in species without distinct morphological subcastes, workers of certain size ranges were shown to perform specific tasks within the colony (Topoff, 1971; Franks, 1985). All Dorylinae and curiously one Ecitoninae species, i.e. *Cheliomyrmex*, have a uninodal waist. Species of the remaining genera possess bi-nodal waists. Although all species possess functional stings, only Ecitoninae and some *Aenictus* species (Maschwitz, pers. comm.) have been reported to use their sting while overwhelming prey or defending themselves (Gotwald, 1995). Eyes are either reduced or absent.

Queens

Army ant queens are dichthadiiform, i.e. they are characterized by a permanently wingless alitrunk, a huge gaster, and an expanded postpetiole (e.g. Fig. A.9 – A.11, Wilson, 1971). While being phyogastric, the abdomen of a queen swells to an unusual degree due to the

hypertrophy of fat bodies and/or ovaries. Physogastric queens are able to lay large amounts of eggs (e.g. a *Dorylus (A.) wilverthi* queen may lay 3 – 4 million eggs a month, Raignier and Van Boven, 1955). In phasic species, the queen regularly alternates between physogastric and non-physogastric states, probably enhancing her ability to follow the frequent emigrations during the nomadic phases (Rettenmeyer et al., 1978).

Males

Army ant males are so unlike other ant males that Linné (1764, cited in: Gotwald, 1995), describing the first army ant, assumed it to be a wasp. Army ant males do indeed resemble wasps, having large and robust bodies and well developed eyes and wings (Fig. A.12 – A.14). Phasic species produce males in large sexual broods (Schneirla, 1971), while the periodicity of male production in most non-phasic species remains unknown. Males of *Labidus coecus* and several *Neivamyrmex* species showed rather distinct flight seasons in the United States (Baldrige et al., 1980). In Uganda, Africa, males of nine *Dorylus* species from five subgenera were shown to swarm throughout the year, but at different times during a night (Haddow et al., 1966). Emergence patterns seemed to be influenced by time, humidity, temperature, and wind (Haddow et al., 1966; Baldrige et al., 1980). In order to mate, army ant males have to find and enter an alien conspecific colony. Males of epigaeically foraging *Dorylus* species respond to chemical trails, which they trace back to their colony-origin (Schneirla, 1971). The mechanisms by which males of hypogaedic species locate and enter an alien conspecific nest are still unknown, although vision might play a role (Schneirla, 1971).

Brood

Army ant larvae have been studied thoroughly (e.g. Wheeler, 1943; Wheeler and Wheeler, 1964; Wheeler and Wheeler, 1974; Wheeler and Wheeler, 1984; Wheeler and Wheeler, 1986a; Wheeler and Wheeler, 1986b). External characters and larval development were found to correlate in larvae of the phasic *Eciton hamatum*, enabling the formulation of a key to separate larvae according to the nomadic day (Tafari, 1955). Colonies of non-phasic species simultaneously contain brood of all developmental stages (Raignier and Van Boven, 1955). Because of the varying brood ages and heterogeneity of worker sizes, it is not possible to differentiate between the larval developmental stages of non-phasic species. Larvae of *Eciton* and *Labidus* spin cocoons, while larvae of *Aenictus* and *Dorylus* do not. As an exception, only sexual brood of *Neivamyrmex* spins cocoons. Nothing is known about the cocooning behavior of *Nomamyrmex* and *Cheliomyrmex* species (Gotwald, 1982).

Colony reproduction

To conduct successful mass raids, colony size can not fall below a critical worker number. Unlike most other ant species, army ant queens, lacking wings, do not leave the colony for a nuptial flight. Insemination takes place within the colony (Rettenmeyer, 1963). Because of these dispersal restrictions, new army ant colonies are formed by fission. Reaching a threshold colony size, workers of an existing colony either choose to stay with their mother or to follow a queen sister to found a new colony. The two dividing colony parts are connected for a few hours via a trail on which workers and brood are exchanged. Later on, this connection breaks and both colonies go their separate ways (e.g. Schneirla, 1971). Colony fission results in an unusual genetic relationship between the two separating colonies (Gotwald, 1995). Workers that stay with their parent queen continue to care for their sisters, with whom they share, on average, 3/4 of their genes. Those that go with their new queen sister will raise their nieces, with whom they share only 3/8 of their genes. Colony fission thus poses a challenge to kin selection theory, since workers following their sister queen may significantly reduce their inclusive fitness (see Marceviz, 1979 for a detailed discussion). Further influencing the level of relatedness, behavioral observations in the laboratory indicated that army ant queens may

mate more than once (Rettenmeyer, 1963). This would lead to virgin queens that are not full sisters of the workers, additionally reducing the genetic benefit of following the new queen. It remains to be shown whether workers will tolerate the insemination of their queen by additional males under natural conditions.

Hypogaecic vs. epigaeic species

Possibly related to increasingly arid environmental conditions, the ancestor of today's army ants transferred its foraging activity into the ground (Gotwald, 1978b). Adapting to the hypogaecic environment, the number of labial and maxillary palp segments were reduced. Eyes were reduced or lost completely. Today's epigaeically foraging species still exhibit these reduced traits, indicating a rather recent resumption of epigaeic activity (Gotwald, 1978b). Epigaeically foraging species represent a small and specialized minority of evolutionary rather young army ant species (Gotwald, 1978b). However, our knowledge about army ants was obtained almost exclusively from the study of epigaeic species. When dealing with stratum-specifications, foraging, nesting, and emigration behavior should be differentiated (Gotwald, 1978b). Conforming with the evolutionary scenario, the majority of species nests, forages, and emigrates hypogaecically. Occasionally, some of these species come to the ground surface to forage under leaf litter at night or in humid weather conditions. In the following, I will refer to all species which conduct the *majority* of their foraging activities below the ground surface as hypogaecic species (i.e. most *Aenictus*, *Cheliomyrmex*, *Dorylus*, and *Labidus* species, and several *Eciton*, *Nomamyrmex*, and *Neivamyrmex* species, Gotwald, 1995). Diverging from these species, epigaeic species frequently conduct epigaeic raids, originating either from a hypogaecic nest (e.g. the remaining *Dorylus* species and several *Aenictus*, *Eciton*, *Labidus*, *Neivamyrmex*, and *Nomamyrmex* species), or from an epigaeic bivouac (e.g. a few *Eciton* and *Aenictus* species). Emigrations of these species are often at least partially epigaeic.

Army ants – a vague definition

Besides the "true" army ants, several species of other subfamilies were shown to mass raid and occasionally emigrate, demonstrating the adaptive value of army ant behavioral patterns in tropical habitats. Having been studied thoroughly, *Leptogenys distinguenda* was shown to conduct mass raids, emigrate frequently, construct bivouacs, and to have a broad food spectrum as well as a single phyogastric queen (Maschwitz et al., 1989; Witte and Maschwitz, 2000). Therefore, this ant species is in all respects a "true" army ant. On the other hand, *Pheidologeton diversus* and *P. silenus* also mass raid and emigrate (Moffett, 1988a; Moffett, 1988b). However, their raids are combined with the use of stable trunk trail systems and emigrations are not frequent enough for the species to be called nomadic (Moffett, 1988a; Moffett, 1988b). Furthermore, young queens conduct nuptial flights and do not become physogastric. Are these species army ants? When compared to epigaeic "true" army ant species, the answer would clearly be no. However, analyzing for the first time the behavior of a hypogaecic species, I will demonstrate in the following that the behavior of this "true" army ant species also diverges from the classical concept. Raids of *Dorylus laevigatus* originate from a stable trunk trail system (Chapter 4), colonies may stay over long periods of time within a foraging area (Chapters 5 and 6), and prey resources can be used in a sustainable way (Chapter 4). Compared to this species, the two *Pheidologeton* species appear already much more like army ants. The only known characteristic shared by all "true" army ants and some other ant species which exhibit many army ant traits (i.e. Leptanillinae, and some Ponerinae), is the occurrence of dichthadiiform females (Wilson, 1971). Anticipating the results of my study, the army ant conception needs to be extended to include the hypogaecic species. The characterizing army ant traits should thus be supplemented as follows:

1. Mass raids. All army ant species are able to conduct mass raids. Raids can have the form of a column, a swarm, or assume intermediate forms. Raids can be either large single events depleting a food source, or persistent small-scale actions, exploiting a food source over some time. Starting-points of raids can be the nest or a trunk trail.
2. Emigrations. Like most ant species army ants are able to move to new nesting sites when necessary. Emigration frequencies can vary between species from regular and predictable over occasional to infrequent. The ability to emigrate is thus a trait not suitable to characterize army ants.
3. Nests. Although the bivouac seems to be a preferred nest form of army ants, a colony can also be dispersed onto several cavities within the soil. Nest form can vary according to the habitat and is thus a trait not suitable to characterize army ants.
4. Queens. All army ants were shown to have queens which are dichthadiiform and can be moderately to extremely physogastric.
5. Colony reproduction: All army ant colonies reproduce through fission.

In accordance with these definitions, army ants can be defined as mass raiding ant species with dichthadiiform queens and fission as means of colony reproduction. This definition includes the "classical" army ants as well some *Leptogenys* species and probably *Leptanilla* species (for which mass raiding behavior remains to be demonstrated).

Chapter 3

Setting the scene: Study sites, studied species, and methods employed

Summary

Introductory to the following chapters, I will shortly discuss the status quo of hypogaecic army ant knowledge prior to my study and how I attempted to investigate the sociobiology of *Dorylus laevigatus*. The reader will be made familiar with the study sites and the scientific history of the studied species. Since not all methods providing data for this study are discussed in the following chapters, I present an overview of all employed methods.

Introduction

Army ants have been studied for more almost two centuries and numerous biological and ecological aspects are now known. However, prior to my work our knowledge of army ants was based almost exclusively on epigaeicly foraging species. Formerly hypogaecic foragers, some army ant species switched to foraging above the soil surface, possibly brought about by a reduced desiccation risk in some areas (Gotwald, 1978b). Epigaeicly foraging species thus represent a specialized and evolutionary rather young minority of army ants. The vast majority of army ant species is restricted in nesting and/or foraging to a hypogaecic lifestyle (Gotwald, 1995). Due to the difficulties confronted with when attempting to find, observe, and follow these cryptic species, their biology long remained unknown.

Only recently, Weissflog and co-workers (2000) observed by chance that the hypogaecic army ant *Dorylus (Dichthadia) laevigatus* recruits to palm oil dripped onto the ground. Although the feeding on palm oil was one of the first traits reported for *Dorylus* army ants (Savage, 1849), Weissflog et al. were the first to perceive the potentials of this trait. By pouring palm oil at regular distances onto the ground and checking these soil baits, we found *D. laevigatus* to recruit to a substantial number of baits within relatively short periods of time (Weissflog et al., 2000). Based on the encouraging results of this study, I developed and tested different methods to study *D. laevigatus* in West-Malaysia and on Borneo. Resultant, I conducted the first behavioral and ecological study of a hypogaecic army ant, which I present in the following chapters.

Study sites

The study was conducted during three field seasons (March – August 2000, November 2000 – Mai 2001, and March – Mai 2002) in Malaysia. Most studies were conducted in the Kinabalu National Park at Poring Hot Springs (6°5' N 116°3' E, Fig. 3.1). The park, comprised at the study plots of lowland and lower montane dipterocarp rainforest, encompasses Mount Kinabalu (4100 m), the highest mountain between Myanmar and New Guinea. The East Ridge, starting at 500 m at Poring Hot Springs, is an altitudinal gradient leading to the top of Mount Kinabalu. Annual rainfall within the area ranges between 2000 mm and 3800 mm with two rainy periods, i.e. between November and February and between June and July (Kitayama, 1992). Rain was collected during the study periods on an open area in Poring Hot Springs. The average rainfall collected during similar periods in all three field seasons showed 2000 to be the most humid year (average rainfall per day, March to Mai: 2000 = 7.9 mm, 2001 = 3.3 mm, 2002 = 3.2 mm). The monthly total rainfall for April amounted to 281.8 mm in 2000, 105.5 mm in 2001, and 110.1 mm in 2002. These values indicate the absence of strong El Niño effects during the study periods (compare to Kitayama, 1996).

To gain an insight into the distribution and possible geographical variations of *D. laevigatus*, I conducted part of the field season of 2000/2001 in West-Malaysia (November 2000 – March

2001). Here, study sites (Fig. 3.1) were established at the Ulu Gombak Field Station of the University Malaya (3°2' N 101°5' E, 250 m a.s.l.) and a privately owned oil palm plantation near Sitiawan (4°2' N 100°5' E, 0 m a.s.l.).



Figure 3.1. Main study sites in Malaysia

To investigate different behavioral aspects and to analyze the overall distribution of *D. laevigatus* in a wide range of habitats, 15 study plots were established during the course of my study (Tab. 3.1). Although not all of these study plots will be included in the following investigations, the data collected on the omitted plots add to and support the data collected on the included plots. Long term study plots were established in March 2000 and were reactivated during the following study periods. Investigations on other study plots were restricted to a single study period.

Table 3.1: Study plot data

Plot Nr.	Site	Habitat*	Height [m]	Size [m ²]	Baits [#]	Bait distance [m]	Remarks
1	Poring	PRF	500	375	24	5	Long-term plot
2	Poring	M	500	100	6	10	
3	Poring	Old SF	500	2200	38	10	Long-term plot
4	Poring	Old SF	500	100	6	5	
5	Poring	M	500	200	15	5	
6	Poring	PRF	550	250	18	5	
7	Poring	PRF	500	100	12	8	
8	Poring	Young SF	500	600	36	5	Long-term plot
9	Poring	PRF	500	Transect	34	50	800 m transect
10	Poring	U	500	100	8	10	
11	Gombak	SF	250	150	12	5	
12	Sitiawan	OPP	0	10829	111	7.5	
13	Sitiawan	OPP	50	900	16	10	
14	Poring	Lower MRF	580 – 1470	Transect	80	5	10 altitudinal transects
15	Sitiawan	RP	0	900	16	10	

* Habitat: M = Meadow, MRF = Montane rain forest, OPP = Oil palm plantation, PRF = Primary rain forest, RP = Rubber plantation, SF = Secondary forest, U = Urban vegetation

Studied species

The focus species of this study, *Dorylus (Dichthadia) laevigatus* (Fig. 3.2), was first collected from Sarawak (Malaysia, Borneo) and described by Smith (1857) as *Typhlopone laevigata*. In 1863, Gerstäcker received a "strange Hymenoptera" without worker ants from Java (Indonesia), which he believed to be the queen of a *Dorylus* army ant. No *Dorylus* queen was known at this time and Gerstäcker (1863) appointed the queen to a new genus, i.e. *Dichthadia glaberrima*. In 1887, a *Dorylus* male, i.e. *D. klugi*, was described from Sumatra (Indonesia, Emery, 1887a). In the same year, Emery (1887b) first suggested *D. laevigata*, *Dichthadia glaberrima*, and *D. klugi* to belong to the same species, i.e. *D. (Dichthadia) laevigatus*. This suggestion was primarily based on the geographic occurrence of the three castes in the absence of recorded workers of other *Dorylus* species. In 1895, Emery (1895a) further supported his union of the species by pointing to the plesiomorphic number of antennal segments. Both, *D. glaberrima* and major workers of *D. laevigatus* had 12 antennal segments, a number never documented for any other *Dorylus* species. Prior to my work, the connection between *D. laevigatus*, *Dichthadia glaberrima*, and *D. klugi* was never actually demonstrated. Nevertheless Wilson, in his key for Indo-Australian army ants (1964), stated without indicating the assumptive nature of this connection, that all castes of *D. laevigatus* are known.



Figure 3.2. Two major and one minor *D. laevigatus* worker

Dorylus laevigatus, including its synonyms, was described from Borneo, Java, Myanmar, Singapore, Sulawesi, Sumatra, and West-Malaysia (Fig. A.24, e.g. Emery, 1887b, 1895a; Rosciszewski, 1995). Prior to my study, *D. laevigatus* was the only *Dorylus* species known to occur on any of the Great Sunda Islands. Although *D. laevigatus* was listed in several faunal inventories, especially around the turn of the 19th century (e.g. Emery, 1887a; Forel, 1901; Bingham, 1903; Forel, 1909), close to nothing was made known about its biology. Emery (1895b) commented on the variability of antennal segments and Forel (1914) noted that H. v. Buttel-Reepen had located a nest, which he would describe at a later time. However, this observation was never published. Being not a known crop pest like the related *D. orientalis* (Roonwal, 1972) and due to its generally hypogaeic lifestyle, *D. laevigatus* was believed to be rather rare and long evaded further investigations.

Study methods

Epigaeically active army ants continuously alter the direction of their raids and regularly move to new foraging areas (Gotwald, 1995). Although the direction of a swarm can be influenced over short distances by offering food (Witte and Maschwitz, 2000), it seemed improbable to draw army ants to a certain area other than by chance. Contrary to this notion, we discovered that *D. laevigatus* recruits predictably and in high numbers to palm-oil baits (Weissflog et al., 2000). Employing this discovery, we were able to gain the first behavioral and ecological data of a hypogaeic army ant species. Palm oil was tested as bait by pouring it directly onto the soil. These soil baits (Fig. 3.3) were checked for *D. laevigatus*' occurrence by digging into the

baited area (Weissflog et al., 2000). Basing on the encouraging results of this study, I further developed the baiting method (Berghoff et al., 2002). Since only the main methods employed to study *D. laevigatus* in the field and laboratory are described at some length in the following chapters, an overview of all employed methods is provided in the following.

Field methods

Soil baits

Soil baits represented a quick and easy method to test a site for the occurrence of *D. laevigatus*.

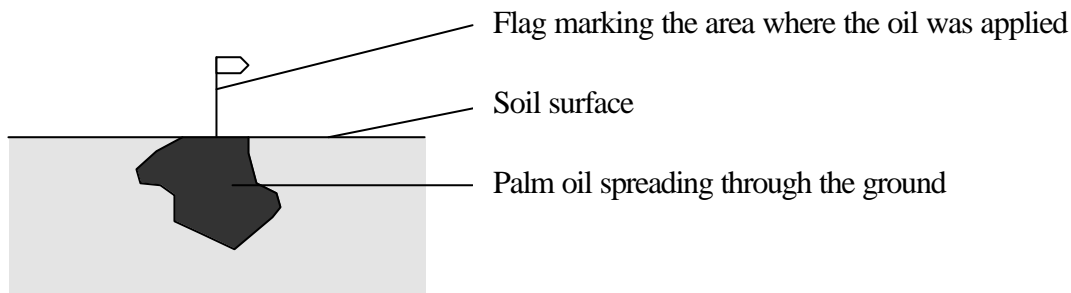


Figure 3.3. Soil bait

The oil (50 ml) was poured directly onto the ground or, in steep terrain, into a small preformed depression to prevent the uncontrolled spread of the oil over the ground. A flag marked the center of the poured out oil. To check a bait, the soil around the flag was excavated and spread out onto a plate in order to uncover occurring ant species. Afterwards, the soil was filled back into the excavated hole.

Sieve buckets

The core of all conducted studies was the establishment of a grid containing regularly spaced sieve buckets (Fig. 3.4).

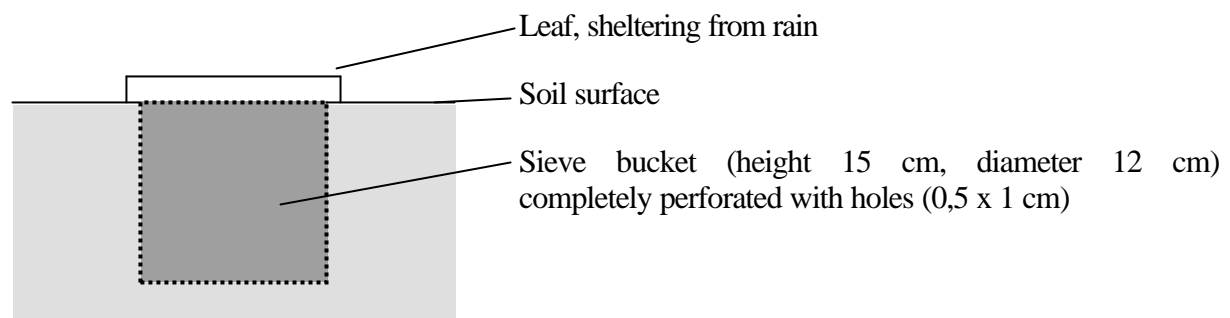


Figure 3.4. Sieve bucket

A sieve bucket contained one liter of soil onto which 50 ml household palm oil was distributed. During a bait check, a sieve bucket was pulled out from the soil via an attached handle (not shown in Fig. 3.4). Ant species and their foraging tunnels could be observed from the bucket's hole remaining in the soil as well as from the sides of the bucket. During each bait check, the number and diversity of ant species, their abundance, location in the bucket's hole, and main foraging direction, as well as observed interactions were noted. Compared to soil baits (Fig. 3.3), sieve buckets allowed more precise abundance estimations and analysis of foraging depth and direction. To conduct reasonably founded abundance estimations for *D. laevigatus*, 12 sieve buckets containing different numbers of ants were collected and the ants counted.

Sieve cavities

Sieve cavities were established in some plots to collect data on ant behavior around baits.

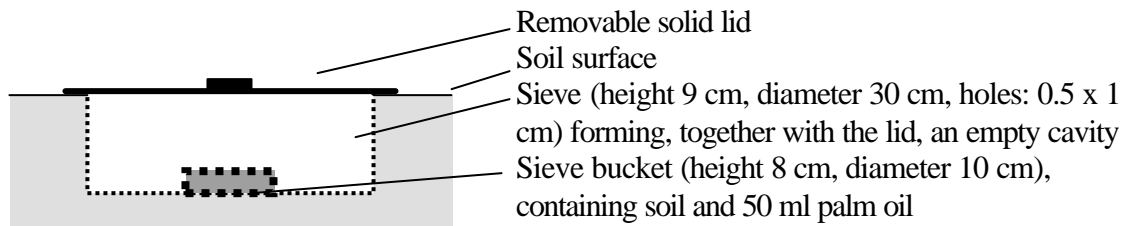


Figure 3.5. Sieve cavity

Since oil could only disperse into the ground below the small sieve bucket contained in the sieve cavity, 10 ml oil were dripped along the walls of the sieve cavity to begin a baiting period. Ants locating the sieve cavity form below or the sides recruited to the central sieve bucket, running freely within the sieve cavity. In the cavity, ant behavior and interspecific interactions could be observed by carefully removing the lid. The lid, closing the 'hypogaeic' cavity, further prevented the oil to be diluted quickly and uncontrollably by sheltering the bait from rain.

Bucket baits

Bucket baits were tested on plots 8 and 1 (Tab. 3.1) to obtain data on foraging depths.

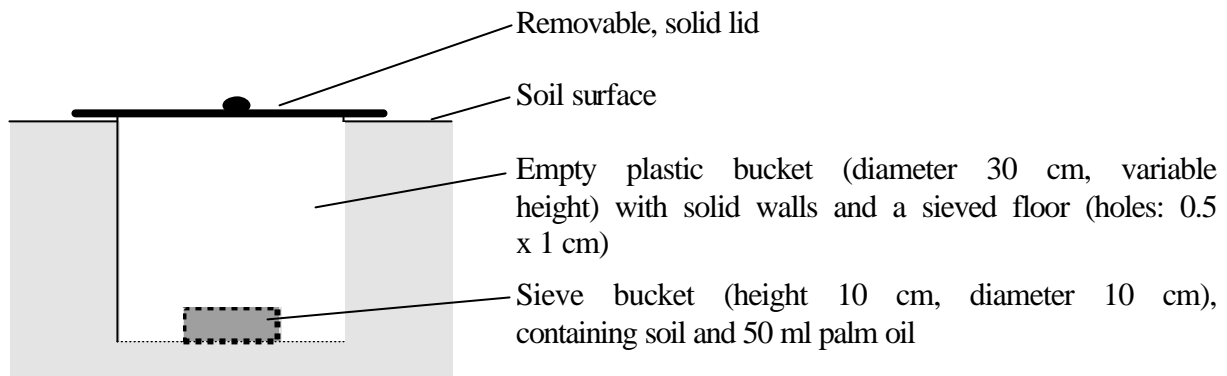


Figure 3.6. Bucket bait

Ants were able to reach the oil in a bucket bait only if they recruited from below the sieved floor of the bucket. By testing buckets with different length of their side-walls, foraging depths of the ants could be investigated. Similar to sieve cavities (Fig. 3.5), ants could be observed running freely in the cavity around the oil bait, enabling behavioral observations. The solid lid sheltering from rain prevented a quick oil dilution into the ground.

Random and search-sampling

Throughout the entire study, the ground of all study plots was repeatedly probed for the occurrence of *D. laevigatus*. This was done either by randomly digging into the ground and searching for ants and their trails in the excavated soil, or by intentionally digging at sites with a higher probability of *D. laevigatus* occurrence (e.g. beneath logs, palm leaf heaps, or garbage, or around termite mounds). The success of each search trial was noted together with a description of the searched site, the date, the time, and the weather conditions. These data added to data of other experiments, providing an estimation of the occurrence and abundance of *D. laevigatus* within an area.

Night observations

Some hypogaeicly foraging army ant species are known to come to the soil surface at night (e.g. Perfecto, 1992). To observe possible epigaeic foraging and to investigate changes in abundance and/or occurrence at baits, the baits of long-term study plots were checked regularly and of other plots occasionally at night. Using a red flashlight, all baits of a plot were checked and the same details noted as during day checks. Observation times were extended for highly occupied baits, noting epigaeic and foraging behavior. Furthermore, the ground of a study plot was carefully examined at regular distances, searching for and noting epigaeicly foraging *Dorylus* workers.

Food-choice experiments

To analyze the food spectrum of *D. laevigatus*, samples of different types of food were offered on plots 6 and 8 (Tab. 3.1) whenever the current experiments allowed such a food introduction. Two neighboring baits, each containing at least 1000 *D. laevigatus* and whose foraging trails indicated a hypogaeic connection, were selected. Halfway between these baits, four different food items were placed directly on the ground in piles approximately 15 cm apart. The area was then shielded from rain and larger animals with a plastic cover (40 cm diameter). The sites were checked once a day and once at night for six consecutive days, after which most offered food was moldy. During the bait checks, ants found around as well as below the food piles were noted. The following materials were offered at different times, in different combinations, and in different repetitions: bananas, melons, pumpkin, different nuts and berries found in the forest, a variety of fresh and boiled vegetables, boiled rice, plain and roasted peanuts, peanut butter, marmalade, syrup, fresh and boiled beef, tuna, oil (palm, olive, sunflower, and corn oil), and paper soaked with urine, honey, sugar, and salt water.

Trail excavations

Sieve buckets not bound into an experiment were used to conduct trail excavations to gain data on *D. laevigatus* foraging trails. In order to distinguish the trails from trails of other species, the excavations were continued only as long as *D. laevigatus* defended the trails. Trails were followed and blocked by inserting a wooden stick five to ten centimeters. The so marked trail section was then carefully excavated and its depth and direction measured (Chapter 4). Trails were hard to follow and often lost a) in fine-grained soil dissolving the form of the trails, b) when the trails branched into several smaller trails, or c) when the excavation was obstructed by one of the numerous roots in forested areas.

Large-scale excavations

On Plot 12, the nest of a *D. laevigatus* colony was successfully excavated (Chapter 5). The excavation was first begun by manpower, using shovels, and later continued using an excavator with a shovel width of 1 m. After the nest was excavated, the excavator opened the ground on most potential foraging and nesting sites of *D. laevigatus* (554 m²). Furthermore, the excavator uprooted one oil palm tree and opened three *Macrotermes* mounds. The data obtained from these additional excavator actions added to the overall data of foraging sites and habitat structure.

Male collections

During the field work for his Ph.D. study, J. Beck collected hawkmoths at UV-Light sources (125 W Mercury-Vapour light) from 18 different sites in Northeast-Borneo. He kindly collected *Dorylus* males for me, which were attracted to the light during his collections. Light trapping was done from April to July 2001 and from November 2001 to March 2002. Study sites included primary lowland rainforest, mountain forest, swamp areas, secondary forests of different degrees of disturbance, as well as highly disturbed habitats such as local gardens and

plantations (oil palm, cocoa). *Dorylus laevigatus* males were collected at five sites (Table 3.2) in the months of January to May and July. An additional male was collected by T. Winter in October 2002 at a similar light trap in a primary forest of the Tawau Hills Park. Generally, one to two and never more than five males were collected per night (J. Beck, pers. comm.).

Table 3.2: Collection sites of *Dorylus* males at UV-light sources in Sabah.

Site	Vegetation	Altitude [m]	Coordinates
East Kalimantan/Indonesia	Secondary forest	150	3°2' N 116°4' E
Tawau	Oil & cocoa plantations	230	4°2' N 117°5' E
Long Pasia	Primary mountain forest	1500	4°3' N 115°4' E
Kinabatangan floodplain	Secondary vegetation	120	5°2' N 118°2' E
Kampung Poring	Local garden area	350	6°1' N 116°5' E

Laboratory methods

Keeping *D. laevigatus*

Early in my work I kept small worker samples (< 100 ants) collected from single baits in plastic containers of variable sizes. The damp tissue used as floor covering was quickly shredded by the ants, which eventually formed one to five piles out of the scraps. No food was accepted and the workers showed no aggression when confronted with workers of alien colonies. The same was true when few workers were kept in containers containing preformed tunnels and cavities in plaster of Paris, covered by a red glass plate. Here, the ants ran below and above the artificial "soil" surface and began to tunnel through the plaster, piling up the excavated crumbs.

More successfully, *D. laevigatus* could be kept when collecting larger worker samples (> 2000 ants) and housing them in containers with at least one liter of soil. The ants tunneled quickly through the soil, constructing a network of tunnels, craters, and soil mountains. Increasing the air moisture, e.g. at night or by keeping a lid on, resulted in increasing numbers of ants visible on the soil surface. Large worker samples kept in such soil-filled containers accepted a variety of food and could also show aggressive behavior when workers of foreign *D. laevigatus* colonies were introduced (see Chapter 6).

Formicary experiments

Formicaries were connected in a variety of experiments to containers housing *D. laevigatus* workers (see previous paragraph). Formicaries enabled the direct observation of hypogaecic behavior, digging methods, and interactions between species and colonies.

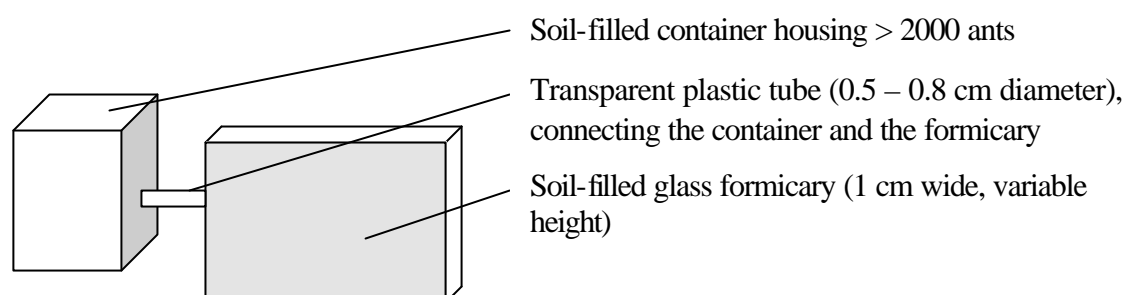


Figure 3.7. Setup of formicary experiments

Whenever a transparent plastic tube was connected to a soil-filled container housing large worker samples (see above), *D. laevigatus* readily dispersed into the tube. Tubes could be connected to other containers housing potential prey objects or worker samples of alien colonies, or to a glass formicary. Formicaries were filled with soil of variable densities,

enabling the observation of foraging behavior in soils of different nature. Due to the small diameter of the formicary the route of most trails could be fully anticipated and single workers could be visually followed through the formicary. Although *D. laevigatus* showed no strong aversion to light, formicaries were set up in a dark corner of the laboratory and ants were observed under red light.

Besides these methods regularly employed to investigate the behavior and occurrence of *D. laevigatus*, I studied other ant species recruiting to the oil baits or interacting with the army ant. This was done by observing the behavior of ants at baits, excavating sample nests, establishing epigaeic and hypogaeic pitfall traps, and conducting experiments on interspecific aggression (Chapter 7).

Morphological measurements

For a morphological analysis of the collected *Dorylus* species and their comparison to data from the literature, seven body proportions were measured for randomly and size selected worker samples, using an ocular micrometer (see Chapters 5 and 6). Furthermore, dry weight was measured on a high precision scale after drying workers at 40°C for 24 hours.

Genetic analyses

A genetic analysis of a 385 basepairs mtDNA was conducted to discriminate between the two sympatric *Dorylus* species recorded on Borneo and the allocation of a collected male to either species (see Chapter 6 for a description of DNA-extraction, amplification, purification, and phylogenetic analysis).

Chapter 4

Foraging of a hypogaeic army ant: a long neglected majority

Summary

Army ants have been studied thoroughly for more than a century. The conduction of column and swarm mass raids, featured by epigaeically active species, is believed to be a central characteristic of army ant behavior. Most army ant species, however, lead a hypogaeic life. Due to the difficulties to observe them, nothing is known about their hypogaeic behavior in the field. Using palm oil baits, trail excavations, and laboratory observations, the hypogaeic foraging of *Dorylus (Dichthadia) laevigatus* was observed in Malaysia. *D. laevigatus* was found to construct stable hypogaeic trunk trail systems providing quick and easy access to all parts of its foraging area. Small column raids were conducted throughout the ground stratum and above the ground surface. These raids were caste specific, with the smallest workers predominantly following existing cracks and tunnels in the soil. In case of food location, larger workers were recruited from nearby trunk trails. Exploratory trails leading to prey had to be widened before larger workers could gain access and help to process the food. Bulky food sources such as baits or termite mounds could be exploited over several weeks to months. Besides raiding in columns, *D. laevigatus* came occasionally to the ground surface at night to conduct swarm raids. This combination of swarm and column raids with the use of trunk trails has never been demonstrated for a classical army ant species. The omnipresence of *D. laevigatus* within its foraging area stands in sharp contrast to epigaeically active species, characterized by a very localized and temporary presence at foraging sites. *D. laevigatus* stayed in the same foraging area for several weeks to months. Having a broad diet and the ability to exploit bulky food sources over long periods of time, *D. laevigatus* seems to follow a sustainable use of the soil fauna. Summing up these particularities demonstrates a remarkable divergence of the hypogaeic foraging of *D. laevigatus* from that of epigaeically foraging army ant species.

Introduction

Originally renowned for their spectacular epigaeic raids with many thousands of participating workers, army ants have captured scientific attention for almost two centuries. They now belong to one of the best studied groups of ants and many essential aspects of their sociobiology have been intensively investigated (e.g. Mirenda et al., 1980; Franks, 1982a; Gotwald, 1982; Hirosawa et al., 2000; Roberts et al., 2000). Originally grouped into a single subfamily, the "classical" army ants were later recognized to belong to three widespread subfamilies, i.e. the Dorylinae, Ecitoninae, and Aenictinae (Bolton, 1990). Species of other subfamilies, including the Ponerinae, Myrmicinae, and Leptanillinae were shown to possess army ant traits as well (e.g. Moffett, 1984; Masuko, 1987; Maschwitz et al., 1989). The behavior of army ants is characterized by a unique combination of colony migration and mass raiding. Some army ant species migrate to new nesting sites on a highly regular basis, while others nest for several months at the same site (e.g. Schneirla, 1945; Rettenmeyer, 1963; Schneirla, 1971). As many non-army ant species are able to change their nesting sites as well, the ability to conduct large mass raids becomes the most outstanding feature of army ant

behavior. The characteristics of these raids have been studied in much detail (eg. Schneirla and Reyes, 1966; Chadap and Rettenmeyer, 1975; Miranda et al., 1980; Franks and Bossert, 1983). The majority of studied army ant species conducts column raids, which are believed to be the more primitive form of mass raiding (Rettenmeyer, 1963). While the fronts of column raids seldom exceed a width of 20 cm, the terminal group of swarm raids, the second known form of mass raiding, can reach a diameter of 20 m. For more details on the raiding forms see e.g. Schneirla (1933; 1934; 1938).

The raiding types are apparently closely linked to the prey taken. Swarm raiding allows the species to include a wide variety of arthropods and even small vertebrates into their diet (Savage, 1847; Gotwald, 1974b; Burton and Franks, 1985). Column raiding species, on the other hand, often exploit bulky food sources such as nests of social insects (e.g. Chadap and Rettenmeyer, 1975; Miranda et al., 1980). Independent of the raiding system used, army ants are very efficient in temporarily decimating the abundance and/or colony size of their prey (Franks, 1982a; Otis et al., 1986). Related to this efficiency is the following common characteristic of both raiding types: All raids are conducted as distinct single events, each leading in a direction different to the preceding raid. Eventually, the raids' advance onto new terrain stops and the ants retreat in a well coordinated manner. This highly specialized mass raiding behavior has been observed in all studied "classical" army ant species. However, studies on army ants have been restricted to a few epigaeicly foraging species. Contrary to these evolutionarily rather young species (Gotwald, 1978b), the majority of army ant species has hypogaeic lifestyles (Gotwald, 1982). These species are virtually unknown in their entire sociobiology, including their raiding behavior. Therefore, the following question remained unanswered: Is the highly organized raiding behavior central to all army ant species, or does it represent an adaptation of epigaeic activity?

Recently we presented a method, finally enabling the study of hypogaeic army ant activity (Weissflog et al., 2000). With a modification of this method, we studied the hypogaeic foraging of the army ant *Dorylus (Dichthadia) laevigatus* F. Smith. *Dorylus laevigatus*, believed to be a phylogenetically rather old species (Wilson, 1964), is the only known species of the subgenus *Dichthadia*. Although the species' existence is long known throughout South-East Asia, its biology is virtually unknown. With a modification of our method we address the following questions: Does *D. laevigatus* show raiding behavior? If so, does it conduct column raids, which is believed to be the raiding form of hypogaeic army ants? Are raids similar to those of epigaeicly raiding species?

Materials and methods

Study sites

Parts of the study were conducted in the Kinabalu National Park and surrounding areas at Poring Hot Springs (Sabah, Malaysia, Borneo; 6°5' N 116°3' O, 550 m a.s.l.), at the Gombak Field Station (Selangor, West-Malaysia; 3°2' N 101°5' O, 250 m a.s.l.), and in Plantations near Sitiawan (Perak, West-Malaysia; 4°2' N 100°5' O, 0 m a.s.l.). Study plot data are given in Table 4.1. Soil profile and vegetation cover was noted for every plot. Temperature was measured at the ground surface and in 1, 5, 10, 20, 30 and 40 cm depth. Data were collected between March and August 2000 and December 2000 and May 2001.

A substantial amount of the following data was obtained from Plot 12, a privately owned oil palm plantation. Therefore, the topography of this plot will be presented in some detail. The 15 year old plantation contained 146 palm trees distributed in 14 rows over an area of 1.1 ha (Fig. 4.1 A). The plantation was surrounded by a water belt; drainage ditches on three and a temporary river on the fourth side. The river contained enough water to flood a land connection to the adjacent oil palm plantation only during the rainy season. Two maintenance

road exits provided continuous land bridges to the surrounding area independent of season. The study was conducted during the rainy season when the ground water level was high, leaving a maximum of 80 cm of dry soil at the highest places. After heavy rain the trenches between palm rows filled with water and lower parts of the plantation were flooded (Fig. 4.1 B). Trenches dried up within one or two days without further rain. Adjacent plantations were occupied by different *D. laevigatus* colonies (unpubl. data).

Table 4.1: Study plots from Borneo and West Malaysia.

RF = rainforest, SF = secondary forest, P = plantation

Plot Number	Location	Study Area [m ²]	Observation time [days]	Vegetation type	Ground Temp. [°C]*	Number of baits	Bait distance [m]
1	Poring	375	109	Primary RF	22.8	24	5
3	Poring	2200	65	Old SF	22.6	38	10
5	Poring	200	10	Meadow	26.8	15	5
6	Poring	250	46	Primary RF	22.7	18	5
8	Poring	600	143	Young SF	25.3	36	5
9	Poring	800 m Transect	19	Primary RF	22.8	34	50
11	Gombak	150	8	Old SF	23.1	12	5
12	Sitiawan	10829	52	Oil Palm P	27.6	111	7.5
15	Sitiawan	900	8	Rubber P	29.1	16	10

*Average ground temperature measured in 10 cm depth.

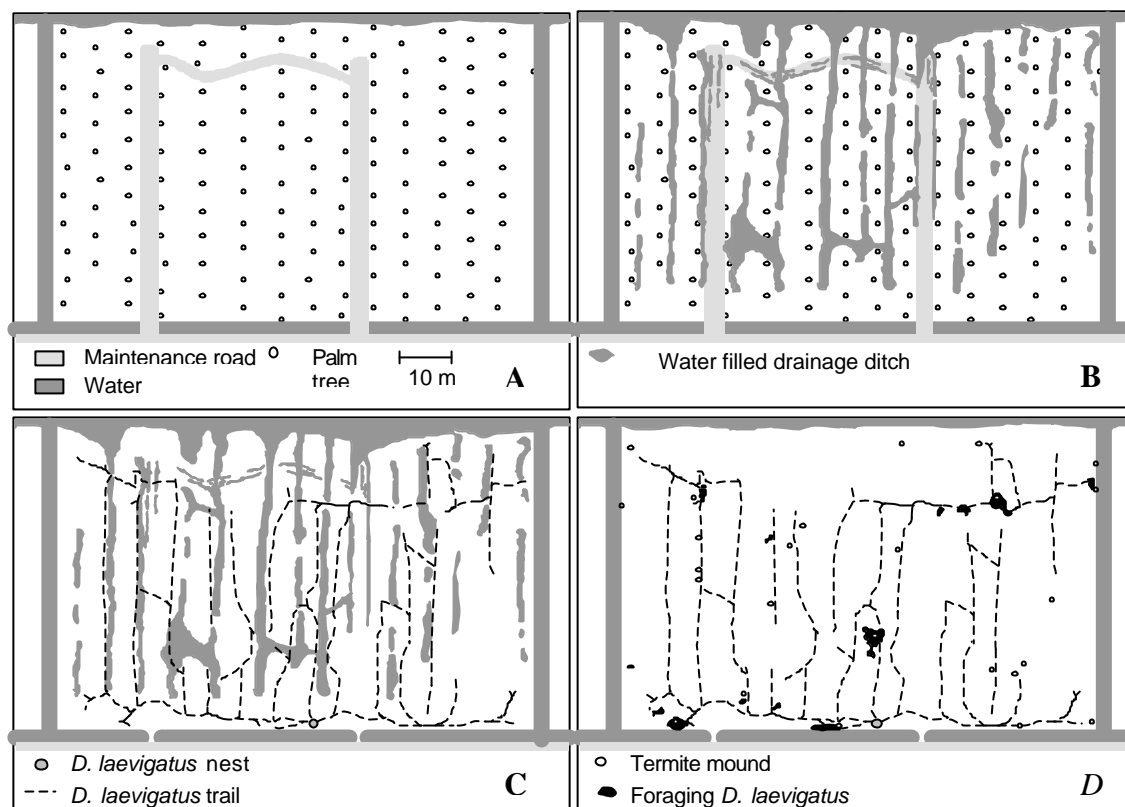


Figure 4.1: Studied oil palm plantation (Plot 12) A: Plantation outline. B: Plantation after heavy rain with trenches filled to a maximum and lower parts of the plantation flooded. C: Distribution of *D. laevigatus* trunk trails within the plantation. D: Location of termite mounds and areas of regular encounter of foraging *D. laevigatus* on exploratory trails.

Ant baiting

The distribution and subterranean movements of *D. laevigatus* were monitored via palm oil baits. The method, originally described by Weissflog et al. (2000), was modified to allow more precise abundance estimations and analysis of foraging depth and direction. Instead of pouring the oil directly on the ground it was applied in "sieve buckets" (Fig. 4.2 A). Each sieve bucket (height 15 cm, diameter 12 cm) held one liter of soil. Including its lid it was covered with holes (0.5 cm x 1 cm), enabling *D. laevigatus* workers of all sizes to pass through. To start a bait, a hole of the size of the bucket was dug into the ground. The bucket was filled with the excavated soil and lowered into the hole. Palm oil (50 ml) was poured onto the soil in the bucket. Finally, the bucket was closed with the lid and covered with a broad leaf to prevent water accumulation through direct rainfall.

Within a study plot baits were evenly distributed with equal distances to neighboring baits (Table 4.1). In some areas, the original baiting area was extended or the original bait distances decreased by inserting new baits. This allowed a closer focus on interesting parts of the foraging area, e.g. parts with high ant abundance or along colony borders. Modifications were generally completed a few days after the first detection of *D. laevigatus* within a plot.

Baits were checked once a day and occasionally additional times during day and night. To check a bait, the bucket was pulled out from the hole via an attached handle. At each bait ant presence was noted. The abundance was visually estimated and assigned to one of five classes: 1) 1-10, 2) 11-100, 3) 100-1000, 4) 1000-5000, 5) >5000 ants. To verify these numbers, baited buckets from areas not included in the study were collected and containing *D. laevigatus* were counted. By removing a bucket, *D. laevigatus*' entrance holes and their depths could be recorded from the buckets' hole remaining in the soil. All buckets were rebaited with 50 ml palm oil when the soil in most buckets of a plot showed a depletion of oil (on average every 10 to 11 days). Such a depletion became evident when the baited soil appeared fine grained and lost its oily touch.

The great advantage of using sieve buckets was that foraging trails to and within a bait were left intact while checking a bait. All data could be collected with a minimum of disturbance.

A second type of bait, the sieve cavity (SC, Fig. 4.2 B), was added in some areas to obtain behavioral data. The SC consisted of a sieve (height: 9 cm, diameter: 30 cm, holes: 0.5 x 1 cm), which was burrowed in the ground up to its rim. The excavated soil was disposed of. A small sieve bucket (height 8 cm, diameter 10 cm) filled with soil and 50 ml palm oil bait was placed in the center of the SC. To start a SC, 10 ml oil were dripped along the SC walls before the cavity was dosed from above with a solid lid. Ants recruiting to the oil droplets along the cavity walls would eventually disperse into the cavity and locate the bait. By carefully removing the lid, ants could be observed running freely in the cavity between the baited sieve bucket and the entry points along the SC walls.

To analyze the trail system, trails were excavated starting at selected baits. In order to distinguish the trails from termite trails, trails were followed only as long as *D. laevigatus* workers defended them. Trails were followed and blocked by inserting a wooden stick five to ten centimeters. The so marked trail section was then carefully excavated and its depth and direction measured.

Spot checks were conducted in all areas to detect foraging trails independent of bait occurrence.

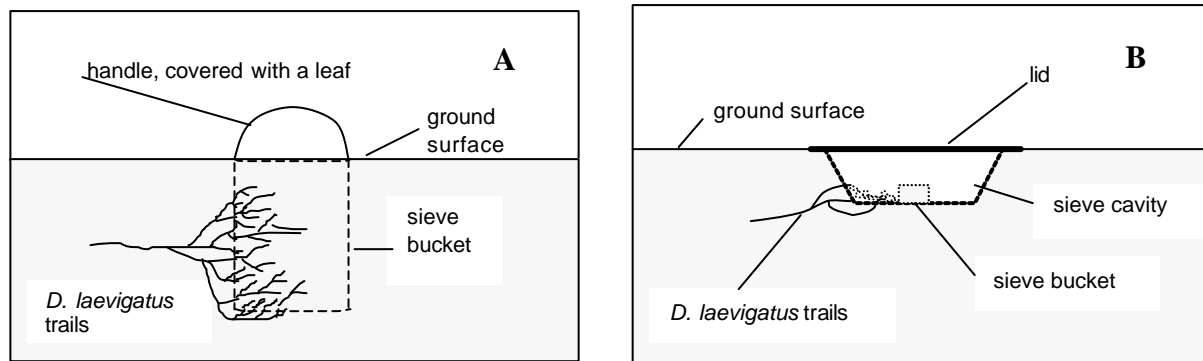


Figure 4.2: Baiting devices to monitor hypogaecic army ant movements (A. Sieve bucket, B. Sieve cavity)

Laboratory observations

Workers of *D. laevigatus* were kept in the laboratory to further analyze their behavior. In order to obtain a most natural behavior, a minimum of 2000 workers had to be collected. The ants were kept in containers filled with 10 liters of soil collected close to the original foraging site. After a maximum of two weeks the ants were returned to the site of collection. Transparent tubes, which were readily used by the ants, were connected to the containers. Running speed and worker behavior were observed in these tubes. The tubes led to soil-filled glass formicaries of 1 cm width and variable sizes, where burrowing activities were observed. Further methods and statistical tests are given at appropriate places in the text.

Results

Bait acceptance

Of the overall 304 baits included in this study (Table 4.1), *D. laevigatus* was recorded at least once at 77.6%. All baits of Plots 1, 3, 6, and 8 were found by workers within the study periods. Located baits were visited by *D. laevigatus* on average after 8.6 days (± 6.8 SD, min. 1 day, max. 29 days). The moment of bait location was observed and monitored on 14 baits. From this moment, ant abundance increased from class 1 to class 3 usually within 2 to 5 hours and to class 4 or 5 within the next 24 hours. Ant abundance was highest (class 4 to 5) two to three days following bait location and after rebaiting (avg. 2.3 days ± 0.9 SD). In the following days (avg. 5.2 days ± 2.6) ant abundance leveled at class 3 before declining to the classes 2 and 1 (avg. 0.8 days ± 0.8). If at this point no rebaiting occurred, *D. laevigatus* would desert the bait. Average ant abundance at occupied baits varied significantly between the study plots (Kruskal-Wallis, $\text{Chi}^2 = 266.85$, $P < 0.002$).

A bait was occupied on average for four days (± 2.8 SD, max. 13 days). However, if rebaiting occurred while *D. laevigatus* occupied a bait, the average occupation time increased significantly (11 days ± 6.4 SD; Mann-Whitney $U = 2008.50$, $P < 0.002$). In this way, a single bait could be continuously attended by varying numbers of *D. laevigatus* workers for a maximum time of 27 days.

Ant abundance at occupied baits was similar between day and night (plot and weather was controlled for; Mann-Whitney $U = 51490.0$, $P = 0.200$). Trails three or more centimeters below ground were used independent of rain or water puddles forming on the soil surface. Most trails accessing a bait were found in such a depth. Ant abundance at baits was independent of weather (plot and time was controlled for; Mann-Whitney $U = 17104.70$, $P = 0.714$). Trails closer to the soil surface were abandoned during rain and were not reused for some time.

Types of trails and raiding patterns

A *D. laevigatus* trail was found by chance only twice, although holes for more than 500 baits (only partially included in this study) were dug and numerous spot checks conducted. However, by backtracking trails originating at baits and inspecting potential foraging sites close to occupied baits, foraging *D. laevigatus* could be found. In this way, three foraging strategies and associated trail types were recorded: the stable hypogaecic trail system, column raids, and swarm raids (Fig. 4.3).

The stable hypogaecic trail system

The topography of Plot 12, with its restrictions to the foraging area of the resident colony, allowed a thorough analysis of *D. laevigatus* trails. A trail system was found, consisting of large trunk trails (TT), (diameter 0.8 to 1.3 cm). To analyze the trail structure without destroying the entire system, 39.45 m trails were excavated and numerous small-scale excavations were conducted. The trails ran at a depth of 8 to 12 cm, where they were unaffected by heavy rain and high ground water levels. The smooth and well maintained walls of the trails indicated that they were used frequently over a long time. Excavated TTs could run up to 4 m in the same depth and direction. Junctions had the form of a T or Y. Trunk trails with the same attributes were found on other study plots as well. Here, however, because of poor accessibility, only small sections of these trails could be excavated.

On Plot 12, baits within a palm row were located by the ants often in a distinct order following the palm row. After rebaiting the ants returned to deserted baits mainly in the opposite direction as they had left the baits. This phenomenon could also be observed at baits of other study plots. Trails originating at different baits within the same palm row could be backtracked to the same TT ($n = 8$). It was found that TTs followed palm rows, where the ground was higher between the trenches (Fig. 4.1 C). They joined in the front of the plantation where there was a connecting strip of high ground and the nest's location. Two rows with occupied baits could be separated by one or two rows without ants at the baits. Trunk trails crossing trenches were excavated in three places. The point of crossover was in each case the highest place of that trench section, providing a maximum time to cross over during flooding. Trails crossing trenches could be reused after drying up again. Trunk trails of other plots were probably arranged differently compared to the well defined topography-related manner found on Plot 12 (Fig. 4.1). However, trails originating at neighboring baits could also be traced to the same TT on other plots.

Trunk trails were well defended during artificial excavation. A cluster of major and large medium workers formed, defending the exposed trail end. Minor and small medium workers quickly closed the opening with soil. These soil blockades could become more than two centimeters thick.

Column raids on exploratory and secondary trails

Minor and small medium workers conducted column raids on small exploratory trails (ET, $n = 153$), (diameter 0.2 to 0.3 cm). Larger workers trying to follow an ET were observed to get stuck in narrow trail sections or entrance holes and had to turn back. ETs were only partially dug by the ants themselves, which readily followed existent cracks or tunnels in the soil. Column raiding workers on ETs could be found within the soil as well as close to or even at the soil surface. Here, leaf litter was used for cover whenever possible. However, epigaeic ETs could also run over open ground for as much as 28 cm. ETs above the soil surface were mostly detected at night (on 49 nights and 8 days). ETs were also found in SCs, excavated soil sections, and under logs or palm leaf heaps. Further observations from formicaries added to the data on ETs. An ET formed when one to eight workers departed from an existing ET and

ran for a few centimeters in a new direction, before turning around. The branching ants dragged their gaster tips on the ground, probably laying a chemical trail. Beginning branches could stop to exist after a few seconds and centimeters or be extended by new worker groups. All ETs had highly variable routes and short life spans. Even well used ETs with up to 300 ants passing a point per minute, changed their routes constantly. An ET generally ceased to exist 10 to 20 minutes after first observing it. No epigaeic ET was found again when its site was checked about four hours later ($n = 38$).

When an ET led to a food source, it was quickly widened to a more stable secondary trail (ST, $n = 58$). These trails (diameter 0.4 to 0.6 cm) allowed the larger sized ants to gain access to the food. If necessary, the prey was protected and cut to pieces and then carried away on the ST. In case of a bulky food source such as an oil bait, a network of STs formed surrounding the bait. This ST network channeled into one to five main STs leading away from the bait ($n = 68$). STs surrounding baits could be used for more than two weeks. During this time their route was often modified.

Contrary to the well defended TTs, ETs were quickly deserted when disturbed. The ants immediately tried to conceal themselves and started to dig alone or in small groups. The defense of STs was intermediate. If the disturbance persisted, the ants would desert a trail section only to block the trail further up the way. This made it extremely hard to follow STs over long distances.

Some STs found beneath wood lying on the ground had thin soil walls connecting ground and wood cover. Such walls or a complete tunnel were never observed when trails led across open ground. Only on one occasion (excavation of a colony, unpubl. data), did scattered colony members build short epigaeic 'tunnels' (1.0 to 3.8 cm long, 0.4 to 0.5 cm wide, and 0.2 to 0.6 cm high). Of these structures, 27% had a soil roof connecting the side walls.

Epigaeic swarm raid

Besides the use of the described hypogaecic trail system and the conduction of column raids, *D. laevigatus* was also able to conduct epigaeic swarm raids. These were observed on three occasions by the senior author. All observations were made between 7:30 p.m. and 11:30 p.m. Workers of all size classes came to the ground surface through multiple holes. Emerging from these holes, the ants spread out in an elliptical to fan-shaped swarm 1.5, 2.0, and 3.5 meters wide. As the swarm progressed, the mass behind the swarm front began to loosen up, forming a tight network of small trails one to four workers wide. The route of these trails changed constantly, disappearing and reappearing beneath leaves, stones, wood, and soil. Ants at the swarm front advanced for a few centimeters in a new direction before turning around. These pioneers were then replaced by other ants extending the new foraging direction. Single ants in all parts of the swarm were observed to start digging. Other swarm members would often overrun these digging ants, but eventually a small group formed, digging a tunnel and disappearing below ground. *Dorylus laevigatus* was never observed to climb vegetation, even when workers of the ant species *Pheidole* sp. and *Pheidologeton affinis* fled from the swarm with their brood into the vegetation. Brood of these two species placed into the path of *D. laevigatus* was carried away by the latter. Most ants participating in the raid had disappeared underground two to three hours after discovering the swarms. During this time, the epigaeic raids had proceeded for 8, 4.5, and 3 m.

All epigaeic swarm raids were observed on nights following afternoons when new baits were inserted between already occupied baits. The hypogaecic discovery of these new baits was quick during the afternoon, with approximately one bait found per hour. After nightfall, the ants came to the ground surface and the swarm proceeded in the same direction of the previously observed hypogaecic advance. In this way, further baits were epigaeically located.

Trail establishment and use

Within SCs, the efficacy of *D. laevigatus* to excavate soil could be observed. The cavity around an occupied bait was filled within 24 hours with an average of 431 ml soil (± 279 SD, min. 50 ml, max. 1100 ml). Heavily occupied sieve buckets had their lids covered with soil and the soil amount within the bucket could decrease by 50%.

In the laboratory, upon reaching a formicary connected to an ant container, *D. laevigatus* started immediately to tunnel through the soil. Minor and small medium workers were the first to arrive. They continued to do the main part of the digging even after larger workers had arrived. Besides the digging methods reported by Weissflog et al. (2000) two additional modes were observed. In loose soil *D. laevigatus* workers would try to squeeze into small cracks where they moved while repeatedly raising and lowering their body. In this way a small tunnel was created by displacing the loose soil. When a new formicary with dense soil was connected to a thoroughly tunneled formicary, ants could be observed to carry pieces of soil from the new back to the old formicary ($n = 29$).

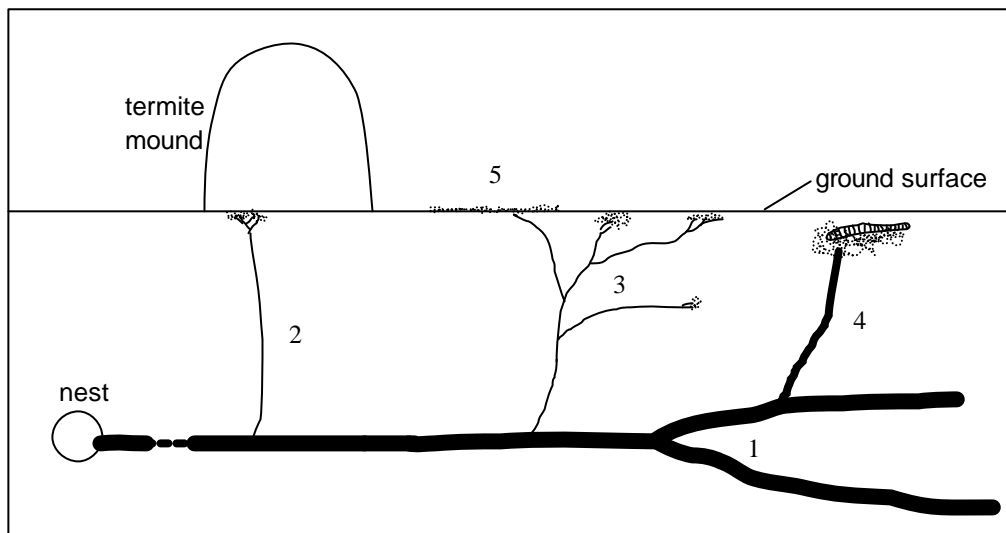


Figure 4.3: Schematic trail and raiding system of *Dorylus laevigatus*. Originating from a stable trunk trail system (1) minor and small medium workers conducted column raids on exploratory trails. These trails could lead to constant food sources such as a termite mound (2) where the workers waited for the opportunity to snatch some prey. The raids could also be conducted underground or at/close to the ground surface (3). In case of food location, the trail was widened to a secondary trail (4). Food was then processed and transported via a nearby trunk trail back to the nest. *Dorylus laevigatus* could also conduct epigaeic swarm raids (5).

Dorylus laevigatus was also observed in the laboratory running through transparent plastic tubes. A maximum of 299 ants per minute could pass a certain point in a tube with a diameter of 0.6 cm (average 77.66 ± 68.67 SD, $n = 335$). Within the tubes, an ant needed on average 4.83 seconds (± 1.01 SD) to cross a distance of 10 cm. In the tube experiments, three size classes were visually distinguished: minor, medium and major workers. Of these, medium and major workers showed no significant differences in running speed (Mann-Whitney $U = 48.00$, $P = 0.833$). Minor workers were significantly slower (minor-medium: $U = 26.00$, $P < 0.002$; minor-major: $U = 6.00$, $P = 0.002$). Minor workers kept to the sides of the ant column and frequently stopped to rest and groom themselves. If they happened to run in the main stream, they were regularly overrun by larger workers, at times literally being kicked aside.

A new tube was first explored by minor and small medium workers. These scout groups consisted of two to five ants which proceeded on average 2.89 cm before turning around (± 2.10 SD). Ants crossing a tube to a new foraging area during the first 30 minutes were significantly slower (average speed: 6.92 sec/10 cm, ± 2.70 SD) than workers using the tube in a constant trail after more than one hour (average speed: 4.95 sec/10 cm, ± 1.64 SD), (Mann-Whitney U-Test: $U = 922.00$, $P < 0.002$).

Prey

The most frequently observed prey of *D. laevigatus* were annelids (observed on four plots, $n = 25$). Once discovered, workers of all sizes joined in covering the earthworm with soil and cutting it to pieces. Groups of workers were discovered on excavated STs and TTs transporting earthworms of 2.6 to 5.5 cm length. Earthworms fed to a laboratory colony were either cut to pieces and transported to the bivouac, or the body fluids were imbibed at the capture site, leaving an empty skin.

Within Plot 12, *D. laevigatus* was found under palm seeds dropped during the harvest (once every 20 days). ETs could reliably be found surrounding regularly checked mounds of *Globitermes sulphureus* and two *Macrotermes* species (Fig. 4.1 D). ETs with varying routes were found in the vicinity of these mounds over the course of two months, even though the area was occasionally disturbed through trail excavation. Foragers collected on STs around termite mounds carried juvenile termites. None of the observed mounds showed any signs of damage due to a large-scale army ant attack. All mounds were alive and well defended when they were partially opened at the end of the study period. On other plots, *D. laevigatus* was occasionally observed to prey on termites at baits, when the species were mixed during a bait check. Termite trails could partially be incorporated into the *D. laevigatus* trail system or they could be used while conducting a termite raid ($n = 4$).

Hypogaecic raids were difficult to observe. However, two column raids could be observed. While excavating a *Diacamma intricatum* nest, *D. laevigatus* workers entered the nest chamber through multiple holes in a 12 cm wide wall section. From here, a column of *D. laevigatus* workers moved into the lower *D. intricatum* brood chamber. After a few minutes, three *D. laevigatus* workers reappeared carrying eggs and a small larva. The raid could not be further observed since all ants were disturbed by the excavation.

On a second occasion, *D. laevigatus* was observed to cross through a SC and disappear on the opposite side into the soil. A few minutes later, *Paratrechina* sp. workers carrying brood appeared on the ground surface and ascended into the vegetation close to the area where *D. laevigatus* had entered the ground. Returning *D. laevigatus* carried larvae and pupae of *Paratrechina* sp. through the SC.

During the three observed swarm raids *D. laevigatus* preyed on a variety of arthropods. Besides the observed raids on *Pheidologeton affinis* and *Pheidole* sp. (see above) further prey included isopods, beetles, annelids, grasshoppers, caterpillars and one *Gryllotalpa* sp.. Food located on the ground surface was immediately lowered into the ground. This was done by removing soil from beneath the food and covering it with soil. No epigaeic food transport was observed. Keeping its position, the main trail leading to a bulky epigaeic food source was transferred below ground. This could be observed especially well at baits located during an epigaeic raid.

Discussion

The characteristics of army ants, gathered from the study of mainly epigaeicly active species are stated in the army ant adaptive syndrome (AAAS) (Gotwald, 1982). Whether the grouped traits apply to the majority of army ant species with partial to complete hypogaecic lifestyles

remained uncertain. The little that is known about hypogaeic species is based predominantly on chance findings and occasional epigaeic appearances. Above ground, the behavior of these species proved to be similar to that of primarily epigaeicly raiding species (Rettenmeyer, 1963; Rettenmeyer et al., 1980; Gotwald, 1982). However, how often these species come to the ground surface, how they behave underground, and whether they meet the postulations of the AAAS remained unknown. In spite of this striking lack of information, hypogaeic army ants were assumed to conduct column raids, to be rather specialized predators, and otherwise to behave similar to epigaeic army ants (Gotwald, 1995).

Like most hypogaeic army ants, *D. laevigatus*, although scientifically known since 1857, has long eluded scientific investigation. With a modification of our method (Weissflog et al., 2000) we could show *D. laevigatus* to be common as well as abundant in a variety of habitats in Malaysia (Table 4.1). The following behaviors were demonstrated, rendering *D. laevigatus* a highly subterranean species (Rettenmeyer, 1963; Rettenmeyer et al., 1980): 1) most activity was hypogaeicly confined, 2) epigaeic activity was mainly nocturnal, 3) epigaeic columns were concealed under leaf litter or vegetation whenever possible, 4) sheltering tunnels around epigaeic columns were an exception, and 5) epigaeic prey objects were immediately covered and lowered into the soil at the site of discovery. As predicted for hypogaeic army ants, *D. laevigatus* was found to conduct column raids. Yet in addition, *D. laevigatus* could also conduct swarm raids at the ground surface. This plasticity in raiding behavior has already been demonstrated for some surface raiding Ecitonine and Aenictine species with mainly hypogaeic lifestyles (Schneirla and Reyes, 1966; Fowler, 1979; Campione et al., 1983). In these species swarm raids formed predominantly at times of high colony excitation. Recruitment overrun was shown to be responsible for army ant swarm development and raid extension (e.g. Witte and Maschwitz, 2000). *Dorylus laevigatus* came to the ground surface after discovering more than the average number of new baits. In such a highly excited colony the resulting strong recruitment and recruitment overrun could bring the foragers to the ground surface, where a quick advance would be less laborious. The observed swarm raids of *D. laevigatus* were rather small, slow, and short-lived when compared to raids of e.g. *Eciton burchelli* or *Dorylus (A.) nigricans* (Gotwald, 1982; Franks et al., 1991)

In addition to observing epigaeic behavior, hypogaeic army ant foraging in a natural environment could be recorded for the first time. The hypogaeic foraging of *D. laevigatus* differed in form, conduction, and related features to epigaeicly active species in three ways. First of all, the existence of stable trunk trails, has never been shown for any classical army ant species. In general, army ants avoid to reuse old raiding trails, thus minimizing the chances to re-raid a previously cropped area (Franks, 1982a). Only during long statary phases could parts of old raiding trails be temporarily reused to launch new raids (Schneirla, 1971; Burton and Franks, 1985). By contrast, *D. laevigatus* established stable trunk trails (best documented at Plot 12, Fig. 4.1). The TT diameter was larger than necessary for food transport, for which STs were sufficient. Trail stability and physical structure correlate (Moffett, 1988a), which indicates the longevity of the large and well maintained *D. laevigatus* TTs. Furthermore, the trails' straight routes in steady depths and their crossing of trenches in the highest places pointed to well established long lasting trails. Workers of *D. laevigatus* moved with average speed of 0.02 m/sec through smooth-walled experimental plastic tubes. With this speed, the well maintained trunk trail system permitted *D. laevigatus* quick and easy access to even remote regions of the foraging area. The thus attained near omnipresence was also demonstrated by a bait acceptance of 77.6%, an average bait localization time of nine days, and an average abundance at baits of 100-1000 ants. This presence of *D. laevigatus* stands in sharp contrast to the temporary and very localized presence of epigaeicly raiding species.

A second difference to epigaeicly raiding species is that *D. laevigatus*' column raids were caste specific. In epigaeic species workers of all sizes participate in raids. Only a very localized recruitment is necessary to attract larger workers to prey. In *D. laevigatus*, the smallest workers explore new terrain. They follow existent soil structures very easily, minimizing time and energy consuming digging. This mode of foraging could be shown in the field as well as in laboratory experiments. Yet, in case of food location, larger workers had to be recruited from a nearby trunk trail. The exploratory trail had to be widened first to give larger workers access to the prey.

A third difference to epigaeicly raiding species was the ability of *D. laevigatus* to exploit bulky food sources over long periods of time. A single bait could be visited non-stop for 27 days. Contrary, epigaeicly raiding species have been reported to desert prey too large to consume or transport during a raid event (Pullen, 1963; Rettenmeyer, 1963).

Combining these differences, the emerging foraging strategy of *D. laevigatus* is remarkably different to those of the classical army ant species. The trunk trail system was not merely a byproduct of a short and temporary raid. At Plot 12, trails were used for at least two months before the colony was excavated (unpubl. data). Observations of bait attendance at other plots indicate even longer use of a foraging area. Trunk trails from which short raids could be launched seem to be an energetically reasonable strategy for a hypogaecic lifestyle. However, the associated long stay within a foraging area requires raiding adaptations. In order to sustain an army ant colony for several weeks to months, a foraging area has to be either very large or the contained food resource must be rich and has to be used in a sustainable way. On Plot 12, the studied colony used a foraging area of one hectare (Table 4.1). In comparison, 0.033 *Eciton burchelli* and 0.315 *Dorylus (A.) nigricans* colonies could be expected per hectare (see respectively Leroux, 1977; Franks, 1982a). On Plot 12, termite abundance was high and palm seeds provided a reliable food source. Despite the notion of being specialized predators (Gotwald, 1978b) analyses of hypogaecic army ant species showed them to be rather generalized feeders (Pullen, 1963; Rosciszewski and Maschwitz, 1994). Likewise, *D. laevigatus* accepted a wide variety of food, probably facilitating the prolonged dependence on a limited foraging area. Termites were preyed on and their mounds could be constantly surrounded by *D. laevigatus*. However, although army ants are known to be able to kill established termite colonies (Darlington, 1985; Korb and Linsenmair, 1999), none of the observed mounds on Plot 12 showed signs of destructive raiding. *Dorylus laevigatus* exploited bulky food sources such as termite mounds or baits over long periods of time. The broad food spectrum and long and continued use of bulky food sources point to a sustainable use of the foraging area.

The ability to conduct mass raids tightly links *D. laevigatus* to other army ant species. On the other hand, the establishment of a trunk trail system and the long-term exploitation of bulky food sources puts the foraging system of *D. laevigatus* in relation to e.g. leaf-cutter and harvester ants (Shepherd, 1982; Beckers et al., 1989; Quinet et al., 1997; Howard, 2001). Away from the classical army ants, myrmicine ants of the genus *Pheidologeton* have been reported to combine as well the foraging strategies of trunk trail use and mass raiding (e.g. Moffett, 1984; Moffett, 1987; Moffett, 1988b).

The current study showed that observations of epigaeic foraging cannot be transferred directly to hypogaecic foraging. The spectacular temporary raids of epigaeicly active species seem to have at least partially developed due to their "new" habitat. Whether the reported foraging strategy is shared by other hypogaecic army ant species needs to be investigated. The detected differences in raiding strategy also hint to differences in migration habits and colony distribution. Looking into these differences (already found for *D. laevigatus*, unpubl. data) will provide a more comprehensive view of "typical" army ant behavior.

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Chapter 5

Nesting habits and colony composition of the hypogaeic army ant *Dorylus (Dichthadia) laevigatus* Fr. Smith

Summary

Epigaeically active species have set the standards for our understanding of army ant behavior. However, the majority of species leads a cryptic hypogaeic life. Being the first of the hypogaeically foraging and nesting army ant species investigated in more detail, we studied the nesting habits and colony structure of *Dorylus (Dichthadia) laevigatus* in Malaysia. By monitoring the species' hypogaeic movements via oil baits we were able to locate and – for one colony - to excavate a nest. The location of the nest was not revealed by epigaeic excavation signs. Within the soil high densities of large and intermediate sized trails indicated the presence of nest cavities. Nest form and number of cavities varied with local conditions.

With an estimated colony size of 325,000 workers the excavated colony was rather small for an army ant. Colony fragments were kept and observed in the laboratory, where emigrations and bivouac formation were documented. Worker morphological traits were measured, showing *D. laevigatus* to lack the large workers of some epigaeic species. In comparison, small workers were more common and conducted more tasks in *D. laevigatus* colonies than in epigaeically foraging species. A description of the queen is provided. The simultaneous occurrence of brood of different developmental stages indicated a non-phasic brood production. Overall, the data obtained for the hypogaeic *D. laevigatus* were compared to known epigaeically foraging *Dorylus* species.

Introduction

A very striking life-form of tropical regions are the so-called army ants, which are characterized by a unique combination of mass raiding and colony migration (Gotwald, 1982). Raid characteristics and mechanisms have been analyzed rather thoroughly for epigaeically active species (subfamilies Aenictinae, Ecitoninae, and Dorylinae; e.g. Schneirla, 1971; Gotwald, 1978a; Gotwald, 1995). On the other hand, for the majority of species, which forage hypogaeically, we are just beginning to look into these traits (Berghoff et al., 2002a). Likewise, colony attributes such as nest form, the way of its construction, and its internal conditions were studied mainly for army ant species which form epigaeic bivouacs (e.g. Beebe, 1919; Schneirla et al., 1954; Jackson, 1957; Rettenmeyer, 1963; Chapman, 1964; Schneirla and Reyes, 1969; Schneirla, 1971). Such epigaeic bivouacs, which are formed by a variety of Ecitoninae and Aenictinae species, are constructed wholly of the bodies of colony members. By altering the space between individuals, a colony is able to maintain an optimal temperature for the brood within the bivouac (Franks, 1989). Of the Dorylinae, which nest strictly hypogaeically (Gotwald, 1995), records on nest structure and conditions within the nest are scarce. The Dorylinae consist of six *Dorylus* subgenera and 61 described species (Bolton, 1995). Of these, nests have been excavated for *D. (Anomma) wilverthi*, *D. (A.) nigricans* subspecies *burmeisteri*, *molestus*, and *sjoestedti* (Raignier and van Boven, 1955; Leroux, 1977; Gotwald and Cunningham-van Someren, 1990), and one unidentified *Dorylus* species (Brauns-Willowmore, 1901). All species had epigaeic foraging trails which could be traced

back to the nest sites. To our knowledge, no nest parameters of a hypogaeicly foraging *Dorylus* species or of a species of a different subgenus have been recorded.

The current study focused on the hypogaeicly foraging and nesting army ant *Dorylus* (*Dichthadia*) *laevigatus* which has been reported throughout most of South-East Asia (Wilson, 1964). Although *D. laevigatus* is scientifically known for almost 150 years and is locally very abundant (Weissflog et al., 2000; Berghoff et al., 2002a), nothing is known about its colony composition or nesting habits. By attracting *D. laevigatus* to palm oil baits we were able to monitor a part of its hypogaeic movements and thus to locate the nest site. We report on the nest structure, colony composition, and morphology of its members, and describe morphological differences between workers allocated to different tasks. Being the first hypogaeicly active *Dorylus* species studied in detail, we compare the recorded characteristics to other *Dorylus* species.

Materials and methods

Study site

The study was conducted in a privately owned oil palm plantation near Sitiawan, Perak, West Malaysia (4°2' N 100°5' E, 0 m a.s.l.). The 15 year old plantation contained 146 palm trees distributed in 14 rows over an area of 1.1 ha (see also Berghoff et al., 2002a). The soil consisted of three distinct zones: 1) an uppermost black humus zone of about 5 cm depth, followed by 2) a yellow clay zone about 40 cm deep, containing a network of palm roots in 20 – 35 cm depth, and 3) a grayish-white zone with red iron streaks reaching the ground water level at a maximum depth of 80 cm. Data were collected at the end of the rainy period between January and March 2001.

Nest excavation and laboratory observations

Distribution of *D. laevigatus* and subterranean movements were monitored via sieve buckets (height: 9 cm, diameter: 30 cm) baited with palm oil (see Berghoff et al, 2002 for a detailed description of the method). The ants recruited in large numbers to the sieve buckets, where they fed on the oil. Presence and abundance of *D. laevigatus* as well as depth and direction of access was recorded daily for each bait. A first set of 30 baits with a bait distance of 14 m was evenly distributed in the plantation. In areas of high ant abundance, new baits were inserted between existent baits, reducing the distance between two baits to 7.5 m. These modifications were completed within the first two weeks, leading to a final number of 111 baits. Baits were refilled with 50 ml palm oil four times during the study period.

For nest excavation we used an excavator with a shovel-width of 1 m. The soil surface was closely examined at a potential nest site before starting an excavation. Then the excavator removed about 2 m long and 10 cm thick strips of soil. The scratched ground surface and the removed soil spread on the ground nearby were examined for signs of *D. laevigatus* before continuing the excavation. Ants were transferred with their surrounding soil to a container (80 cm diameter, 1 m high), which was brought into the laboratory at the end of the excavation. The soil was manually reduced as much as possible before the container was slowly filled with water, forcing the ants to accumulate close to the surface. The topmost dry soil containing ants and brood was transferred to a new container where it was spread out. From here the ants readily emigrated through provided plastic tubes to connected soil-filled nest boxes (40 x 30 x 30 cm). The nest boxes were connected via transparent plastic tubes to soil-filled glass formicaries of 1 cm width and variable sizes. Ants crossing the tubes in either direction were counted at regular intervals. Workers from the two excavated nest parts were observed for 23 and six days, respectively. Afterwards, remaining ants and brood were counted and conserved in ethanol. The approximate numbers of ants lost due to flight, death,

or foraging activity were visually estimated during each stage of the excavation and laboratory observations. Adding this estimated number to the preserved worker and brood numbers allowed us to make a prediction of colony size.

Morphological measurements

For a morphological description of *D. laevigatus* and its comparison to other *Dorylus* species, 330 workers collected from the nest were chosen at random and 20 workers to sample for size extremes. On these 350 workers and the queen, the following body portions were measured using an ocular micrometer:

- 1) Body length (L)
- 2) Head width across the midline of the head (HW)
- 3) Head length from the anterior clypeal margin to the occipital margin of the head (HL)
- 4) Alitrunk length (AtL)
- 5) Pronotum width (PnW)
- 6) Hind tibia length (HTL)
- 7) Petiolar width along its posterior margin (PtW)
- 8) Number of antennal segments (AS)

The dry weight (DW) was measured on a high precision scale after drying workers at 40°C for 24 hours. An additional 110 workers were collected at baits and on exploratory foraging trails. The HW, HTL and DW was recorded for these workers. All characters were transformed to their natural logarithms for further analysis. To estimate possible allometric growth for *D. laevigatus*, we followed the definition of Wilson (1953), who defines allometry by the following equation: $\log y = \log b + k * \log x$, where X is the size of the allometric organ and Y is the size of the organ against which X is compared. A significant deviation of the slope k of the regression line from one indicates differential growth, i.e. allometry. Since the X as well as the Y value contained measuring errors, we used a Multiple Means Regression (Model II regression) to estimate the parameters of the allometric equation. Departure of slopes from unity was tested using a t -Test (Köhler et al., 1996).

Further methods are given at appropriate places in the following text.

Results

Nest excavations

Although *D. laevigatus* is well-known locally as well as scientifically, a nest has never been documented. Plantation workers, acquainted with these common ants, assured us that "these ants have no nests". These circumstances hint to the difficulties confronted with when searching for a *D. laevigatus* nest. Although the studied plantation was well suited for such a task, we had to use an excavator to obtain the nest. In this rather destructive way a single nest was collected. Nevertheless, in consideration of the lack of information about hypogaeic army ants, we believe that the understanding of army ant biology will profit from the following description of a singleton.

In the following, the first discovery site of the colony is numbered nest site 0, followed by nest sites 1 and 2 where the ants were collected consecutively.

Nest site 0

We analyzed the pattern of bait acceptance and frequentation for 34 days. Baits close to the plantation's front were found very early during the study period and were frequented on most observation days. Combining bait observations with the plantation's topography, the nest site

was traced down to one potential area. In this area (15 m long, 4 m wide), the ground was probed with a shovel. Under a pile of palm leaves, which was pushed aside in order to examine the ground surface, a 1 m² area was found (NS0, Fig. 5.1) containing numerous well frequented *D. laevigatus* trails. A hole (25 cm diameter) dug into this area revealed a dense three-dimensional network of *D. laevigatus* trunk trails (0.8 – 1.3 cm diameter) and interconnecting secondary trails (0.4 – 0.6 cm diameter, for further trail descriptions see Berghoff et al., 2002a). Trunk trails were found up to a depth of 47 cm. The ground water level was at 70 cm depth. On two trunk trails workers transporting earthworm pieces were observed. Due to heavy rain and nightfall, we interrupted the pre-excitation and sheltered the site from rain. The site was probed 14 hours later, first by manpower and then via an excavator. No *D. laevigatus* workers were found at NS0 or the surrounding area (25.16 m²).

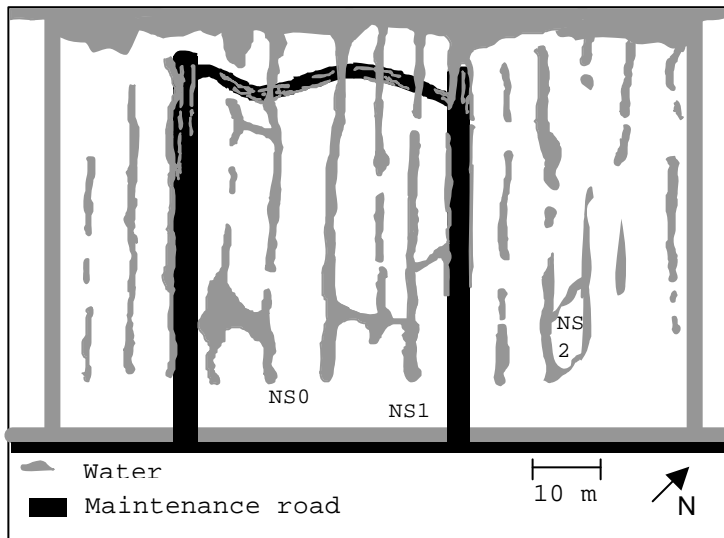


Figure 5.1. Position of the nest sites (NS0, 1, and 2) within the plantation. As shown, the trenches between palm rows filled with water and lower parts of the plantation were flooded after heavy rainfall.

Nest site 1

Since *D. laevigatus* had left NS0 we extended our search for the new nest site. The excavator continued to probe the ground within a radius of 20 m and NS1 (0.80 x 1.00 m, Fig. 5.1) was located 13 m away from NS0. Similar to NS0, NS1 was covered by a pile of dried palm leaves and contained highly frequented trails with diameters between 0.3 and 1.1 cm. Digging deeper at the site of high trail concentration, the nest was found in a depth of 20 cm. The nest consisted of an approximately round cavity with a diameter of 20 cm. It contained a dense cluster of ants and brood. The cavity was located in the soil zone with high root density and contained eight roots itself. In an area of approximately 2.5 x 3.0 m around NS1 numerous cavities of variable shapes were found which were filled with fine grained soil. Soil of this consistence was often found around baits, indicating recent and heavy digging activity of *D. laevigatus* (see also Berghoff et al., 2002a).

Observations of the collected ants and bait frequentation after nest excavation showed that only a fraction of the colony and no queen were collected. Because of this, the remaining colony was allowed to reunite and foraging movements were monitored via baits for another 39 days.

Nest site 2

Workers and brood could be found in the soil around NS1 for six days. One day after the excavation at NS1, *D. laevigatus* occupied still 79% of the previously visited baits. A shift in bait frequentation during the following weeks connoted a shift of the colony to NS2, where it was excavated after 39 days (Fig. 5.1). Previous exceptionally heavy rainfall left only 25 cm of dry soil in the nest area on the excavation day. The colony was distributed onto at least

three larger (6 to 10 cm long and 5 to 8 cm high) and several smaller nest cavities (4 to 6 cm diameter). The cavities were dispersed over an area of 1.5 x 2 m and were located about 10 cm below the soil surface. They contained clustered workers as well as brood. As for NS1, nest presence was revealed by high trail densities above the nest cavities. Although we crossed NS2 daily while checking the baits we never detected any epigaeic signs indicating hypogaecic activity. After the completed excavation we opened the ground at all potential nest sites within the plantation (554 m²) to ensure no part of the nest was missed.

Morphology and colony composition

Until now, details on colony size, worker numbers, and worker polymorphism are lacking for hypogaecic Dorylinae. In the following we provide the first detailed data.

Workers

The DW of a worker was positively correlated to its L and HW (DW:L, Spearman's R = 0.979, P < 0.002; DW:HW, R = 0.986, P < 0.002). Because of this, DW will be used as a measure of worker size. Since the worker DW did not differ between NS1 and NS2 (Mann-Whitney U Test, U = 13212.00, P = 0.513) workers from the two nest parts were pooled.

The largest worker weighted 115 times as much as the smallest (Tab. 5.1). An allometric relationship was found for only two pairs of measured body parts, i.e. HW-HL: $k = 0.949$, $r^2 = 0.96$, P < 0.02, and HTL-PnW: $k = 1.041$, $r^2 = 0.92$, P < 0.05. No break of the regression line was found when plotting the data. *Dorylus laevigatus* thus demonstrates monophasic allometry without distinct morphological subcastes.

The average DW of workers found at baits was significantly higher than that of workers collected from the nest (Fig. 5.2; Mann-Whitney U = 9182.000, P < 0.002). On the other hand, workers collected from exploratory trails were on average significantly lighter than workers collected from the nest or from baits (Fig. 5.2; Mann-Whitney U-Test, nest: U = 3933.500, P < 0.002, baits: U = 323.500, P < 0.002). To classify collected workers without measurement and to compare their results and those of former and following studies we established four arbitrary worker classes: 1) Minimum: DW < 0.25 mg, HW 0.5 – 0.8 mm; 2) Minor: DW 0.25 – 1.00 mg, HW 0.9 – 1.2 mm; 3) Medium: DW 1.00 – 2.50 mg, HW 1.3 – 1.6 mm; 4) Major: DW > 2.5 mg, HW > 1.6 mm. The morphological ranges of workers in these classes are given in Table 5.1. When previously measured workers were visually distributed onto these classes, 68% were correctly assigned to the corresponding class. Combined with the behavioral differences, the majority of workers could be assigned visually to the classes during field observations.

Of all workers measured for morphological traits (i.e. 460 workers), 114 workers (25%) belonged to the minimum class. Only in this class workers were found with less than ten antennal segments (i.e. 71 individuals, 62% of minimum workers). Most of these small workers were found within the nest (92%) and a few on exploratory trails (8%).

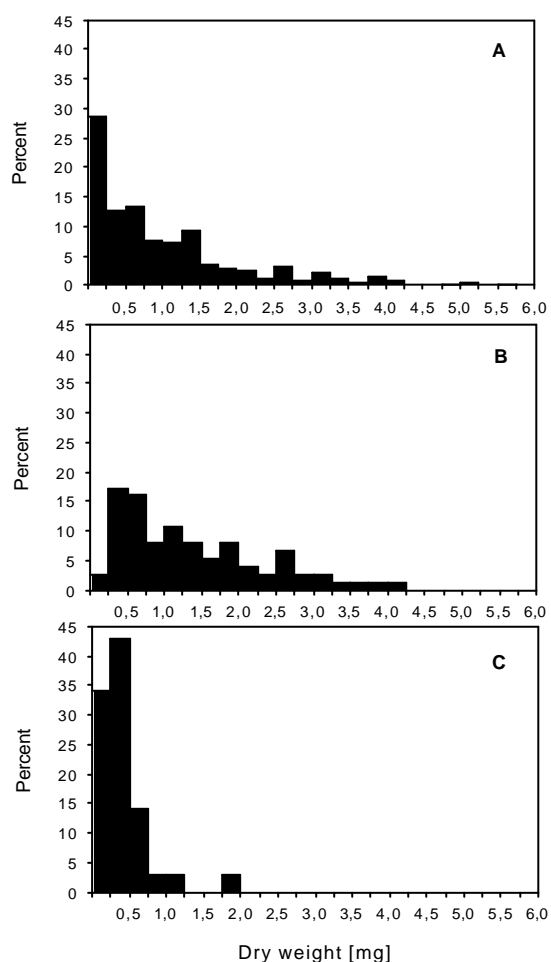
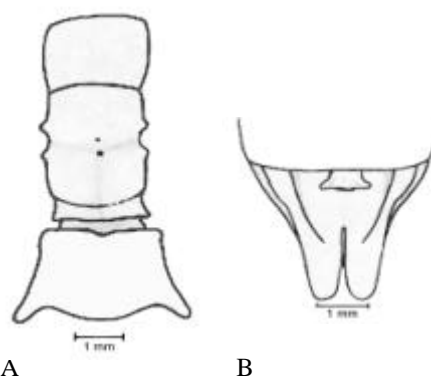
Queen

The queen was found among the excavated cavities of NS2 and was transferred with her surrounding retinue of 58 workers onto the soil of a separate container. Of the retinue, major and medium workers were surrounding and protecting the queen while medium and minor workers tried to lower her into the ground. This was done by covering her with soil removed from beneath. The queen was barely able to walk on her own and made no noticeable progress. While trying to move, being slightly physogastric, she laid a small cluster of 63 eggs. Each egg had the size of 0.4 x 0.2 mm.

The measurements of the queen are given in Table 5.1. Her external morphology conformed with the detailed description of Gerstäcker (1863). Barr and co-workers (1985) provided a list

Table 5.1. Morphological measurements of a queen and 350 *D. laevigatus* worker assigned to four classes. For abbreviations and definitions of worker classes refer to text.

		Minimum		Minor		Medium		Major		Range	Queen
		Mean	SD	Mean	SD	Mean	SD	Mean	SD		
DW	[mg]	0.14	0.05	0.57	0.20	1.42	0.37	3.09	0.79	0.05 - 5.75	71.70
L	[mm]	2.90	0.33	4.45	0.60	6.05	0.73	8.03	0.61	2.25 - 9.30	28.00
HW	[mm]	0.65	0.08	1.00	0.15	1.35	0.13	1.75	0.11	0.48 - 1.98	4.60
HL	[mm]	0.70	0.08	1.00	0.13	1.35	0.17	1.85	0.19	0.48 - 2.35	4.05
AtL	[mm]	0.84	0.11	1.30	0.18	1.70	0.17	2.20	0.17	0.50 - 2.80	5.15
PnW	[mm]	0.40	0.05	0.63	0.10	0.85	0.09	1.15	0.08	0.25 - 1.28	2.50
HTL	[mm]	0.45	0.07	0.73	0.10	0.95	0.09	1.18	0.11	0.30 - 1.40	2.05
PtW	[mm]	0.29	0.03	0.43	0.07	0.58	0.06	0.75	0.06	0.18 - 0.90	4.10
AS	[#]	9	0.89	11	0.66	12	0.35	12	0.00	8 - 12	12
n		100		117		93		40			1

**Figure 5.2.** Dry weight distributions of *D. laevigatus* worker samples. (A) 350 workers collected from NS1 and NS2, (B) 75 workers collected at five baits, and (C) 35 workers collected from exploratory raiding trails.**Figure 5.3.** Morphology of the *Dorylus (Dichthadia) laevigatus* queen: (A) alitrunk and petiolus and (B) hypopygium.**Figure 5.4.** Vertical soil filled, 1 cm wide glass formicary, showing a cavity excavated and used by *D. laevigatus* as bivouac site and associated tunnels. The dashed line encompasses the position of brood within the bivouac.

of queen morphology traits considered to be of taxonomic importance for *Dorylus* subgenera. Since no *Dichthadia* queen was available, this was the only *Dorylus* subgenus they had to omit in their study. Figure 5.3 completes their data. Our specimen missed the last one to two tarsal segments and the claws on all legs.

Colony size

The nest fragment excavated at NS1 contained an estimated 80,000 workers and 60,000 brood, of which 92% were pupae and 8% larvae. No eggs were found. The second colony fragment excavated at NS2 contained approximately 50,000 workers and 55,000 brood. Of the brood, 84% were pupae and 16% larvae. Eggs were only found as a small egg cluster laid by the queen. Because of the heterogeneity of worker sizes it was not possible to differentiate between larvae of different ages. Pupae ranged in both nest fragments between young and just beginning to differentiate, and already pigmented, old pupae.

Adding the data of both nest parts to the estimated number of workers and brood lost during the excavation, the total colony size approximates 325,000 workers and 120,000 brood.

Laboratory observations

The following observations are based on about 30,000 workers and 12,000 brood excavated at NS2.

Emigration and bivouac

A transparent plastic tube (0.6 cm diameter, 1.25 m length) connected the nest box to a soil-filled glass formicary (F1, 44 x 28 cm). Almost immediately after connection the tube was explored by minor and small medium workers. After 20 minutes larger workers frequented the tube, and after 40 minutes workers crossed the tube in a continuous stream. After 90 minutes, a cluster of workers (1 cm diameter) had accumulated in a preformed cavity between the soil and the F1 wall. The first workers transporting brood into F1 were observed at this time.

Ninety minutes after the onset of brood transport *D. laevigatus* had excavated a cavity of 1 cm diameter in the middle of F1. All incoming brood was transported into this cavity. Around the cavity's entrances and at widened places within the tunnel system small groups of ants were found standing in a threatening position on extended legs with opened mandibles. During the next eight hours minor, medium, and major workers enlarged the cavity by removing soil particles from its periphery and carrying them to cavities existent within the soil or back to the nest box. After 12 hours the new-formed cavity was 9.8 cm high and 11 cm wide (Fig. 5.4). Workers and brood had accumulated in the cavity, forming a bivouac. The bivouac consisted of a tight cluster of minor and small medium workers. These were motionless and about 80% were oriented with their heads downwards. Minor and minimum workers moved along stable paths between the bodies of their nestmates. The majority of brood was concentrated to a defined bivouac region where it was loosely dispersed between the ants' bodies (Fig. 5.4).

While the last brood was still carried into F1 (22 hours after immigration onset) brood began to be carried back to the nest box. During the next eight hours the ants forming the bivouac showed minor positional shifts, resulting in an unsteady bivouac appearance and temporary gaps in its structure. After another four hours brood was carried around within the bivouac, which had now lost its calm and orderly structure. A permanent 3 cm wide gap had formed and the cavity was clearing from the side opposite to the main entrance. Brood was now transported predominately out of F1, back into the nest box, and from here into a second formicary (F2). The emigration out of F1 lasted about 33 hours. We observed a similar order of events for F2 and a third formicary. The formation of a cavity or a bivouac were never observed in numerous previous experiments when we kept *D. laevigatus* without brood.

Feeding

While keeping the colony fragments in the laboratory, we provided oil, arthropods, and earthworms in a feeding container connected via a tube to the nest container. Living prey was always instantly attacked, killed, and covered with soil. Prey was either consumed in the container or cut to pieces and transported back to the nest container. However, we observed actual feeding, e.g. the complete imbibing of an earthworm, only during the first four to five days of captivity. After a week of captivity, earthworms were killed but left mostly untouched. On the third day of laboratory observations we provided oil dyed with Sudan III Red. Workers feeding on the red oil were discernible by a red spot visible through their gasters. When the ants emigrated to a formicary about 24 hours later, we observed 16 larvae with a distinct red color. We never observed red larvae prior to dying the oil or larvae being transported into the feeding container.

Discussion

Generally, *D. laevigatus* trails are very difficult to find by chance alone since foraging ants are restricted to small, ephemeral exploratory trails and a few trunk trails (Berghoff et al., 2002a). We had opened the ground during innumerable previous occasions when burrowing baits, looking for trails, and excavating nest. However, the large three-dimensional trail network indicating the nest presence at NS1 and NS2 had only been found at NS0 before. This supports the indication of the pattern of bait acceptance that NS0 was the original nest site of the colony. Contrary to *D. (Anomma) nigricans* and *D. (A.) wilverthi* (Raignier and van Boven, 1955), no epigaeic excavation craters revealed the presence of the *D. laevigatus* nests. While digging, *D. laevigatus* can either displace loose soil with its body or carry soil particles off to other places (Berghoff et al., 2002a). The hypogaeic shift of excavated soil could explain the observed cavities filled with fine grained soil at NS1 where the nest was probably still under construction.

Nest and emigration

Raignier and van Boven (1955) classified two general types of *Dorylus* nests: one exemplified by *D. wilverthi*, featuring a large central cavity, the other represented by *D. nigricans*, consisting of several smaller interconnected cavities. Later, Leroux (1977) showed that *D. nigricans* nests found in the savanna consisted of dispersed cavities while the more common nests found in forested areas contained a central cavity. Similar to *D. nigricans* *D. laevigatus* is able to alter the number of nest cavities with habitat conditions. With only about 25 cm of dry soil available the establishment of a central cavity, as observed at NS1, was probably not possible at NS2.

The formation of a nesting cavity and bivouac assembly was anticipated in laboratory formicaries. The structure of the bivouac was similar to bivouacs of epigaeic species (Rettenmeyer, 1963; Schneirla, 1971). Cavity formation seemed to be elicited by the presence of brood, since it was never observed in all-worker samples.

Contrary to the regular emigrations of *Eciton* species (e.g. Schneirla, 1945; Schneirla, 1957; Rettenmeyer et al., 1980), between one and 164 days can elapse between two partially epigaeic *Dorylus* emigrations (Raignier and van Boven, 1955; Raignier et al., 1974; Gotwald and Cunningham-van Someren, 1990). Our observations of the *D. laevigatus* colony prior to the excavation and of other colonies (unpubl. data) indicate a residency of several weeks to several months at the same site. Probably due to the disturbance of the pre-excavation, the colony emigrated from NS0 to NS1. The colony had about 14 hours at their disposal before the nest at NS1 was excavated. Laboratory emigrations of colony fractions lasted 22 and 33 hours. Considering the long emigration times of *D. wilverthi* colonies (e.g. 56.3 hours, Raignier and van Boven, 1955) it is likely that the emigration was not yet completed when we

excavated the nest at NS1. This could also explain why we did not collect the queen at this site. Although able to emigrate when forced to do so it remains to be shown if and how often *D. laevigatus* emigrates under natural conditions.

Colony population and composition

Ever since Raignier and van Boven (1955) reported estimated colony sizes of two to 20 million workers for *D. wilverthi*, Dorylinae were quoted as having the most numerous colonies – even among army ants. Besides for *D. wilverthi* estimations of army ant colony sizes have only been attempted for *D. nigricans* (i.e. 1,000,000, Vosseler, 1905). With an estimated colony size of 325,000 workers, the excavated *D. laevigatus* colony was small compared to these *Dorylus* colonies and medium sized for other army ants (range: 30,000 to 1,000,000 workers, Rettenmeyer, 1963; Schneirla and Reyes, 1966; Schneirla, 1971; Fowler, 1979; Franks, 1982; Franks, 1985). Large colony sizes have been linked to the development of group predation and a broad diet (Hölldobler and Wilson, 1990). Although *D. laevigatus* preys on a variety of soil animals, it seems to use available food resources in a sustainable way over long periods of time (Berghoff et al., 2002a). Without the need of constant mass raids extreme colony sizes may never have gained adaptive value. Furthermore, the confined hypogaeic space probably demarcates the operation of large masses.

Workers ranged in body length between 2.3 and 9.3 mm (Tab. 5.1) and were thus lacking the large individuals of *D. nigricans* (2.5 – 12.3 mm, Hollingsworth, 1960) and *D. wilverthi* (2.3 – 13 mm, Raignier et al., 1974). As for *D. nigricans* (Hollingsworth 1960), *D. laevigatus* showed monophasic allometry. Although no morphological subcastes were discernable army ant workers of certain size ranges perform often different tasks within colonies. In *D. wilverthi*, medium workers dominated at raids, where minor workers contributed only 5 – 6% (Raignier et al., 1974). Similar results were found for *Eciton burchelli* (Franks, 1985). Contrary, minimum and minor *D. laevigatus* workers dominated on exploratory raiding trails (Fig. 5.2 B), while baits were occupied mainly by minor and medium workers (Fig. 5.2 C). This comparative overrepresentation of small workers can be anticipated when the foraging strategy of *D. laevigatus* is taken into account. Raids are caste specific, with large workers being recruited only when prey was located (Fig. 5.2, see also Berghoff et al., 2002a). These foraging peculiarities, which are probably an adaptation to its hypogaeic lifestyle, are reflected in the morphology of *D. laevigatus*.

Another notability of *D. laevigatus* is its large range in antennal segments (8 – 12 AS, Tab. 5.1), making it the most variable army ant species in this respect. Since 92% of these small workers were found within the nest previous reports of collected foragers never documented individuals with less than ten AS (Smith, 1857; Emery, 1895a; Bingham, 1903; Wilson, 1964).

A queen is known for 19 of the 132 *Dorylus* species and subspecies (Bolton, 1995). Gerstäcker (1863) was the first to describe a "strange Hymenoptera" which he supposed to be the queen of a new *Dorylus* genus, i.e. *Dichthadia*. Although no further information about this queen or associated workers were available, Emery (1895) assumed it to be the queen of *D. laevigatus*. Our excavated *D. laevigatus* queen in fact fits the original description of Gerstäcker (1863) and its unity with *D. laevigatus* is thus finally confirmed. Like our *D. laevigatus* queen, all described functional *Dorylus* queens had mutilated tarsi (e.g. Gerstäcker, 1863; Emery, 1895b; Menozzi, 1927; Raignier and van Boven, 1955). Emery (1895) speculated that the tarsi break off while pulling and crawling through hypogaeic tunnels during migration, while Raignier (1972) found young *D. wilverthi* queens to loose their tarsi already prior to the first emigration. Possibly due to this mutilation, the *D. laevigatus* queen was not able to notably proceed on her own. While *Eciton* queens run under their own power

(Rettenmeyer et al., 1978) *Dorylus* queens probably have to be assisted by workers during emigrations. This maladjustment of *Dorylus* queens to walk could actually render emigrations more difficult and might be linked to the lower emigration rates.

The regular emigrations of epigaeicly active Ectoninae and Aenictinae species are closely linked to a cyclic brood production (e.g. Schneirla, 1957; Schneirla, 1971; Rettenmeyer et al., 1980). At any one day the brood of these species is of similar age and developmental stage (Schneirla, 1945). Due to their irregular emigration patterns, hypogaeic army ants, including all Dorylinae, are generally believed to be non-phasic (Gotwald, 1982; but see Raignier et al., 1974). *Dorylus wilverthi* colonies excavated at different times of the year contained larval percentages between seven and 29% (Raignier and van Boven, 1955). The larval percentages recorded for *D. laevigatus* fall within this range (8% at NS1 and 16% at NS2). Simultaneous presence of brood in all developmental stages indicate a non-phasic brood production.

By attracting *D. laevigatus* to palm oil baits it became possible to study the species' foraging and nesting habits. Since army ants are believed to have only limited ability of trophallaxis (Eisner, 1957; but see Rettenmeyer, 1963) *D. laevigatus* workers feeding on palm oil were supposed to use it mainly for their own nutrition (Weissflog et al., 2000). However, we found red-colored larvae after feeding oil dyed red to *D. laevigatus* workers in the laboratory. Although the role of palm oil baits in colony nutrition and their possible influence on the time of colony residency remains to be shown, they still provide a unique tool to gain a first insights into hypogaeic army ant behavior.

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Chapter 6

Sociobiology of hypogaecic army ants: description of two sympatric *Dorylus* species on Borneo and their colony conflicts

Summary

Army ants, although known as fierce predators, are rarely reported to prey on other army ants and most observed interspecific contacts were resolved comparatively peacefully. Of the four Asian Dorylinae, *Dorylus (Dichthadia) laevigatus* was believed to be the only species occurring on Borneo, sharing its habitat only with *Aenictus* and *Leptogenys* army ants and mass raiding *Pheidologeton* species. Using palm oil baits, we monitored the hypogaecic movements of *D. laevigatus* in Sabah (Malaysia, Borneo) and found a second species, i.e. *D. cf. vishnui*, also recruiting to the baits.

To describe the new species and differentiate it from *D. laevigatus*, we compared them in nine morphological traits. Hind tibia length, petiole shape, and number of antennal segments showed to differ significantly. Both species foraged predominately hypogaecically and were found in similar habitats and altitudes. However, differences were found in bait utilization and foraging strategy. Furthermore, *D. cf. vishnui* seemed to be more likely to come to the soil surface than *D. laevigatus*. A phylogenetic analysis based on 385 basepairs of mtDNA confirmed the distinctiveness of both species. Interestingly, *D. laevigatus* showed considerable intraspecific differences between subpopulations from Java, West Malaysia, and even within Borneo, which might indicate that *D. laevigatus* is a species complex containing multiple cryptic species. A single male, collected from a light trap in Sabah, could be assigned to *D. laevigatus* using the same phylogeny, confirming this previously only assumed association.

Encounters between the two species were observed at 11 baits, leading in ten cases to fierce fights. We provide the first detailed description of such interspecific fights, in which major workers were the fighters in both species. Experiments with intra- and interspecific mixing of workers in the laboratory showed *D. laevigatus* to have a higher aggressive level towards *D. cf. vishnui* than towards foreign conspecific colonies. No intraspecific fights between neighboring *D. laevigatus* colonies were observed in the field.

Introduction

"Classical" army ants belong to the subfamilies Aenictinae, Ecitoninae, and Dorylinae. Long believed to be a monophyletic group, they were later on agreed to have evolved independently (Gotwald, 1977; Bolton, 1995). However, this view is now again challenged by recent genetic analyses (Brady, 2002). Ecitoninae are restricted to the neotropics, while Aenictinae have a predominately Asian and Dorylinae an African distribution (Gotwald, 1977). Like all army ants, Dorylinae possess apterous queens and colonies reproduce through fission. This form of reproduction significantly decreases the effectiveness of army ant dispersal (Gotwald, 1977). Probably originating in Africa (Gotwald, 1977), 57 African and four Asian *Dorylus* species are known. Dorylinae are regarded to be still in a state of early dispersal (Brown, 1973), with a rather recent immigration into Asia (Gotwald, 1979). Of the Asian species, which are all hypogaecic foragers, *Dorylus (Alaopone) orientalis* is widest distributed. It has been reported from south China, Nepal, north to central India, Sri Lanka, and south-west as far as lower

Myanmar (Wilson, 1964). *Dorylus* (*Typhlopone*) *labiatus* is known from India (Wilson, 1964), and *D. (A.) vishnui* was once collected in Myanmar (Wheeler, 1913). As the only member of its subgenus, *D. (Dichthadia) laevigatus* overlaps in its distribution only marginally with the former species, having been reported from Myanmar to Sumatra, Java, Borneo, and Sulawesi (Emery, 1901b; Forel, 1901; Bingham, 1903; Wilson, 1964). Due to the ancestral number of antennal segments of large workers, and lacking other prominent modifications, *D. laevigatus* is believed to be a relatively primitive Dorylinae species (Wilson, 1964). Aside from Myanmar, *D. laevigatus* was long thought to share its habitat with no other Dorylinae army ant.

Here, we report on the first finding of a second *Dorylus* species on Borneo. The species are compared in morphological, genetic, and life history traits. Furthermore, we provide the first detailed description of recurrent interspecific army ant conflicts.

Materials and methods

Study sites

The study was conducted in the Kinabalu National Park at Poring Hot Springs, Sabah, Malaysia, Borneo (6°5' N 116°3' E, 500 – 1470 m a.s.l.). Within the park, three long-term study plots (Plots 1, 3, and 8) and three temporary plots (Plots 6, 9, and 14) were established (Table 6.1). At Plot 8, 12 additional baits could be activated if necessary, increasing the total bait number to 48. The transect of Plot 9 contained bait pairs separated by 50 m. On Plot 14, transects containing eight baits each were established every 100 m in altitude between 580 m and 1470 m. Long-term study plots were set up in March 2000 and were reactivated during the next two study periods in the following years. Short-term study plots were treated only within one study period. Data were collected between March and August 2000, March and May 2001, and March and May 2002.

Table 6.1. Study plot data

Plot	Study area [m ²]	Vegetation type	Baits	Bait distance [m]
1	375	Primary rainforest	24	5
3	2200	Old secondary forest	38	10
6	250	Primary rainforest	18	5
8	600	Young secondary forest	36	5
9	800 m longitudinal transect	Primary rainforest	34	50
14	900 m altitudinal transect	Primary rainforest	80	5

Field and laboratory observations

Within the study plots, the occurrence and distribution of *Dorylus* was studied via palm oil baits. The oil was applied in sieve buckets and sieve cavities, which allowed the estimation of ant abundance and foraging directions with minimum disturbance to the ants' hypogaecic foraging activity (see Berghoff et al., 2002a). Sieve cavities further allowed the observation of worker behavior around baits. Baits of long-term study plots were checked daily and when necessary additional times during day and night. Baits of other study plots were checked at regular intervals.

Whenever possible, foraging habits and food preferences were recorded in the field. Large worker samples (> 2000 workers) of both species and different colonies were kept in the laboratory in separate containers (24.5 cm diameter, 23 cm high), each partially filled with soil. To analyze colony conflicts, single ants were transferred from one container onto the soil of a container occupied by a different colony or species. After these initial checks, containers were connected via transparent plastic tubes (0.8 cm diameter) either directly to each other or to opposing sides of a soil-filled glass formicary (1 cm wide, 50 cm long, 30 cm high).

Conflicts between the species or colonies could be observed within the formicary or on the soil of the containers.

Morphological and genetic analyses

Following Wilson's key for army ants of the Indo-Australian region (1964), the newly detected *Dorylus* species could not be identified unequivocally. Appertaining to the subgenus *Alaopone*, our species was most similar to *D. vishnui*. However, known only from a single collection of a dozen workers (Wheeler, 1913), the number of antennal segments of small *D. vishnui* workers diverges between Wilson's key (1964) and Wheeler's (1913) original description. Due to this discrepancy and the overall rather imprecise morphological descriptions of the species key (Wilson, 1964), our species will be termed *D. cf. vishnui* until a revision of the genus clarifies its status.

In order to provide a good morphological description of the conceivably new species and to compare it to the sympatric *D. laevigatus*, we randomly collected 50 *D. cf. vishnui* and 50 *D. laevigatus* workers from three colonies, respectively, at baits. These workers were measured for the following traits using an ocular micrometer (16x magnification):

1. Body length (L)
2. Head width across the midline of the head (HW)
3. Head length from the anterior clypeal margin to the occipital margin of the head (HL)
4. Alitrunk length (AtL)
5. Pronotum width (PnW)
6. Hind tibia length (HTL)
7. Petiole width along its posterior margin (PtW)
8. Number of antennal segments (AS)

The dry weight (DW) was measured on a high precision scale after drying workers at 40°C for 24 hours.

To analyze size ranges of workers engaged in interspecific colony conflicts, 84 *D. laevigatus* and 49 *D. cf. vishnui* workers were collected at random from fights at two baits. Another 45 fighting pairs were randomly collected at one bait. Since the workers were partially dismembered, the HW of each individual was measured as an indication of worker size (see Berghoff et al., 2002b). These measures were compared to the HW of foraging workers collected at different baits.

The first Dorylinae species were described almost 200 years ago. Since then, 61 species and 71 subspecies with 43 synonyms have been described; 22 species are known only from the male caste (Bolton, 1995). Lacking a key for 57 of the species, nothing is known about geographical variability and even the most common species can not be identified unequivocally. Furthermore, the status of the subgenera remains uncertain; five of which may be elevated to genus level (Gotwald, 2002). In consideration of this taxonomic confusion, we wanted to ascertain whether the observed interactions occurred between two different or a single, morphologically variable, species. For that reason, we conducted a phylogenetic analysis, sequencing 385 basepairs of the mtDNA gene cytochrom oxidase I of the two *Dorylus* species. Comparisons were made between one individual each of different colonies collected from the following locations:

1. *D. cf. vishnui* from Plots 1 (D.vishBO1) and 14 (680 m: D.vishBO14.6 and 960 m: D.vishBO14.9)
2. *D. laevigatus* from Plots 1 (D.laevBO1), 3 (D.laevBO3), and 6 (D.laevBO6)

3. *D. laevigatus* from three locations in West Malaysia (D.laevWM)
4. *D. laevigatus* from Java (D.laevJA)

Additionally, we included two samples of *D. (Anomma) nigricans* from the Ivory Coast (D.nigrIC) and as outgroups three ant species from three different subfamilies (*Myrmecocystus mimicus*: Formicinae; *Pogonomyrme rugosus*: Myrmicinae; *Odontomachus rixosus*: Ponerinae, unpublished data courtesy of C. Strehl and T. Bickel).

Since only a single *Dorylus* species was known for Borneo, collected males had until now always been assigned to *D. laevigatus* (Emery, 1895b; Bingham, 1903). However, no male was ever collected in association with workers. The collection of the sympatric *Dorylus* species rendered the relation of males to *D. laevigatus* uncertain. To shed some light onto this matter and to supplement our species descriptions, we included one male (D.maleBO) collected at a light trap in Tawau (Sabah, Borneo) in our genetic analysis.

DNA-extraction, amplification, purification, and phylogenetic analysis

The head and alitrunk of specimens were ground in liquid nitrogen and a classical phenol/chloroform extraction protocol was used for DNA isolation (Gadau et al., 1996). A single set of primers was used for all amplifications: "Jerry" is a universal insect primer (Simon et al., 1994) and "BenR" was designed by T.R. Schultz (Smithsonian Institution). For detailed primer and PCR information see Brady et al. (2000). PCR products were purified by ethanol precipitation in the presence of 4 M NH₄Ac. The precipitated DNA was washed twice with 70% ethanol. DNA was recovered in 30µl HPLC purified H₂O. Purified PCR products including the sequencing primers were sent to a sequencing facility (Sequence Laboratories Göttingen GmbH) and directly sequenced by cycle sequencing with Big Dye. All DNA sequences could be unambiguously aligned by eye. Phylogenies were estimated under Maximum Parsimony (MP) using PAUP 4.0b10 (Swofford, 2002). MP phylogeny was obtained by branch and bound search with all sites weighted equally. Character optimization was set to ACCTRAN, starting trees were obtained via stepwise addition, and TBR branch swapping algorithm was used. Bootstrapping (1000 replicates of heuristic searching) was used to determine the strength of support for individual nodes.

Results

Morphological and genetic characterization

The morphological measures of *D. cf. vishnui* and *D. laevigatus* are given in Table 6.2. The significant differences between the species in HTL, petiole shape, and number of AS (Table 6.2) also enabled the identification of the species in the field.

A total of 385 characters were used in the analysis, of which 305 were constant, 15 parsimony-uninformative, and 65 parsimony-informative. A parsimony analysis with the branch and bound algorithm produced six most-parsimonious trees with a length of 224 steps (CI = 0.71; RI = 0.74). A bootstrap analysis (heuristic search; 1000 bootstrap replicates) supported the existence of two distinct species, i.e. *D. cf. vishnui* and *D. laevigatus*, on Borneo and unambiguously assigned the male caught at the light trap to *D. laevigatus* (Fig. 6.1). Although *D. cf. vishnui* was always the sister taxon of *D. laevigatus* in our phylogenetic analyses, this relationship was not supported by significant bootstrap values (Fig. 6.1). Therefore, the phylogenetic relationship of *D. laevigatus*, *D. nigricans*, and *D. cf. vishnui* remains open and in the need of further analysis.

Table 6.2. Morphological measures of 50 *D. laevigatus* and 50 *D. cf. vishnui* workers collected from baits and the statistical comparison of each trait (Mann-Whitney U-Test).

?	Mean	<i>D. cf. vishnui</i>			Mean	<i>D. laevigatus</i>			U-Test, P =
		SD	Min	Max		SD	Min	Max	
DW	1.001	1.155	0.148	5.117	1.058	0.976	0.157	4.084	0.812
L	6.000	1.647	3.100	9.450	5.575	1.482	3.000	9.150	0.218
HW	1.200	0.357	0.650	2.050	1.275	0.338	0.675	1.900	0.458
HL	1.450	0.453	0.750	2.450	1.250	0.367	0.750	2.150	0.068
AtL	1.725	0.493	0.800	2.750	1.625	0.410	0.900	2.450	0.131
PnW	0.700	0.197	0.375	1.150	0.750	0.214	0.400	1.250	0.417
HTL	1.000	0.299	0.480	1.800	0.950	0.229	0.500	1.375	0.039*
PtW	0.450	0.118	0.250	0.750	0.550	0.137	0.300	0.825	0.001*
AS	9.000	0.000	9.000	9.000	11.000	0.797	10.000	12.000	0.000*
Color		reddish-brown				reddish-brown			
Pet-S		rectangular and flat				rounded and erect			
Subpet-S		non-pointed				tapered			

? All measures in mm except for DW [mg] and AS [#]. For abbreviations refer to text. Pet-S = Petiole shape, Subpet-S = Shape of subpetiolar process.

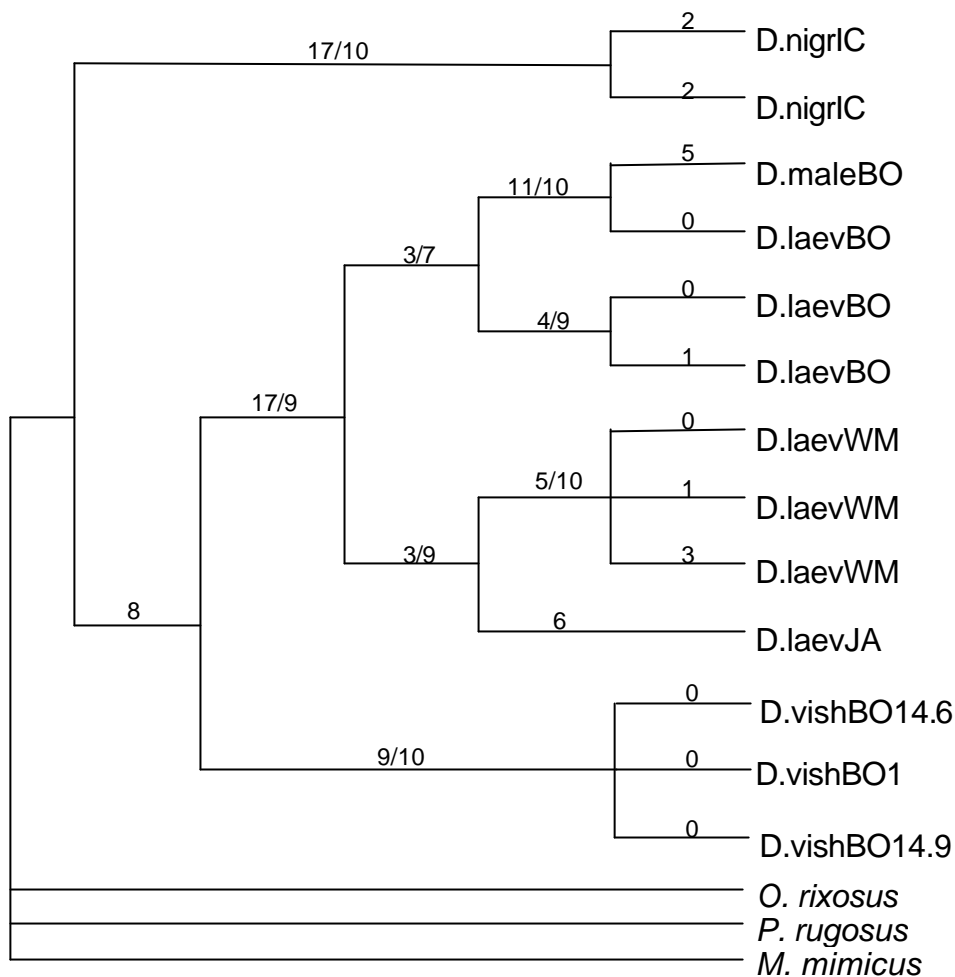


Figure 6.1. One of six most parsimonious trees (tree length = 224, CI = 0.71; RI = 0.74) of *D. laevigatus* (from Borneo, West-Malaysia, and Java), *D. cf. vishnui* (Borneo), *D. nigricans* (Ivory Coast), and a *Dorylus* male (Borneo). Numbers on the branches refer to branch length and bootstrap values (based on 1000 replicates), respectively. If only a single number is given on the branches it refers to branch length and no significant bootstrap value supported this branch. For exact sampling locations refer to the text.

Life history traits of D. laevigatus and D. cf. vishnui

For an overview of some general life history traits see Table 6.3.

Table 6.3. Trait comparison of the sympatric *D. laevigatus* and *D. cf. vishnui*.

	<i>Dorylus laevigatus</i> *	<i>Dorylus cf. vishnui</i>
Habitats	lowland & lower montane rainforest, secondary & urban vegetation	lowland & lower montane rainforest, secondary vegetation
Recorded altitudes	0 m – 1280 m a.s.l.	500 m – 960 m a.s.l.
Digging method	all sizes participate, carry soil pieces off to other places or pass soil beneath their bodies to on-following ants	all sizes participate, carry soil pieces off to other places or pass soil beneath their bodies to on-following ants
Food	oil, tuna, cookies, boiled rice, bananas, peanut butter, annelids, Homoptera, Blattodea, Hymenoptera, Chilopoda, Coleoptera, Dermaptera	oil; further food preferences are unknown
Visited plots (n = 6)	Six	Five
Avg. baits located per plot and study period	76.7% (min. 38%, max 100%)	25.3% (min. 0%, max 78%)
Avg. time to first bait location in a plot ¹	4.6 days ± 3.24 SD (min. 1 day, max 10 days)	13.67 days ± 6.38 SD (min. 5, max 23 days)
Baits visited per day ²	51.7%	56.3%
Maximum recorded stay within a plot	53 days	132 days

* For additional information on altitudinal occurrence and digging methods see Berghoff et al. (2002 a, b).

¹ Only plots with at least one located bait per study period were included. *D. cf. vishnui* did not locate any baits in 40% of study plots during the study periods.

² Only plots and days with at least one occupied bait were included in the calculation.

Foraging strata

At night, both species were observed to come to the soil surface. However, *D. laevigatus* did so only occasionally in the vicinity of heavily occupied baits. Surfacing during the day was even less common and litter was used for cover wherever possible (Berghoff et al., 2002a). *Dorylus cf. vishnui*, on the other hand, was regularly found on short ephemeral epigaeic trails around occupied baits. Twice we observed a trail of the species running for several centimeters in bright sunlight. At one of these occasions, *D. cf. vishnui* ascended 15 cm onto a dead log before disappearing in its interior. *Dorylus laevigatus* was never observed to leave the ground (see also Berghoff et al., 2002a). Further indicating increased epigaeic activity, *D. cf. vishnui* was found in pitfall traps surrounding one of six sieve buckets, which were not yet baited with palm oil (unpubl. data). After baiting the sieve buckets, *D. laevigatus* was abundant at all six baits, yet was not recorded in any of the surrounding pitfall traps.

Occurrence and bait utilization

Both species readily recruited to palm oil baits. During the first days of bait location, both species visited baits in similar numbers, exceeding 5000 ants per liter baited soil. When a new study area was created or a deserted area rebaited, *D. laevigatus* was always the first of the two species to recruit to a bait. Besides finding baits more efficiently (Table 6.3), *D. laevigatus* also occupied more baits during any study period. *Dorylus laevigatus* was found on all study plots and long-term plots were visited in each study period. On the other hand, *D. cf. vishnui* located only five of the six study plots and some long-term plots were visited only during a single study period (Table 6.3).

Dorylus laevigatus proved to be rather predictable in its recruiting to the baits of a study area. In all three study years, *D. laevigatus* located always one of two neighboring baits at its first day of appearance in Plot 8. When baits were regularly rebaited with new oil, *D. laevigatus* could recruit to baits of a plot over long periods of time (Table 6.3). If the oil was depleted, *D.*

laevigatus left the baits successively. A sudden desertion of well occupied baits was never observed. *Dorylus* cf. *vishnui*, on the other hand, could suddenly leave well occupied baits after occupying them for a few days or weeks. Rebaiting had no apparent effect on the species' return to the baits. When *D.* cf. *vishnui* reentered a study plot at a later time, the first occupied baits could be far away from the baits first located during its initial stay.

Feeding habits

Laboratory worker samples of *D. laevigatus* fed on a wide variety of foods (Table 6.3). Live arthropods were immediately attacked, covered with soil, and dismembered, while dead arthropods were only covered with soil but not consumed. Similar numbers of *D.* cf. *vishnui* workers kept in the laboratory rejected all offered food including palm oil. Live arthropods were killed, partially dissected, and covered with soil but not consumed.

Intra- and interspecific interactions

Field observations

Conflicts between two *D. laevigatus* colonies were never recorded in the field. However, fights between *D. laevigatus* and *D.* cf. *vishnui* colonies could be observed at baits on all long-term study plots. Fights were observed at 11 baits, including sieve buckets as well as sieve cavities.

When both *Dorylus* species occurred within a study plot, occupied baits were allocated to the different colonies, allowing us to monitor the respective colony movements. The approximate distribution of two neighboring colonies was best documented on Plot 8; Figure 6.2 illustrates the progress of the two colonies for an exemplary 14 days. Both colonies could be observed with varying numbers and locations of occupied baits for seven weeks. Recorded fights between the species varied in intensity. Evading a direct confrontation, a *D. laevigatus* colony occupying a sieve cavity was able to prevent the access of *D.* cf. *vishnui* to the bait: Major *D. laevigatus* workers were positioned around several entrance holes of the *D.* cf. *vishnui* colony, preventing it to enter the sieve cavity. Minor and medium workers engaged in closing the alien tunnels with soil. Only a few ants appeared to be killed on both sides and the resident colony maintained the bait ownership. In the event of the species actually fighting at a bait the fights were generally fierce, resulting in hundreds of dead workers. Eight of ten such fights were decided within 24 hours, when one of the colonies dominated the bait on the following days and no further fighting activity could be observed. However, when the conflict could not be resolved, fighting continued for two to three days without noticeably reduced intensity. Of the eleven observed fights, *D.* cf. *vishnui* apparently won five fights, i.e. occupied the bait in question on the days following the fight, while *D. laevigatus* won in four cases. In two cases both species had left the bait the next day and no victorious contestant could be determined. Neither of the two species retrieved any dead workers.

Morphological description of interspecific fights

The average HW of workers engaged in interspecific fights was for both species significantly larger than for workers collected at baits (*D.* cf. *vishnui*: Mann-Whitney U = 694, P < 0.002; *D. laevigatus*: Mann-Whitney U = 1012.5, P < 0.002; Fig. 6.3). Of the collected 45 workers engaged in single combat, participating *D. laevigatus* workers had overall significantly larger HW than participating *D.* cf. *vishnui* workers (Mann-Whitney U = 364, P < 0.002). However, the HW of a fighting pair were significantly correlated (Spearman's R = 0.45, P = 0.002), with the head of *D. laevigatus* on average 0.29 mm \pm 0.19 SD wider than its opponents. In 71% of the fighting pairs, *D. laevigatus* was the species which had locked its mandibles into the opponent's body. However, of all pairs, *D. laevigatus* was dismembered and reduced to head or head and alitrunk in 28 cases, i.e. 62%. In none of the pairs was *D.* cf. *vishnui* damaged.

Furthermore, of 45 heads collected at random at the same battlefield, 40 belonged to *D. laevigatus*.

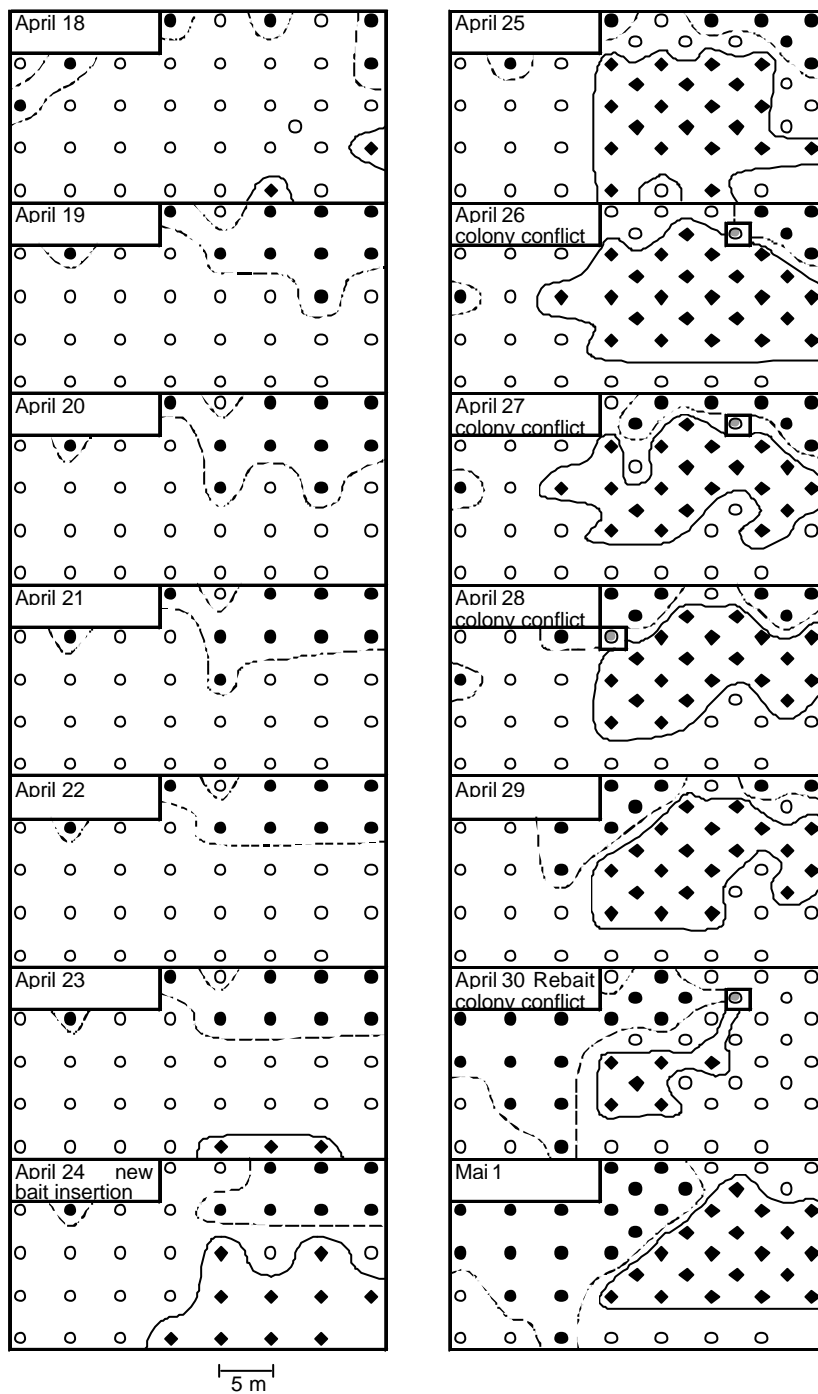


Figure 6.2. Approximate extent of neighboring *D. laevigatus* (dashed line, circles) and *D. cf. vishnui* (solid line, rhombs) colonies on Plot 8. Black circles and rhombs represent occupied, white circles unoccupied baits. Interspecific fights occurred at hatched baits surrounded by a frame.

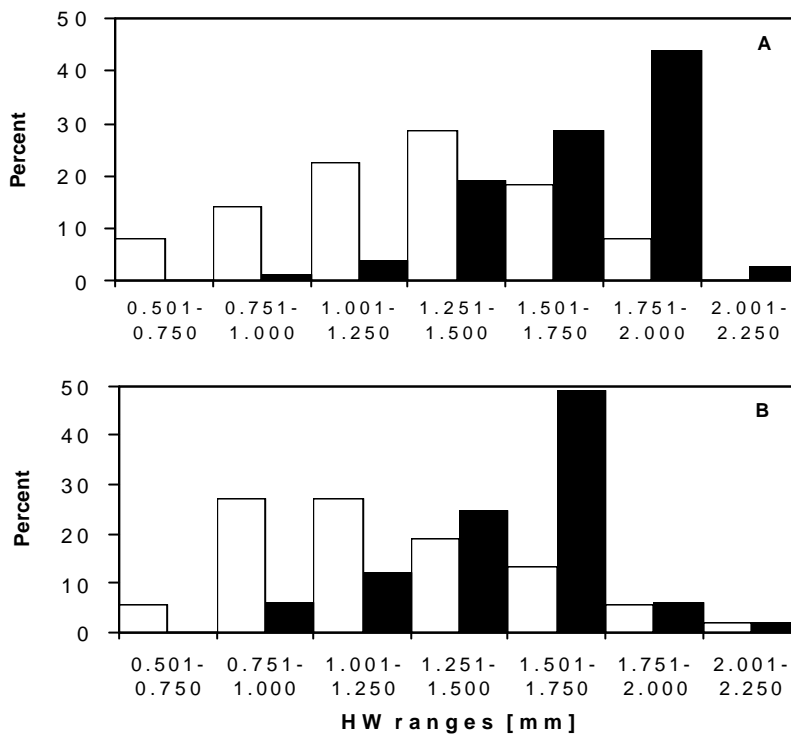


Figure 6.3. Head width distributions of *D. laevigatus* (A) and *D. cf. vishnui* (B) workers collected foraging at baits (white bars) and engaged in interspecific fights (black bars).

Interactions between laboratory worker samples

Because of the sporadic finding of *D. cf. vishnui*, worker samples of only three colonies could be collected and kept in the laboratory. After one day both species could be observed on the soil surface of their containers. Single ants of *D. cf. vishnui* and *D. laevigatus* were set free in containers occupied by *D. laevigatus*. The results for conspecific introductions were equivocal. Despite numerous contacts with "resident" ants, introduced *D. laevigatus* individuals joined one of the ant trails and disappeared unhampered underground in 69% of the separate introductions ($n = 71$). However, on two colony-pairings eight and seven from ten introduced individuals, respectively, were immediately seized and killed. In seven other single introductions resident ants attacked the introduced ant but let go of it after a while. How many ants were attacked within the soil is not known.

Container connections of different *D. laevigatus* colonies resulted always in some fighting ($n = 12$ separate connections). Eventually, one of the colonies dispersed into the other colony's container. Marking one of the colonies prior to the experiment by feeding them oil dyed with Sudan III Red, we observed that at least some ants survived the mixing of the colonies and joined the victor.

Towards *D. cf. vishnui*, *D. laevigatus* reacted much more aggressively. Here, single *D. cf. vishnui* workers placed on *D. laevigatus* soil appeared highly agitated and did not join an ant trail or try to get below the soil surface. As soon as the ant was encountered by *D. laevigatus* it was attacked and killed ($n = 26$). The same results were obtained when *D. laevigatus* individuals were released in *D. cf. vishnui* containers. Connecting containers of both species in an experiment to opposite sides of a formicary, *D. cf. vishnui* started to recruit into the formicary after two minutes. In previous formicary connections, *D. laevigatus* only came to the soil surface of the formicary after it had thoroughly tunneled through the soil. Contrariwise, the first tunnel dug by *D. cf. vishnui* in the formicary led straight up to the soil surface. After crossing the formicary over the surface, workers started to dig on the opposite

side at the border between glass and soil where the soil was loosest. In this way, *D. cf. vishnui* reached the *D. laevigatus* container only ten minutes after starting the experiment. Despite the quick recruitment of *D. laevigatus* to the site of entry, *D. cf. vishnui* was able to disperse into the container where fights ensued between the species. Two hours later the soil was covered with fighting, dead, and dying ants of both species. After six hours *D. laevigatus* had regained the ownership of the container and was fending off *D. cf. vishnui* from the tube's entry point. This situation was maintained until the experiment was ended after three days. A second connection of different colonies of the two species via a formicary led to similar results. Since the three *D. cf. vishnui* colonies were collected during different study periods, we were not able to test them for intraspecific interactions.

Discussion

Dorylus (Dichthadia) laevigatus was first described in 1857 on Borneo (Smith, 1857). Up to now, it was believed to be the only *Dorylus* species occurring this far into South-East Asia. As for the majority of army ant species, the hypogaecic lifestyle of *D. laevigatus* had made it very difficult to investigate the biology of the species and for a long time no more than its existence was known. By employing our recently developed method of attracting *D. laevigatus* to palm oil baits (Weissflog et al., 2000), we were able to detect a second hypogaecic *Dorylus* species on Borneo.

Morphological and genetic species characterization

Worker samples of the two species collected at baits differed significantly in their number of AS, petiole shape, and HTL (Table 6.2), allowing a differentiation of the two species also in the field.

The phylogenetic analysis, supported by high bootstrap values, showed that *D. laevigatus* and *D. cf. vishnui* exist as distinct species sympatrically on Borneo (Fig. 6.1). Due to their permanently apterous queens and production of new colonies by fission, army ants in general have low dispersal abilities (Gotwald, 1995). Small rivers can already pose impassable barriers and thus enhance the formation of genetically isolated subpopulations. These dispersal restrictions could explain the closer clustering of the geographically closer Java and West-Malaysian *D. laevigatus* samples (Fig. 6.1). Furthermore, different *D. laevigatus* subpopulations were discernible even within the Borneo population (Fig. 6.1), indicating the possibility of *D. laevigatus* being a species complex containing multiple morphologically similar species. However, this needs further analysis.

The single male included in our study proved to be a male of *D. laevigatus*. Its allocation to the subgenus *Dichthadia* is thus confirmed, which was previously only assumed and subsequently supplemented with morphological data (Barr and Gotwald, 1982). Twenty-seven males, which showed obvious morphological differences to the analyzed male, were collected at light traps in Sabah during 10 of 28 collection nights (unpubl. data). The absence of *D. cf. vishnui* males, which still await discovery, could indicate different flight periods or lower colony densities of this species.

Niche differences

The biological comparison of *D. laevigatus* and *D. cf. vishnui* showed both species to forage below the soil surface, to occur in similar habitats and altitudes, and to feed on palm oil (Table 6.3). The prey of *D. cf. vishnui* are not known. However, like *D. laevigatus*, all army ant species recorded to feed on oil had broad food spectra (Rettenmeyer 1963; Savage, 1849; Roonwal, 1972; Moffett, 1986). It is therefore possible that the food spectra of the two *Dorylus* species overlap at least a partially. Besides these similarities, our results indicate

differences in foraging strategies. Unlike epigaeically foraging army ant species, which only rarely reuse old foraging trails (e.g. Schneirla, 1945; Rettenmeyer, 1963; Franks, 1982a), *D. laevigatus* was shown to establish stable hypogaeic trail systems (Berghoff et al., 2002a). Formerly unknown for army ants, such a system consisted of well maintained trunk trails providing access to most regions of a colony's foraging area. The same foraging area could be used over long periods of time. The use of stable trails interlacing an area could explain the observed similar recruitment pattern to individual baits and the comparatively quick bait localization (Table 6.3). Furthermore, the high percentage of located baits (Table 6.3, see also Berghoff et al., 2002a) points to high colony densities.

Contrary to the long-term exploitation of bulky food sources seen in *D. laevigatus* (Berghoff et al., 2002a) mass raids of epigaeically active species substantially reduce the abundance of their prey (Franks, 1982b). The amount of available food was shown to influence emigration frequencies (Topoff and Mirenda, 1980; Witte and Maschwitz, 2000). By depleting their foraging areas, epigaeically active species alter the direction of each raid and eventually move to a new foraging area (e.g. Raignier and Van Boven, 1955; Rettenmeyer, 1963; Schneirla and Reyes, 1966; Franks and Fletcher, 1983; Gotwald, 1995). In order to prevent raiding over recently cropped areas, the density of such migrating species should be lower than for more stationary species. If baits would be distributed in an area occupied by a few colonies of migrating species altering their foraging directions, bait localization would most likely be random and unpredictable. Located baits could suddenly be abandoned when a colony moved its foraging site. The observed occurrence of *D. cf. vishnui* at baits was very similar to this predicted pattern of bait occupation. This implies a foraging strategy more similar to epigaeically active army ant species than to *D. laevigatus*. Similarities to epigaeically active species are further supported by the overall higher probability of *D. cf. vishnui* to come to the ground surface.

Intra- and interspecific interactions

Although most army ant species prey at least to some extent on other ants, other army ant species are generally avoided (Chapman, 1964; Gotwald and Cunningham-Van Someren, 1976; Franks and Fletcher, 1983). The concentration of foragers onto stable trail systems could reduce massive aggressive confrontations between neighboring *D. laevigatus* colonies, as observed e.g. for *Pogonomyrmex* species (Hölldobler, 1974; Hölldobler, 1986). The lack of observed aggressive conflicts between *D. laevigatus* colonies in the field and the varying but moderate level of aggressiveness in the laboratory further support the assumption of intraspecific avoidance strategies.

On the other hand, interspecific fights could be observed when *D. laevigatus* and *D. cf. vishnui* met at a bait (Fig. 6.2). These fights could proceed for several days and result in hundreds of dead workers on both sides. Both species selectively recruited large workers to the battlefields (Fig. 6.3). Apart from their evident role in fighting, major workers found at baits were either feeding or protecting the bait (Fig. 3, see also Berghoff et al., 2002b).

Despite their similar HW ranges (Table 6.2), the HW of fighting *D. laevigatus* workers collected from two baits were on average 0.29 mm wider than those of their direct opponents. Nevertheless, the majority of *D. laevigatus* workers was badly injured. The ownership of the two baits from which these fighting workers were collected was attained in both cases by *D. cf. vishnui*. This indicates that beside colony and worker sizes factors such as fighting ability and strategy, as e.g. the observed successful tunnel-plugging strategy, influence the outcome of a fight.

Boswell and co-workers (2001) proposed that arms-races between army ant colonies may account for the colony gigantism reported for some African *Dorylus* colonies. Besides the ability to exploit the food source, they assumed a colony can benefit from a fight by

incorporating the dead bodies into its biomass (Boswell et al., 2001). However, of the few reports on army ant fights, only three mention actual retrieval of dead bodies, i.e. *D. (Typhlopone)* spp. preying on *D. (A.) nigricans* (Leroux, 1979; Gotwald, 1995) and *Nomamyrmex esenbeckii* preying on *Eciton dulceum* (P. Valette pers. comm. in Borgmeier, 1955). Neither *D. laevigatus* nor *D. cf. vishnui* retrieved any bodies from their battlefields. Furthermore, a *D. laevigatus* colony excavated in an oil palm plantation was rather small for a *Dorylus* colony (Berghoff et al., 2002b). However, this excavation was conducted in West-Malaysia, where *D. cf. vishnui* did not recruit to baits during the study period. Whether other *D. laevigatus* colonies, within other habitats, and in competition with *D. cf. vishnui*, contain more workers remains to be investigated.

The hypogaeic lifestyle and sporadic occurrence of *D. cf. vishnui* has probably concealed it from scientific notice on Borneo. Our study showed that the two sympatric *Dorylus* species compete at least for palm oil but might also reduce competition by using different foraging strategies. Further studies need to show how and how many colonies of the two species are actually able to co-exist within an area.

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Chapter 7

Influence of the hypogaecic army ant *Dorylus (Dichthadia) laevigatus* on tropical arthropod communities

Summary

The majority of army ant species forages hypogaecically. Due to the difficulties in observing these ants their potential influence on hypogaecic and epigaeic arthropod communities has not yet been investigated. Being the first hypogaecically foraging army ant studied in detail we attracted *Dorylus laevigatus* to areas monitored for their arthropod diversity. Here, for the first time, the same sites were sampled before and after an army ant raid. Furthermore, interactions between *D. laevigatus* and the five most common ground-nesting ant species were noted and their life history traits compared, allowing first inferences on possible mechanisms of their coexistence.

The occurrence of *D. laevigatus* within a study plot had no evident effect on the number of arthropod taxa or individuals collected with epigaeic and hypogaecic pitfall traps. Likewise, juvenile arthropods, which are less mobile and thus a potentially easier prey for *D. laevigatus*, showed no differences in their collected numbers before and after the army ant had visited a plot. However, significantly fewer ant species were collected with hypogaecic traps after *D. laevigatus* had been within the study plots, indicating a possible predation of *D. laevigatus* especially on two *Pseudolasius* and one *Pheidole* species. The five most common ground foraging ant species demonstrated their ability to avoid, to kill, and even to prey on the army ant. The reaction of *Lophomyrmex bedoti* towards *D. laevigatus* indicated it to be a potential prey species, while *Pachycondyla* sp. 2 showed signs of 'enemy specification'. *Odontoponera diversus* and *O. transversa* actively preyed on *D. laevigatus*, while *Pheidologeton affinis* fought with *D. laevigatus* over resources. All ant species could co-occur with *D. laevigatus* at palm oil baits. Adding to the differences detected in previous studies between *D. laevigatus* and epigaeically foraging army ant species, the occurrence of this hypogaecic army ant seems to have not as devastating effects on arthropod community compositions as that of epigaeically mass raiding species.

Introduction

The ability to conduct highly organized mass raids, which can take the form of a column or swarm (Schneirla, 1934), is one of the most characteristic traits of army ants (Gotwald, 1982). Within a day's raid an army ant colony can remove large amounts of booty, e.g. 40 g of dry animal matter may be harvested by an *Eciton burchelli* colony (Franks, 1982a) or 90,000 insects by an *E. hamatum* colony (Rettenmeyer et al., 1980). Removing such large amounts of animal matter, army ants represent the top predators of leaf litter arthropods and even of small vertebrates in some areas (Brosset, 1988; Roberts et al., 2000). A raid can temporarily reduce the overall arthropod abundance and the diversity of taxa in the leaf litter (Otis et al., 1986). Areas raided by *Eciton burchelli* were found to contain a substantial number of patches in different states of recovery (Franks and Bossert, 1983). In this way, army ants are presumed to prevent the establishment of climax communities and thus to enhance arthropod diversity (Gotwald, 1995).

Due to the easier accessibility, most studies concentrated on epigaeically active army ant species. However, the majority of species forages hypogaeically (Gotwald, 1982). These species prey at least to some extent on soil-structuring animals such as termites, ants, and earthworms (e.g. Gotwald, 1974a; Gotwald, 1978b; Darlington, 1985; Berghoff et al., 2002a). Despite their potential importance for soil communities, the influence of hypogaeic army ant species on soil faunas was not yet investigated. Besides their foraging being concealed, this was at least partially due to the hard to predict foraging movements of hypogaeic ants. Epigaeically active army ants continuously alter the direction of their raids and eventually move to new foraging areas (Gotwald, 1995). Although the direction of a swarm can be influenced over short distances by offering food (Witte and Maschwitz, 2000), it seemed improbable to draw these ants to a certain area other than by chance. Being the first hypogaeic army ant studied in detail, *Dorylus (Dichthadia) laevigatus* was shown to recruit to palm oil baits in large numbers, locating the majority of baits within short periods of time (Berghoff et al., 2002a). This difference in bait utilization to epigaeically active species was linked to differences in foraging and raiding strategies, which included the long-term exploitation of bulky food sources and the establishment of stable trail systems (Berghoff et al., 2002a). The foraging peculiarities enabled us to draw *D. laevigatus* to census areas and thus to study the impact of a hypogaeic army ant on the soil and ground arthropod fauna. The arthropod diversity was monitored in census areas before and after *D. laevigatus*, which has a broad diet (Weissflog et al., 2000; Berghoff et al., 2002a), was attracted to the areas. The effects of army ant raids are often especially visible in ground ant communities, exhibiting reduced species and colony numbers in raided areas (Franks 1982a; Perfecto, 1992; Hirosawa et al., 2000). Because of this, we analyzed the recorded ant communities in more detail, comparing species and individual numbers before and after *D. laevigatus* had visited the areas. Furthermore, we report on the interactions between *D. laevigatus* and the five most common ground foraging ant species, indicating possible mechanisms of coexistence.

Materials and methods

Study sites

The study was conducted in the Kinabalu National Park and surrounding areas at Poring Hot Springs (Sabah, Malaysia, Borneo; 6°5' N 116°3' E). Data were collected between March and August 2000, March and May 2001, and March and May 2002. Study plots ($n = 7$) were established in different habitats to evaluate the occurrence and abundance of *D. laevigatus* and other ground foraging ant species. Habitats included a meadow, young and old secondary forests, primary lowland and lower montane rainforest (for details on study plot data see Berghoff et al., 2002a). Long-term study plots were established during the first study period and were reactivated during the following two years. Studies on short-term study plots were restricted to a single study period.

Baits

On all study plots, ants were baited using sieve buckets buried into the ground. Each bucket held one liter of soil and was baited with 50 ml palm oil (for a detailed description of the method see Berghoff et al., 2002a). Ants were able to access the baits either from the soil surface or through the surrounding soil. In this way, epigaeically as well as hypogaeically foraging ants could be recorded during the regular bait checks. During each bait check the sieve buckets were removed from the ground and the occurrence, abundance, and location of all ant species were recorded. Abundance was visually estimated and assigned to one of five classes: 1) 1-10, 2) 11-100, 3) 100-1000, 4) 1000-5000, and 5) >5000 ants. Samples of occurring ant species were collected, preserved in 75% ethanol, and later identified with the

key of Bolton (1994). Species were compared to the reference collection of the University of Würzburg and unidentified species were assigned morphospecies numbers. Voucher specimens were included in the reference collections at the University of Würzburg, Germany and the Sabah Parks Headquarter, Malaysia.

Census areas

After monitoring the occurrence of *D. laevigatus* in two long-term study plots (one in primary rainforest and one in old secondary forest) during two study periods, we selected these plots to investigate the possible influence of *D. laevigatus* on ground communities during the third study period. On each of the two plots, six sieve buckets were selected at random. Around each of these 12 sieve buckets a 1 m² areas ('squares') was established, containing the sieve bucket in its center (Fig. 7.1). The minimum distance between two squares was 8 m. To monitor the diversity and abundance of potential prey of *D. laevigatus*, four pitfall traps (6.5 cm diameter) were established in each square (Fig. 7.1). Each trap was covered with a leaf to prevent water accumulation and to collect predominately species which stayed close to the soil surface. Since *D. laevigatus* forages predominately hypogaeically, two hypogaeic pitfall traps were burrowed in the soil of each square (Fig. 7.1). A hypogaeic pitfall trap consisted of a rectangular container (16 cm high, 5 cm wide) with three opening slits (0.5 cm high, 4 cm wide, 2.5 cm apart) on each side. Each container was tightly fitted into a dug hole, bringing the surrounding soil close to the opening slits. Afterwards, containers were completely covered with soil, making them accessible only for animals which dug through at least some soil. After epigaeic traps were allowed to settle for four days, hypogaeic traps were inserted and all traps within a study area were opened, filled with 2% Formalin, and left to collect for three consecutive days. After removing the collected animals, epigaeic traps were closed and hypogaeic traps were extracted from the soil. For data analysis, the four epigaeic as well as the two hypogaeic traps were pooled for each square. On the day following trap collection, all sieve buckets of a study plot were baited with palm oil. Sieve buckets were checked daily and occurrence of *D. laevigatus* and other ant species was noted. Since *D. laevigatus* can be observed occasionally at the soil surface at night (Berghoff et al., 2002a), a plot was checked an additional time during the night once the army ant had entered a square. To investigate potential changes in the arthropod communities due to the presence of *D. laevigatus*, epigaeic pitfall traps were opened and hypogaeic traps were inserted in the same holes as before on each square whose sieve bucket was occupied for three days by *D. laevigatus*. All traps were left to collect for three days. Collected arthropods were sorted to orders and ants to species.

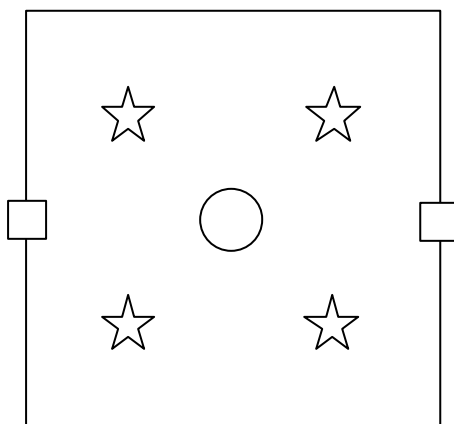


Figure 7.1. Trap arrangement in each of 12 1m² census areas (squares) to which *D. laevigatus* was attracted. Circle: sieve bucket; stars: epigaeic pitfall traps; squares: hypogaeic pitfall traps.

Interactions

To further analyze the interactions between *D. laevigatus* and ground foraging ant species, we focused on the five most common species, i.e. *Pheidologeton affinis*, *Lophomyrmex bedoti*,

Odontoponera transversa, *O. denticulata*, and *Pachycondyla* sp. 2. Except for *O. denticulata*, which was restricted to non-forested study plots, data were collected for all species on all seven study plots. All species recruited to palm oil baits, where they were observed alone as well as co-occurring with *D. laevigatus* during innumerable bait checks. In case of these species co-occurring with *D. laevigatus*, a bait check was regularly extended to observe interactions. Besides noting the behavior at baits, foraging habits of each species were observed and food samples were taken. Nest structure was analyzed by excavating five nests for each species, except for *Pachycondyla* sp. 2. To test the species' reaction toward the army ant, 20 *D. laevigatus* were released in the field close to entrances of ten different nests of each species. Since no nest was found for *Pachycondyla* sp. 2, it was confronted with *D. laevigatus* in the laboratory. In separate experiments, two *Pachycondyla* sp. 2 were united in a Petri dish with two individuals of *D. laevigatus*, *O. transversa*, *P. affinis*, and *Dolichoderus* sp., respectively (n = 6 repetitions for each species). Respective behavior was noted during the course of ten minutes.

To analyze the interactions between *D. laevigatus* and its strongest competitor at baits, i.e. *P. affinis*, we kept in a separate laboratory experiment large worker samples (> 2000 ants) of both species in separate soil-filled containers. After 24 hours, the containers were connected via plastic tubes to opposite sides of an arena (20 x 20 cm) covered with a thin layer of soil. Respective behavior and interactions were observed continuously for the first three hours and afterwards every hour for the next three days.

Results

Arthropod communities

Overall, epigeaic and hypogaeic pitfall traps collected 12660 individuals. Of these, 7509 individuals were ants (59.3%) and 578 individuals (4.6%) represented juvenile arthropod stages (Table 7.1). Since ants will be treated separately, they are not included in the following analyses.

Table 7.1. Collected individuals of the most common taxa in epigeaic and hypogaeic pitfall traps before and after *D. laevigatus* recruited to the squares. Included are only the ten squares in which *D. laevigatus* was recorded; 1338 individuals, including 658 Formicidae and 46 juveniles, were collected on the two excluded 'control' squares.

	Epigeaic pitfall traps		Hypogaeic pitfall traps	
	before	after	before	after
Acarina	203	322	85	116
Araneida	45	35	4	6
Chilopoda	4	7	31	8
Coleoptera	173	112	84**	19**
Collembola	700	985	109**	228**
Formicidae	1050	2002	717	3082
Hemiptera	49	61	8	6
Isopoda	55	65	1	15
Isoptera	30	8	139	16
Juveniles	135	248	83	66
Others*	41	78	54	37
<i>Sum</i>	2485	3923	1315	3599

*Contains 14 taxa, none of which contributed 50 or more specimen to any trap category.

**Sign. differences (Wilcoxon-Test) Coleoptera: Z = -2.2552, P = 0.011; Collembola: Z = -2.668, P = 0.008.

Epigeaic traps of a square yielded on average 10 arthropod orders \pm 1.89 (SD) and 166 individuals \pm 81.86 (SD). Hypogaeic traps – of which there were only half as many per square, collected significantly fewer orders (average = 6 \pm 1.95 SD) and individuals (average

= 53 ± 27.39 SD), (Wilcoxon Test, orders: $Z = -3.071$, $P = 0.002$; individuals: $Z = -2.824$, $P = 0.005$). However, looking at juvenile stages of arthropods, both trap types yielded similar numbers of individuals (Wilcoxon Test $Z = -1.897$, $P = 0.058$). Ensifera and Caelifera were the only taxa exclusively found in epigaeic pitfall traps. Species of all hypogaecicly collected orders were recorded also in epigaeic traps.

After baiting the sieve buckets with oil, they were located on average 11.67 days ± 2.24 SD later by *D. laevigatus*. The sieve buckets of two squares in the old secondary forest were not located by *D. laevigatus* within the study period (approximately three weeks). To minimize potential environmental variations due to long study periods, the traps of these two 'control' squares were opened following the schedule of the last occupied square (22 days after completing the first trapping period). Due to the low number of these controls, they will be excluded from the following analyses.

No significant differences were detected in the overall number of collected orders or individuals before and after *D. laevigatus* had recruited to the squares (Wilcoxon-Test, orders - epigaeic traps: $Z = -1.723$, $P = 0.085$, hypogaecic traps: $Z = -7.680$, $P = 0.442$; individuals - epigaeic traps: $Z = -1.376$, $P = 0.169$, hypogaecic traps: $Z = -0.530$, $P = 0.078$). Due to their limited mobility, juvenile arthropods are thought to be more vulnerable than adults to fall prey to army ants (Gotwald, 1974b). However, neither the number of juveniles nor the number of termites, another likely prey of *D. laevigatus* (Berghoff et al., 2002a), differed significantly between the collections before and after *D. laevigatus* visited the squares (Table 7.1). Earthworms, also commonly preyed on by *D. laevigatus*, were collected in too low numbers (i.e. 47 within all squares and collections) to evaluate any potential changes in their abundance. Comparing the collections of the main taxa for an effect of *D. laevigatus*, only the numbers of Coleoptera and Collembola collected in hypogaecic traps before and after *D. laevigatus* had recruited to the squares differed significantly differences (Table 7.1). However, the number of Coleoptera showed a similar decline from eight to one collected specimen in the hypogaecic traps of the two control squares. The number of Collembola, on the other hand, stayed much the same in hypogaecic traps of control squares between the first (19 specimen collected) and the second (22 specimen) trapping period.

Ant communities

Summarizing the yield of epigaeic and hypogaecic pitfall traps 93 ant species from 37 genera were collected (Table 7.2). As before, the two plots to which *D. laevigatus* did not recruit during the study period will not be included in the following calculations. Of the remaining 87 species, 45 were recorded with at least three individuals (Table 7.2). Of these, 16 species (36%) were collected exclusively with epigaeic and 22% exclusively with hypogaecic traps; 42% of the species were collected with both traps (Table 7.2). As for the overall arthropod diversity, epigaeic traps collected more ant species per square (average 8.57 ± 2.82 SD) than hypogaecic traps (average 5.57 ± 2.31 SD).

Dorylus laevigatus was found in none of the traps prior to baiting the sieve buckets (Table 7.2). After baiting with palm oil, *D. laevigatus* recruited to the sieve buckets of ten squares, which it visited for three days, when the traps were opened. During the three-day trapping period, *D. laevigatus* deserted eight of the ten occupied sieve buckets. The army ant was found in eight hypogaecic traps on six of the ten occupied squares.

Comparing the number of species collected by epigaeic traps before and after *D. laevigatus* had recruited to the squares, no significant differences were found (Wilcoxon-Test, $Z = -0.535$, $P = 0.593$). However, hypogaecic traps collected significantly fewer species after *D. laevigatus* had recruited to the squares than before (Wilcoxon-Test, $Z = -2.673$, $P = 0.008$).

Table 7.2. Ant individuals collected with epigaeic (n = 40) and hypogaeic (n = 20) pitfall traps before (BD) and after (AD) *D. laevigatus* was attracted to the study plots (squares, n = 10). The two excluded control squares collected six additional species and overall 658 ant individuals.

	<u>Epigaeic pitfall traps</u>		<u>Hypogaeic pitfall traps</u>		# occupied squares
	BD	AD	BD	AD	
Aenictinae					
<i>Aenictus</i> sp. 8	3				1
<i>Aenictus</i> sp. 9			37		1
Cerapachyinae					
<i>Cerapachys</i> sp. 4	1				1
Dolichoderinae					
<i>Dolichoderus</i> sp. 2	1				1
<i>Dolichoderus</i> sp. 3		2			1
<i>Tapinoma</i> sp. 1	1				1
<i>Technomyrmex</i> sp. 1		1			1
<i>Technomyrmex</i> sp. 2	1				1
Dorylinae					
<i>Dorylus laevigatus</i>				970	6
<i>Dorylus</i> cf. <i>vishnui</i>	17				1
Formicinae					
<i>Acropyga</i> sp. 1			20	1	2
<i>Camponotus</i> sp. 2		2			1
<i>Camponotus</i> sp. 3	1				1
<i>Camponotus</i> sp. 4	1				1
<i>Camponotus</i> sp. 5			1		1
<i>Paratrechina</i> sp. 7	2	3			1
<i>Paratrechina</i> sp. 8	3	4	1		5
<i>Pseudolasius</i> sp. 2			1		1
<i>Pseudolasius</i> sp. 5			31		1
<i>Pseudolasius</i> sp. 6		1	7	5	3
<i>Pseudolasius</i> sp. 7		10	54		2
Leptanillinae					
<i>Leptanilla</i> sp. 1			3		1
Myrmicinae					
<i>Crematogaster</i> sp. 5	1				1
<i>Lophomyrmex bedoti</i>	493	849	117	338	10
<i>Monomorium</i> sp. 3	1				1
<i>Myrmecina</i> sp. 1	2	1			3
<i>Myrmecina</i> sp. 2			1		1
<i>Myrmecaria</i> sp. 3	3	6			3
<i>Oligomyrmex</i> sp. 1			4	15	3
<i>Oligomyrmex</i> sp. 2	2	14	5		2
<i>Oligomyrmex</i> sp. 6		1			1
<i>Oligomyrmex</i> sp. 7	2		1	1	1
<i>Oligomyrmex</i> sp. 8	36	1	17	6	3
<i>Oligomyrmex</i> sp. 9			93	4	6
<i>Pheidole cariniceps</i>	1	2			2
<i>Pheidole clypeocornis</i>				2	1
<i>Pheidole plagiaria</i>	1	1			1
<i>Pheidole sabahna</i>		2			1
<i>Pheidole spinicornis</i>		1			1
<i>Pheidole</i> sp. 1		4	1		1
<i>Pheidole</i> sp. 17	2				1
<i>Pheidole</i> sp. 18			13		4

Table 7.2 continued

	<u>Epigaeic pitfall traps</u>		<u>Hypogaeic pitfall traps</u>		# occupied squares
	BD	AD	BD	AD	
<i>Pheidole</i> sp. 19	3	3	19	52	5
<i>Pheidole</i> sp. 20	1				1
<i>Pheidole</i> sp. 21	3	1			3
<i>Pheidologeton affinis</i>	168	458	145	1609	10
<i>Pheidologeton pygmaeus</i>	1	2	5		4
<i>Pheidologeton</i> sp. 1	217	505		55	3
<i>Proatta butelli</i>	1	2			3
<i>Recurvidris</i> sp. 1		3			1
<i>Smithistruma</i> sp. 1				3	1
<i>Smithistruma</i> sp. 2		1			1
<i>Solenopsis</i> sp. 1	4	1	16	6	3
<i>Strumigenys</i> sp. 2		2			2
<i>Strumigenys</i> sp. 3	2				2
<i>Strumigenys</i> sp. 4		1			1
<i>Tetramorium</i> sp. 5				1	1
<i>Tetramorium</i> sp. 7		1			1
<i>Tetramorium</i> sp. 8		3			1
<i>Tetramorium</i> sp. 9	2	1			2
<i>Tetramorium</i> sp. 10	1				1
<i>Trichoscapa</i> sp. 1				1	1
Ponerinae					
<i>Anochetus</i> sp. 2	2				2
<i>Diacamma intricatum</i>	1	1			2
<i>Gnamptogenys</i> sp. 2	1				1
<i>Gnamptogenys</i> sp. 3			1		1
<i>Hypoponera</i> sp. 1	1	1			2
<i>Hypoponera</i> sp. 2	3	2	8	1	3
<i>Hypoponera</i> sp. 8			2		1
<i>Hypoponera</i> sp. 9	1				1
<i>Leptogenys mutabilis</i>		19	11	4	4
<i>Leptogenys</i> sp. 2		45			1
<i>Leptogenys</i> sp. 4	5	5			6
<i>Leptogenys</i> sp. 5	2	4		1	4
<i>Leptogenys</i> sp. 6	2				1
<i>Odontomachus rixosus</i>	1	1			1
<i>Odontomachus</i> sp. 1	14	3			1
<i>Odontoponera transversa</i>	20	13		2	9
<i>Pachycondyla sharpi</i>	1	2	7		4
<i>Pachycondyla tridentata</i>	2	4			4
<i>Pachycondyla</i> sp. 1	11	12		1	2
<i>Pachycondyla</i> sp. 2			95	4	7
<i>Pachycondyla</i> sp. 4	3				1
<i>Pachycondyla</i> sp. 12	1				1
<i>Pachycondyla</i> sp. 13		1			1
<i>Ponera</i> sp. 1			1		1
unidentified genus	1				1
Individuals	1050	2002	717	3082	
Species	50	46	29	22	

Night checks around baits occupied by *D. laevigatus* revealed no increased epigaeic ant activity or nest evacuations.

During the after-*Dorylus* trapping period, five squares were raided by mass-raiding ants. These raids were indicated by traps of a square with more than 100 individuals of such species, i.e. *Pheidologeton* sp. 1 (one occasion, 505 ants), *P. affinis* (two occasions, 1181 and 184 ants), and *D. laevigatus* (three occasions, 102, 121, and 612 ants). Since the high numbers of raiding individuals may conceal abundance changes of other ant species, the above individual numbers were not included in the comparison of collected individuals. Epigaeic as well as hypogaeic traps collected similar numbers of individuals before and after *D. laevigatus* had visited the squares (Wilcoxon-Test, epigaeic traps: $Z = -0.969$, $P = 0.333$; hypogaeic traps: $Z = -1.274$, $P = 0.203$).

Interactions between D. laevigatus and selected ground ant species

Some life history traits of the five focus species are summarized in Table 7.3. All species were active independent of time of day.

Table 7.3. Life history traits of five common ground foraging ant species.

	<i>Lophomyrmex bedoti</i>	<i>Odontoponera denticulata</i>	<i>Odontoponera transversa</i>	<i>Pachycondyla</i> sp. 2	<i>Pheidologeton affinis</i>
Habitat ¹	U, SF, PF	U	PF	U, SF, PF	U, SF, PF
Height [m] ²	1060	500	880	680	1470
Colony size	> 100	> 100	> 100	> 100?	> 10,000
Nest type	Polydomous soil nests	Polydomous soil nests	Polydomous soil nests	Unknown	Multichambered soil nest
Nest/square ³	0.92 ± 0.79	Unknown	0.58 ± 0.67	Unknown	0.92 ± 0.67
Foraging stratum	Hypogaeic and epigaeic	Predominately epigaeic	Predominately epigaeic	Hypogaeic	Hypogaeic and epigaeic
Foraging strategy ⁴	Single foragers, TT	Single foragers	Single foragers	Single foragers	Single foragers, TT
Observed food	Oil, tuna, honey, cookies, Homoptera, arthropods	Oil, tuna, honey, cookies, arthropods	Oil, tuna, honey, cookies, arthropods	Oil, arthropods, annelids	Oil, tuna, honey, cookies, arthropods, annelids, seeds
Class/baits ⁵	2: 11-100 ants	1: 1-10 ants	1: 1-10 ants	1: 1-10 ants	4: 1000-5000

1: U = Urban vegetation, SF = Secondary forest, PF = Primary rain forest

2: Height up to which the species was recorded at oil baits along an altitudinal transect reaching 1470 m

3: Average number of nests (± SD) found by baiting twelve 1 m² study areas (squares)

4: TT = Trunk trails

5: Mean abundance class on the second day of bait occupation

Lophomyrmex bedoti nests belonged to two types: satellite nests with up to five entrances housing workers, brood, and Hemiptera, and main nests consisting of several soil nests interconnected via hypogaeic tunnels. *Dorylus laevigatus* workers released around entrances of satellite nests were generally avoided. Twice the release of *D. laevigatus* resulted in the temporary evacuation of a satellite nest. Contrary, when *D. laevigatus* was released at main nest entrances, *L. bedoti* workers accumulated at the entrances and occasionally attacked the army ant.

The abundance of *L. bedoti* at baits did not differ significantly between baits with and without *D. laevigatus* (Mann-Whitney U = 306.00, $P = 0.537$). Co-occurring with *D. laevigatus*, it restricted its bait access mainly to the top of the bait and retreated upon contact. Regularly, *L. bedoti* collected dead *D. laevigatus* workers from baits (e.g. left after fights with *Pheidologeton affinis*, see below).

Odontoponera denticulata and *O. transversa* exhibited very similar life history traits (Table 7.3). The nests of both species were connected to neighboring nests via hypogaeic tunnels. Probably due to these tunnels, all nests were evacuated when the experimental excavations

reached the nesting chambers. Without other species present at a bait, both *Odontoponera* species removed pieces of soil soaked with oil. However, when *D. laevigatus* joined at a bait, both *Odontoponera* species switched to hunting the army ant. While the abundance of *O. transversa* did not differ significantly between baits with and without *D. laevigatus* (Mann-Whitney U = 3282.00, P = 0.665), it increased in the presence of *D. laevigatus* for *O. denticulata* (Mann-Whitney U = 231.00, P = 0.002). When releasing *D. laevigatus* close to nest entrances of both *Odontoponera* species, workers of the latter species effectively guarded their nest entrances, preventing the army ants' descend into the nest-tunnel. Incoming foragers started to hunt dispersed *D. laevigatus* and carried them into the nest.

Pachycondyla sp. 2 nests could not be detected, as the species quickly retreated into the soil when encountered during a bait check. On 14 occasions, *Pachycondyla* sp. 2 shared a bait with *D. laevigatus*, where its abundance did not differ significantly from its mean abundance (Mann-Whitney U = 412.00, P = 0.899). Twice, five to six *Pachycondyla* sp. 2 were observed to successfully maintain a small bait area although co-occurring with more than a thousand *D. laevigatus*. When the species were mixed during the bait check, a few interspecific fights could be observed, after which *Pachycondyla* sp. 2 retreated into the ground. On the following days, no *Pachycondyla* sp. 2 were found at these baits. Mixing *Pachycondyla* sp. 2 with *O. transversa*, *P. affinis*, and *Dolichoderus* sp., respectively in the laboratory, the species quickly retreated whenever they met. However, when mixed with *D. laevigatus*, *Pachycondyla* sp. 2 immediately attacked the army ant. Each *D. laevigatus* worker was repeatedly stung by one or both *Pachycondyla* sp. 2. All *D. laevigatus* were paralyzed within the first minute of the experiments.

Pheidologeton affinis immediately recruited large numbers of nestmates and attacked and killed *D. laevigatus*, when it was released close to *P. affinis*' nest entrances. At baits, the abundance of *P. affinis* did not differ significantly between baits with and without *D. laevigatus* (Mann-Whitney U = 8799.00, P = 0.622). However, at least some fighting activity could always be observed when both species co-occurred at a bait (Fig. 7.2). A fight (n = 33) was judged as won when one species maintained the lone bait ownership for three consecutive days. The outcome of a fight seemed to be related to the order in which the species arrived at a bait (Table 7.4). When worker samples were connected to an arena in the laboratory, both species dispersed onto the arena within one hour. Upon contact, *D. laevigatus* assumed an aggressive posture but caught *P. affinis* only rarely. On the other hand, single *D. laevigatus* workers were overwhelmed by groups of *P. affinis* workers, pinning *D. laevigatus* to the ground. After three hours of the experiment, *D. laevigatus* used two trails across the arena. These trails were lined with medium and major workers, shielding the trails from surrounding *P. affinis*. After 24 hours, *D. laevigatus* had moved across the arena and into the container of *P. affinis*, which accumulated at the soil surface. This situation was maintained until the end of the experiment.

Table 7.4. Interspecific fights between *Pheidologeton affinis* and *Dorylus laevigatus* at baits. The percentage in which *D. laevigatus* won and lost the bait ownership depending on the order of arrival is given. The outcome was called a draw when both species left the bait on the same day.

1 st species at the bait	Bait ownership by <i>D. laevigatus</i>			N =
	Won [%]	Lost [%]	Draw [%]	
<i>P. affinis</i>	14	21	64	14
<i>D. laevigatus</i>	58	25	17	12
Both species	71	14	14	7

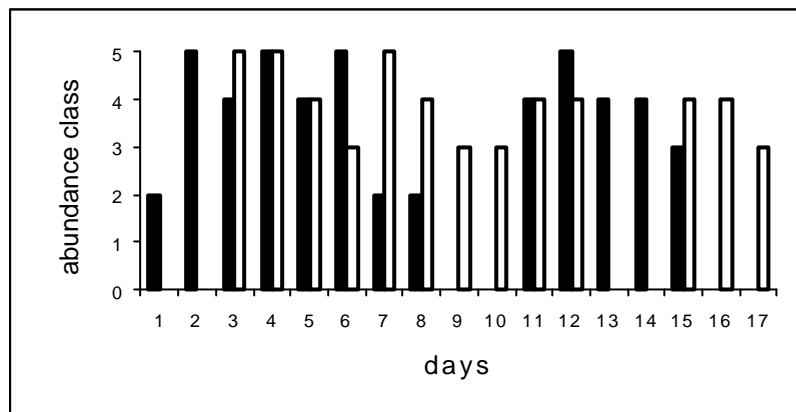


Figure 7.2. Abundance of *Pheidologeton affinis* (black bars) and *Dorylus laevigatus* (white bars) co-occupying a single bait. Interspecific fights could be observed on days with co-occurring species. For abundance classes refer to text.

Discussion

A variety of methods has been developed to sample ground and litter arthropod communities. Litter techniques (e.g. Winkler sifting or Berlese funnel) represent methods enabling the effective collection of litter fauna, while direct and intensive sampling methods are well suited to gain an inventory of ant species richness (Bestelmeyer et al., 2000). However, all these methods cause major disturbances to the soil and litter fauna, preventing the possibility to re-sample the same area after a short while. Although pitfall traps will not catch all species (Greenslade, 1973; Bestelmeyer et al., 2000), the combination of epigaeic and hypogaeic traps should provide a reasonable collection of potential *D. laevigatus* prey species. The high numbers of juveniles in hypogaeic traps indicated the soil stratum to be rich of this potential prey. Ants comprised 59% of all collected specimen and they dominated in all traps (Table 7.1). Most ant species with more than two collected specimen were restricted either to epigaeic (36%) or hypogaeic (22%) traps. Similar species restrictions to epigaeic and hypogaeic traps were also found by Quiroz-Robledo and Valenzuela-González (1995).

The possibility to attract *D. laevigatus* predictably and within short periods of time to a bait enabled the first study of the potential influence of a hypogaeic army ant on soil fauna. However, the presence of the bait could also influence the species' foraging behavior. Although oil is probably fed to some extent to the larvae (Berghoff et al., 2002b), other food, in particular proteins, should be needed to rear the larvae (Weissflog et al., 2000). Because of this, *D. laevigatus* would need to extend its foraging also beyond baits. When army ants locate a food source during a mass raid, foragers are recruited from the swarm to that site (Witte and Maschwitz, 2000). Not all arriving foragers stop at the prey but proceed a little further into the surrounding area (Witte and Maschwitz, 2000). This 'recruitment overrun', which is closely linked to the spatial development and extension of raids, was described for mass raiding species such as *Neivamyrmex*, *Pheidologeton*, and *Leptogenys* (Topoff et al., 1980; Moffett 1988a; Witte and Maschwitz, 2000). With initial abundances of more than 5000 ants per sieve bucket (Berghoff et al., 2002a), a bait literally flows over with *D. laevigatus* workers, some of which disperse due to the recruitment overrun into the surrounding area. If prey is discovered, nestmates will be recruited further into the area, as was observed for *D. laevigatus*, extending its foraging into the soil surrounding a recently located bait, where they preyed on *Paratrechina* sp. (Berghoff et al., 2002a). As indicated by the presence of *D. laevigatus* in hypogaeic pitfall traps, the squares should thus have been subject to at least some raiding activity. Most sieve buckets were deserted by *D. laevigatus* after three to five days, indicating that the oil was not sufficient to keep the ants within the area. This should further increase the likelihood of raids into the surrounding area.

When comparing areas recently raided by epigaeically foraging *Eciton burchelli* or *Aenictus* species to control areas, a strong influence of the army ants on litter arthropods was shown

(Franks, 1982a, b; Otis et al., 1986; Hirosawa et al., 2000). While prey ants took about 100 days to recover to half their original abundance, populations of crickets and roaches quickly recovered due to individual migration to the site (Franks 1982a). Migration of succession species to empty patches increased also the ant diversity after a raid (Franks and Bossert, 1983). Because of this, effects of an army ant raid are most likely to be seen a few days after a raid. Arthropods were trapped three days after *D. laevigatus*, which preys on earthworms and a wide variety of arthropods including termites and brood of ground-nesting ants (Weissflog et al., 2000; Berghoff et al., 2002a, b), had entered a square. No significant differences were found in the number of arthropod orders, individuals, or juveniles collected with epigaeic or hypogaeic traps. A decrease in Coleoptera numbers in hypogaeic traps was also seen in control squares and was thus probably linked to some external factor. The significant increase in Collembola collected in hypogaeic traps after *D. laevigatus* was recorded in the squares, may be linked to the epigaeic and hypogaeic mass raids, which probably flushed Collembola from the leaf litter during this trapping period. Similar to overall arthropod numbers, ants showed no effect in their number of collected individuals. However, hypogaeic traps, collecting in the preferred foraging stratum of *D. laevigatus*, collected significantly fewer ant species after *D. laevigatus* had visited the squares. In particular the disappearance of two *Pseudolasius* and one *Pheidole* species, which were numerous in the first collection (Table 7.2), could indicate predation by *D. laevigatus*. The effect of the only reported hypogaeic raid of an army ant species, i.e. *Labidus coecus*, on an ant community resulted in one dead colony out of 23 colonies attacked (Perfecto, 1992). A similar impact of *D. laevigatus* would hardly be detectable by the here applied methods. However, the lower species numbers in traps after *D. laevigatus* had visited the squares could also be related to the mass-raids of three other ant species in the same time frame. Most prey ant species seem to flee into the vegetation (Hirosawa et al., 2000; Berghoff et al., 2002a) or to related nests (LaMon and Topoff, 1981; Droual, 1984) during a raid, which can temporarily reduce ant abundance in a raided area. The use of satellite nests, also recorded for three of the five most common ant species in this study (Table 7.3), can thus provide refuges during army ant attacks (Droual, 1984; Perfecto, 1992). The five focus species were able to coexist with *D. laevigatus* despite conformities in habitat, foraging strata, and food preferences (Table 7.2, Berghoff et al., 2002a), showing different strategies to cope with the army ant. All species were able to maintain exclusive bait sections when co-occurring with *D. laevigatus*. The induced nest evacuations and defensive behavior observed for *L. bedoti* in the presence of *D. laevigatus* were recorded in similar experiments also for prey species of *Neivamyrmex* (LaMon and Topoff, 1981; Droual, 1984). The reaction of *L. bedoti* thus identifies it as a possible prey species of *D. laevigatus*. However, due to their high density of associated nests (Table 7.3) mature colonies will probably be able to survive an attack (Hirosawa et al., 2000). The high aggressiveness of *Pachycondyla* sp. 2 towards *D. laevigatus* in arena tests indicates a possible 'enemy specification' of *D. laevigatus*, signifying it to be a serious enemy of *Pachycondyla* sp. 2 (Wilson, 1975; Hölldobler, 1979). Since hypogaeic *D. laevigatus* raids are conducted by minor workers (Berghoff et al. 2002 a), a strong defensive reaction by *Pachycondyla* sp. 2 could probably ward off an attack. Contrary to *Pachycondyla* sp. 2, the two *Odontoponera* species not only killed but actively preyed on *D. laevigatus*. Such a behavior was up to now reported only for *Oecophylla* species (Gotwald, 1995). The predatory efficiency and the use of interconnected nests probably enable these fast-moving *Odontoponera* species to restrain raiding *D. laevigatus* digging through to their nest cavity and to evacuate their nests before too many army ants arrive on the scene. A low predation pressure is further supported by the mild reaction towards *D. laevigatus* workers released at *Odontoponera* nests (compare to LaMon and Topoff, 1981). On the other hand, when releasing *D. laevigatus* close to *Pheidologeton affinis* nests, or when the species met at a bait, interspecific fights would always develop. Fights at baits could continue for several days (Fig. 7.2). However, *D.*

laevigatus was more likely to gain the bait ownership when it arrived prior to or at the same time with *P. affinis* (Table 7.4). In a laboratory experiment, *D. laevigatus* was shown to shield its columns from attacking *P. affinis*, and thus to maintain its position or to slowly advance. A similar strategy could also be demonstrated for fights between the sympatric *D. laevigatus* and *D. cf. vishnui* (Chapter 6). Combining the observations at baits and in the laboratory, *D. laevigatus* showed to gain and maintain new terrain by slowly advancing in tight formation and defending the gained areas at strategic points. Compensating its lower ability to defend and retain a bait, *P. affinis* had high nest (Table 7.3) and forager densities, enabling it to localize most baits within 24 hours (Berghoff, unpubl. data). *Dorylus laevigatus*, on the other hand, needed on average 8.6 days to locate a bait (Berghoff et al., 2002a).

Although known to conduct hypogaeic column and occasionally epigaeic swarm raids and to prey on a wide variety of arthropods (Berghoff et al., 2002a), *D. laevigatus* showed only little effect on hypogaeic and none on epigaeic arthropod communities. Even when *D. laevigatus* recruited to a sieve bucket it could occur in none or only one of the squares' hypogaeic pitfall traps. Concentrating its foraging onto a few stable trails, from which single raids originate, *D. laevigatus* can exploit larger resources over long periods of time (Berghoff et al., 2002a). In this way, only occasionally single ant colonies should fall prey to a *D. laevigatus* raid. The possible effect of *D. laevigatus* on earthworms and termites, a seemingly preferred prey (Berghoff et al., 2002a), might have been underestimated due to their low individual numbers in traps (Table 7.1). The five most common ground-nesting ant species were able co-occur even with more than 1000 *D. laevigatus* at a bait by employing different strategies. Adding to the differences separating *D. laevigatus* from epigaeically raiding army ant species (Berghoff et al., 2002a, b) this hypogaeic ant thus seems by far not as fierce a predator as e.g. the epigaeically swarm raiding army ant *D. nigricans*.

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Chapter 8

Baited sieve buckets: an easy method to include hypogaeic ant species into ground ant diversity studies

Summary

Numerous studies have been conducted to investigate the diversity of ground ant communities. However, despite their potential importance for tropical ecosystems, hypogaeicly foraging ant species were often neglected or only marginally touched by these studies. This was mainly due to the difficult sampling of these cryptic species. We successfully used palm oil baited sieve buckets to study ground and especially hypogaeicly foraging ant species on Borneo. We suggest the inclusion of sieve buckets into future studies of ground ant communities to obtain a more comprehensive record of the hypogaeic ant fauna than could be sampled with the methods hitherto applied. As expected, the species yield was with 85 collected species out of 32 genera lower than in studies employing several and more generalized sampling methods. However, a large proportion of our collected species (48%) had not been collected during a previous study extensively sampling the same area. Of the collected species, 55% foraged at least partially below the soil surface, 47% of which had not been collected by Winkler litter sifting in a previous study in the same area. Furthermore, by employing sieve buckets, we could show different hypogaeic species to be undersampled by other studies using different methods in the same area. Although the oil was accessible to epigaeicly as well as hypogaeicly foraging species, only 45 species demonstrably fed on the oil. The attractiveness of oil for ant species of different genera is discussed. Since oil was not a generally attractive baiting substance, we successfully tested sieve buckets baited with tuna and cookies in a preliminary way. We conclude that sieve buckets represent a quick and easy method well suited to supplement other methods, finally enabling the inclusion of hypogaeic ant species into ground ant diversity studies.

Introduction

Tropical rain forests are known for their exceptionally high arthropod diversity, a large contribution to which is made by ants. With their diverse lifestyles, including gardening and farming habits, and their often predatory feeding preferences, ants interact in manifold ways with their surrounding fauna and flora (e.g. Hölldobler and Wilson, 1990). Their high abundance, combined with the ability to influence the composition of arthropod communities (Petal, 1978; Grant and Moran, 1986; Hölldobler and Wilson, 1990), render them an important factor in tropical ecosystems. Linked to this role, numerous studies were conducted investigating ant diversity and community composition (e.g. Andersen, 1986; Basu, 1997; Xu et al., 1999). Ants were found to be abundant in the canopy, the vegetation, as well as in the ground leaf litter (e.g. Verhaagh, 1990; Tobin, 1995; Floren and Linsenmair, 1997; Brühl et al., 1998; Ito et al., 2001). A variety of methods was developed to evaluate ant diversity within a particular stratum (e.g. Winkler litter sifting, canopy fogging, pitfall traps, hand sampling). While most studies concentrated on one method and a single stratum, a few studies combined different methods to record the overall ant diversity of an area (e.g. Verhaagh, 1990; Brühl et al., 1998; Malsch, 2002). Since most sampling methods are biased (Bestelmeyer et al., 2000) different methods should always be combined to gain a

representative synopsis of a stratum's ant fauna (Delabie et al., 2000). However, due to the poor accessibility, hypogaecic ant diversity was only marginally touched by ground sampling studies and was often completely neglected (but see Delabie and Fowler 1990, 1995). The soil-structuring activities and the potential predation on ground-dwelling ants, termites, and juvenile arthropods, indicate an important role of hypogaecic ants in tropical ecosystems. With these points in view, studies on ground ant diversity should attempt to include hypogaecic ant species.

We studied the ground ant community recruiting to palm oil baits on Borneo. The oil was applied in special baiting containers, which allowed us to observe epigaeically as well as hypogaecically foraging species. We point to differences between the oil-recruiting ant community and ant communities recorded by other authors within the same area. Furthermore, the suitability of the employed baiting containers to supplement ground ant diversity studies is discussed.

Materials and methods

Study sites

The study was conducted in the Kinabalu National Park at Poring Hot Springs (Sabah, Malaysia, Borneo; 6°5' N 116°3' E). Data were collected between March and August 2000 and February and May 2001.

Ants were studied at palm oil baits (see below). Included in this study are 182 baits distributed onto five plots:

Plot 1 containing 24 baits in primary lowland rainforest (500 m a.s.l.).

Plot 3 containing 30 baits in old secondary forest (500 m a.s.l.).

Plot 6 containing 12 baits in primary lowland rainforest (550 m a.s.l.).

Plot 8 containing 36 baits on an old meadow partially covered with young secondary forest (500 m a.s.l.).

Plot 14 (East Ridge, Mount Kinabalu) containing 80 baits distributed onto ten altitudinal transects between 580 m and 1470 m a.s.l.

For further details on study plot data see Berghoff et al. (2002a).

Baits

To study epigaeically and hypogaecically foraging ant species recruiting to palm oil baits we applied the oil in sieve buckets (see also Berghoff et al., 2002a). A sieve bucket (height 15 cm, diameter 12 cm) held one liter of soil and was completely perforated (holes: 0.5 cm x 1 cm). It was buried into the ground up to its rim and filled with the excavated soil. In this way, hypogaecically foraging ants could move freely from the surrounding soil through the bucket's holes into the bucket. Epigaeically foraging species could access the soil inside the bucket through the bucket's lid, which was also perforated. As bait we used kitchen palm oil (50 ml), which was poured onto the soil in the bucket. To prevent quick washing out of the oil and water accumulation, buckets were sheltered from rain by covering each with a broad leaf.

Ant occurrence at baits was recorded at regular intervals. To check a bait, the bucket was pulled out from the hole via an attached handle. Ants were collected for later identification from the bucket's hole remaining in the ground and from the sides of the bucket. Judging from the point of entry into the bucket's hole, a species' foraging was classified as predominately hypogaecic or epigaeic or, when both strata were used, as not stratum specific.

To test whether sieve buckets were suitable to sample hypogaecic ant species which did not recruit to palm oil, canned tuna and household cookies were used as alternative baiting substances. For these trials, the soil of six sieve buckets was mixed with cookie crumbs or canned tuna, respectively. The soil mixtures were then covered with an extra layer of plain soil to render bait access more difficult for epigaeically foraging species. The baits were

distributed randomly at the edges of Plots 3 and 8. Baits were checked daily for six consecutive days.

Ant identifications

Collected species were preserved in 75% ethanol and later identified to the genus level with the key of Bolton (1994). The species were compared to the reference collection of the University of Würzburg, which contains leaf litter ants collected in Sabah (Poring Hot Springs: 560 –1530 m, Danum Valley Conservation Area, Sepilok Forest Reserve, Kebun Cina Forest Reserve, and Deramakot Forest Reserve) using pitfall traps and Winkler litter sifting (Brühl, 1996; Brühl et al., 1998, 1999). Unidentified species were assigned morphospecies numbers. Voucher specimens were deposited within the reference collections of the University of Würzburg, Germany and the Sabah Parks Headquarter, Malaysia.

Results

Overall, 85 species from 32 genera and seven subfamilies were recorded at sieve buckets baited with palm oil (Tab. 8.1). Of these, 22 species, i.e. 26 percent, represented predominately hypogaecicly foraging species (Tab. 8.2). Another 25 species (29%) foraged hypogaecicly as well as epigaecicly. The comparison to the reference collection showed that 48 percent of the species found at sieve buckets were new to the collection. Of these new species, 14 (34%) foraged predominately hypogaecicly and eight species (20%) above as well as below the ground (Tab. 8.2).

Table 8.1. Taxonomic composition of ants recorded at palm oil baits

Subfamily	Genera		Species	
	Species	Percentage	Species	Percentage
Aenictinae	1	3.2	2	2.4
Cerapachyinae	1	3.2	2	2.4
Dolichoderinae	2	6.3	4	4.7
Dorylinae	1	3.2	2	2.4
Formicinae	3	9.4	7	8.2
Myrmicinae	15	46.9	41	48.2
Ponerinae	9	28.1	21	31.8
Sum	32	100.0	85	100.0

Of the species recorded at baits, 53% were demonstrably feeding on the oil (Tab. 8.2). Oil feeding was not unequivocal for 22 species (26%) due to their rare occurrence and/or low abundance at baits. The remaining species (21%, Tab. 8.2) used the sieve buckets as nesting site (e.g. *Camponotus* sp. 1, *Cerapachys* sp. 1, *Leptogenys* spp., and *Strumigenys* sp. 1), as hunting site (e.g. *Anochetus* sp. 1 and *Odontomachus* spp.), or represented chance encounters (e.g. *Aenictus* spp. and *Tetramorium* spp.). Some species showed mixed strategies of bait utilization. For example, *Odontoponera transversa*, *O. denticulata*, and *Odontomachus* sp. 1 regularly visited baits and carried away soil pieces soaked with oil. However, when other ant species recruited in large numbers to the baits, the three ponerine species partially or completely switched to preying on co-occurring ants.

Species such as *Dorylus (Dichthadia) laevigatus*, *Pheidole* sp. 1, and *Pheidologeton affinis* visited baits over a wide range of plots and altitudes (Tab. 8.2). Other species, i.e. 21 of the 44 species recorded on Plot 14, were found only on one or two neighboring altitudinal transects (Tab. 8.2).

Table 8.2. Ant diversity recorded at sieve buckets baited with palm oil.

	Stratum ¹	Oilfeeding	Plots	Height ² [m]	Status ³
Aenictinae					
<i>Aenictus</i> sp. 3	E	no	14	7	new
<i>Aenictus</i> sp. 4	E	no	3, 14	5, 9, 11	new
Cerapachyinae					
<i>Cerapachys</i> sp. 1	HE	no	8	5	1, 2
<i>Cerapachys</i> sp. 2	H	yes	8, 14	5, 6, 8, 11	2
Dolichoderinae					
<i>Loweriella</i> sp. 1	HE	yes	3, 8, 14	5, 6	new
<i>Technomyrmex</i> sp. 1	E	yes	6	5	1, 2
<i>Technomyrmex</i> sp. 2	E	no	8	5	1
<i>Technomyrmex</i> sp. 4	E	yes	8	5	new
Dorylinae					
<i>Dorylus laevigatus</i>	H	yes	1, 3, 6, 8, 14	5, 6, 7, 8, 10, 12	1
<i>Dorylus</i> cf. <i>vishnui</i>	H	yes	1, 3, 8, 14	5, 6, 9	new
Formicinae					
<i>Camponotus</i> sp. 1	HE	no	8	5	2
<i>Paratrechina</i> sp. 1	HE	?	8	5	new
<i>Paratrechina</i> sp. 2	E	?	8	5	new
<i>Paratrechina</i> sp. 3	E	?	8	5	new
<i>Pseudolasius</i> sp. 1	H	?	14	6	new
<i>Pseudolasius</i> sp. 2	HE	?	8, 14	5, 8	new
<i>Pseudolasius</i> sp. 4	H	?	6	5	new
Myrmicinae					
<i>Crematogaster</i> sp. 1	E	yes	1, 8, 14	5, 6, 7	new
<i>Lophomyrmex bedoti</i>	HE	yes	1, 3, 6, 8, 14	5, 6, 8, 10	1, 2
<i>Monomorium</i> sp. 1	E	yes	14	6, 7	1, 2
<i>Monomorium</i> sp. 3	H	yes	6	5	new
<i>Myrmecina</i> sp. 1	E	yes	1, 3	5	1
<i>Myrmecaria carinata</i>	E	yes	8	5	1, 2
<i>Myrmecaria</i> sp. 2	E	?	14	11	new
<i>Oligomyrmex</i> sp. 1	E	?	14	6	1, 2
<i>Oligomyrmex</i> sp. 2	E	?	8, 14	5, 6	new
<i>Oligomyrmex</i> sp. 4	E	?	6	5	new
<i>Oligomyrmex</i> sp. 5	HE	?	14	10	new
<i>Oligomyrmex</i> sp. 6	HE	?	14	5	new
<i>Pheidole annexus</i>	E	yes	1, 3, 8	5	1, 2
<i>Pheidole aristotelis</i>	E	?	6	5	1, 2
<i>Pheidole cariniceps</i>	HE	yes	1, 3, 14	5, 6	1, 2
<i>Pheidole clypeocornis</i>	E	yes	6, 8, 14	5, 6, 9	1, 2
<i>Pheidole lucioccipitalis</i>	E	?	6, 14	5, 12	1, 2
<i>Pheidole plagiaria</i>	HE	yes	3, 14	5, 14	2
<i>Pheidole sabahna</i>	E	yes	1, 8	5	2
<i>Pheidole spinicornis</i>	E	yes	1, 3, 8, 14	5, 7	2
<i>Pheidole</i> sp. 1	HE	yes	1, 3, 6, 8, 14	5, 7, 9, 10	1, 2
<i>Pheidole</i> sp. 2	E	yes	8	5	new
<i>Pheidole</i> sp. 3	E	yes	8	5	new
<i>Pheidole</i> sp. 12	E	?	14	11	new
<i>Pheidole</i> sp. 17	HE	yes	6	5	1

Table 8.2 continued

	Stratum ¹	Oilfeeding	Plots	Height ² [m]	Status ³
<i>Pheidologeton affinis</i>	HE	yes	1, 3, 6, 8, 14	5 - 14	1, 2
<i>Pheidologeton pygmaeus</i>	E	yes	1, 3, 14	5, 6, 8	new
<i>Pheidologeton</i> sp. 1	HE	yes	1, 3, 8, 14	5, 6, 7, 8, 10	new
<i>Pheidologeton</i> sp. 4	HE	yes	8	5	new
<i>Recurvidris</i> sp. 1	E	yes	6	5	new
<i>Rhoptromyrmex wroughtonii</i>	E	yes	6, 8	5	2
<i>Solenopsis</i> sp. 1	HE	yes	1, 3	5	1, 2
<i>Strumigenys</i> sp. 1	HE	no	8	5	new
<i>Tetramorium neshena</i>	HE	no	1, 8	5	1, 2
<i>Tetramorium</i> sp. 1	E	?	3	5	1, 2
<i>Tetramorium</i> sp. 2	H	no	8	5	1, 2
<i>Tetramorium</i> sp. 5	E	?	14	6	new
<i>Tetramorium</i> sp. 6	H	?	6	5	new
<i>Vollenhovia</i> sp. 1	H	yes	1, 3, 8, 14	5, 9, 11	2
<i>Vollenhovia</i> sp. 2	H	?	14	11	new
<i>Vollenhovia</i> sp. 3	H	yes	14	7, 9	new
Ponerinae					
<i>Anochetus</i> sp. 1	E	no	8	5	new
<i>Diacamma intricatum</i>	E	no	1	5	1, 2
<i>Gnamptogenys</i> sp. 1	H	?	8	5	new
<i>Hypoponera</i> sp. 1	H	yes	1, 8	5	new
<i>Hypoponera</i> sp. 3	HE	?	14	11	1, 2
<i>Hypoponera</i> sp. 4	H	yes	14	14	new
<i>Hypoponera</i> sp. 7	H	yes	14	10	1
<i>Leptogenys mutabilis</i>	HE	no	1, 3, 8, 14	5, 6, 8	2
<i>Leptogenys</i> sp. 2	H	yes	1, 3, 6, 8, 14	5, 9	1, 2
<i>Leptogenys</i> sp. 3	E	no	3	5	new
<i>Leptogenys</i> sp. 4	E	no	6	5	new
<i>Myopone</i> sp. 1	H	no	8	5	new
<i>Odontomachus rixosus</i>	E	no	1	5	1, 2
<i>Odontomachus</i> sp. 1	E	yes	3	5	1
<i>Odontomachus</i> sp. 3	E	no	14	10	new
<i>Odontoponera denticulata</i>	HE	yes	8	5	2
<i>Odontoponera transversa</i>	HE	yes	1, 3, 6, 8, 14	5, 6	1, 2
<i>Pachycondyla sharpi</i>	H	yes	1, 3, 8, 14	5, 8	2
<i>Pachycondyla tridentata</i>	E	no	3	5	1, 2
<i>Pachycondyla</i> sp. 2	H	yes	1, 3, 6, 8, 14	5, 6, 7	1, 2
<i>Pachycondyla</i> sp. 3	HE	yes	3, 6	5	1
<i>Pachycondyla</i> sp. 4	H	yes	1, 3, 14	5, 6	new
<i>Pachycondyla</i> sp. 5	E	no	6	5	1, 2
<i>Pachycondyla</i> sp. 6	H	yes	3, 6, 8, 14	5, 13	new
<i>Pachycondyla</i> sp. 8	H	?	14	11	new
<i>Pachycondyla</i> sp. 9	HE	yes	3, 14	5, 10, 11, 14	1, 2
<i>Pachycondyla</i> sp. 11	HE	yes	14	9, 10, 13, 14	1

¹Stratum of bait access: H = hypogaecic, E = epigaecic, HE = hypogaecic and epigaecic

²Height of research plot: 5 = 500-580m, 6 = 680m, 7 = 790m, 8 = 880m, 9 = 960m, 10 = 1060m, 11 = 1160m, 12 = 1280m, 13 = 1400m, 14 = 1470m

³Status: 1 = recorded by Brühl (1996), 2 = recorded by Brühl (2001)

Sieve buckets baited with tuna were visited by 12 ant species from nine genera and three subfamilies (Tab. 8.3). Hypogaecic foraging species were represented by *Dorylus laevigatus*, *Pachycondyla* spp. 4 and 5, and *Probolomyrmex* sp. 1. Except for *D. laevigatus* and *Pheidole*

sp. 1, which were found on the third day of bait control, all species could be collected during the first two days of the experiment. Beginning on the second day, species diversity decreased as *Pheidologeton affinis* dominated an increasing number of baits. Contrary to its long stays at oil-baited sieve buckets, *D. laevigatus* visited tuna baits for less than 24 hours. Tuna baits began to mould already on the second day of the experiment.

Sieve buckets baited with cookies were visited by 12 species from eight genera (Tab. 8.3). Hypogaecicly foraging species were represented by *Dorylus laevigatus* and *Pachycondyla* sp. 4. Most baits, i.e. five from six, were dominated by *Pheidologeton affinis* already on the first day, limiting the bait access of other species through its high numbers and aggressiveness. On the third day of bait control most cookie crumbs were consumed and apart from a few single individuals the baits were deserted. Of the species recorded at sieve buckets baited with tuna or cookies, five species were never recorded at palm oil baits and four species were new to the reference collection (Tab. 8.3).

Table 8.3. Ant species found at sieve buckets baited with tuna or cookie crumbs

	Stratum ¹	Bait	At oil baits	Status ¹
Dorylinae				
<i>Dorylus laevigatus</i>	H	Tuna, Cookie	yes	1
Myrmicinae				
<i>Lophomyrmex bedoti</i>	HE	Tuna, Cookie	yes	1, 2
<i>Mayriella</i> sp. 1	E	Cookie	no	1, 2
<i>Myrmecina</i> sp. 2	E	Tuna	no	new
<i>Oligomyrmex</i> sp. 1	E	Cookie	yes	1, 2
<i>Oligomyrmex</i> sp. 7	HE	Cookie	no	1, 2
<i>Pheidole clypeocornis</i>	E	Tuna, Cookie	yes	1, 2
<i>Pheidole poringensis</i>	E	Cookie	no	2
<i>Pheidole</i> sp. 1	HE	Tuna, Cookie	yes	1, 2
<i>Pheidologeton affinis</i>	HE	Tuna, Cookie	yes	1, 2
<i>Pheidologeton pygmaeus</i>	E	Tuna	yes	new
Ponerinae				
<i>Hypoponera</i> sp. 1	H	Tuna	yes	new
<i>Odontoponera denticulata</i>	HE	Tuna, Cookie	yes	2
<i>Odontoponera transversa</i>	HE	Tuna, Cookie	yes	1, 2
<i>Pachycondyla</i> sp. 2	H	Tuna, Cookie	yes	1, 2
<i>Probolomyrmex</i> sp. 1	H	Tuna	no	new

¹For abbreviations refer to the legend of Table 8.2.

Discussion

The ground ant abundance was recorded in Poring Hot Springs by Brühl (283 species, 1996), Malsch (250 species, 2002), and Mohamed et al. (95 species, 1996) (only ground-foraging species are included in the following calculations). These authors used different sampling methods: Mohamed et al. collected ant species using pitfall traps and hand collection at 500 m a.s.l.; Brühl and Malsch collected ants along the East Ridge altitudinal transect, Malsch by employing Winkler litter sifting, baiting, and nest collections, Brühl by using Winkler litter sifting and pitfall traps. Winkler sifting efficiently samples litter ant species and also collects cryptic species (Olson, 1991). Pitfall traps, although having a lower species yield, collect larger epigaeicly active species often undersampled in Winkler sifting (Olson, 1991). The above authors combined different sampling methods, generating a general overview of occurring ground ant species at Poring Hot Springs. Representing a rather selective sampling method, the number of species recorded at sieve buckets was with 85 species lower than the

diversity recorded by the above authors. Although the oil baits were accessible also for most epigaeically foraging species found in other studies, only few species (i.e. 53% of recorded species, Tab. 8.2) seemed to be able to feed on palm oil. Of common ground foraging ant genera (Brühl, 1996; Mohamed et al., 1996; Malsch, 2002), *Polyrhachis* and *Smithistruma* were never found at an oil bait, while other genera (e.g. *Camponotus*, *Crematogaster*, *Myrmecina*, and *Strumigenys*) were apparently undersampled (Tab. 8.2). Although some ant species recruiting with single foragers to the oil could have been missed by the employed method, other authors found (peanut) oil to be of low attractiveness as well (Brinkman et al., 2001). For a few species, on the other hand, palm oil was highly attractive; e.g. *Dorylus laevigatus* recruited over several weeks and in large numbers to the baits (Berghoff et al., 2002a). These ants could be found also below oil palm seeds fallen to the ground (Berghoff et al., 2002a). Fruits, seeds, and elaiosomes of a variety of plant species (Strasburger et al., 1991; Jordano, 2000) as well as many arthropod larvae (e.g. Inaoka et al., 1999; Finke, 2002) are rich in lipids, representing natural sources of oil for ants. Oil-feeding has been reported also for other *Dorylus* species (Savage, 1849; Weissflog et al., 2000), and *D. orientalis* represents a serious crop pest of peanuts (e.g. Roonwal, 1972).

Genera represented by mainly hypogaecially foraging species, i.e. *Cerapachys*, *Dorylus*, *Hypoconera*, *Pachycondyla*, *Pseudolasius*, and *Vollenhovia*, represented 28 percent of all collected species in this study (Tab. 8.2), but only 17 percent in Brühl (1996), 15 percent in Malsch (2002), and 5 percent in Mohamed (1996). In addition to these differences in species richness, the abundance of some hypogaecic species seemed to be underestimated by other sampling methods as well. For example, *Dorylus laevigatus* was recorded only once in the studies of Brühl (at 800 m, 1996) and Malsch (at 580 – 620 m, 2002), and never by Mohamed (1996). The use of oil-baited sieve buckets, however, showed *D. laevigatus* to be very common and abundant in all study plots and to occur up to an altitude of 1280 m (Tab. 8.2). Likewise, two common hypogaecic species in this study, *Pachycondyla* sp. 2 and *Hypoconera* sp. 1, were only once or twice recorded by Brühl (1996) and Malsch (2002), respectively.

Since our results indicated oil to be a substance attractive not to all ant species, we tested sieve buckets baited with other generally accepted baiting substances in a preliminary study. Despite the low bait number and short time of exposure, four predominately hypogaecially foraging species could be collected (Tab. 8.3). Of these, *Probolomyrmex* was never recorded at oil baits. In Poring, *Probolomyrmex* was collected only once by Malsch (2002) and never by Brühl (1996) or Mohamed (1996). Species of this genus are believed to be rare and to occur in small numbers (Taylor, 1965). However, *Probolomyrmex* sp. 1 recruited after 24 hours with more than 100 ants to a tuna bait, indicating that at least this species might be underestimated in its frequency of occurrence and abundance due to its hypogaecic lifestyle. The other three hypogaecic species, i.e. *D. laevigatus*, *Hypoconera* sp. 1, and *Pachycondyla* sp. 2, were also rare or absent in Winkler litter sifting and pitfall traps (see above).

Sieve buckets proved to be effective in sampling hypogaecic ant species, many of which had previously not been collected, despite extensive sampling (Tab. 8.2). Our results indicate that tuna in oil should be an attractive and suitable baiting substance (see also Brinkman et al., 2001). Since tuna and cookies were a) quickly depleted or partially began to mold already on the second day of exposure and b) most species were collected during the first two days of bait control, we suggest an application time of 24 hours. In this way, sieve buckets represent a quick and easy method to sample hypogaecic ant species. We suggest the combination of Winkler litter sifting, pitfall traps, and sieve buckets for future studies to attain an inclusive view of ground ant diversities. How much still remains to be discovered in the soil is indicated by the recent unearthing of a new hypogaecic ant subfamily (Brandao et al., 2002).

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Chapter 9

Myrmecophilous Staphylinidae (Coleoptera) associated with *Dorylus (Dichthadia) laevigatus* (Hymenoptera:Formicidae) in Malaysia with studies of their behavior

Summary

Three new genera are described here; *Berghoffia* (type species, *B. spectabilis* new sp.); *Pseudolydorus* (type species, *Pseudolydorus linsenmaieri* new sp.); and *Pygoplanus* (type species *P. subterraneus* new sp.) *Berghoffia* represents the first record of the tribe Dorylogstrini outside of Africa. The three new species above are all associated with *Dorylus (Dichthadia) laevigatus* in Perak, Malaysia as are other new species here listed. These are *Doryloxenus coecus* new sp., *Zyras (Rhynchodonia) praedabunda* new sp. and *Trachydonia dichthadiaphila* new sp. *Micropolemon subahensis* new sp. was collected from palm oil baits in Poring Hot Springs, Sabah associated with the same antspecies. Additionally both *Doryloxenus groveri* and *Micropolemon malayensis* were collected associated with the same host. These species had been previously described from specimens associated with termites, most likely left behind after raids of the ants had subsided. A revised phylogeny of the Pygostenini is presented which incorporates the 2 new pygostenine genera. The behavior of most of the species is described. The range of behavior is from predation [*Zyras (Rhynchodonia)*, and *Trachydonia*] to close association (all of the Pygostenini). Within the Pygostenini, the limuloid genera (*Doryloxenus*, *Pseudolydorus*, & *Pygosplanus*) seem to be more closely integrated into the ant colony than the more elongate species (*Micropolemon*). The progenitors of all the Pygostenini is in Africa where the more primitive genera are found with the more epigeal species of doryline ants. The subgenus *Zyras (Rhynchodonia)* is presently known only from the Indomalayan zoogeographic region, but since the majority of the known species of *Zyras* (*s. lat.*) are from Africa, it is likely that the ancestral link will ultimately be with some of the larger bodied African *Zyras*. *Trachydonia* has far more species in Africa than in the Orient so the few species in Malaysia and Indonesia may be the result of invasion after the move of the Indian subcontinent onto the rest of Asia.

Introduction

The purpose of this paper is to report on the myrmecophiles captured by Stefanie Berghoff in Malaysia. Beetles were collected around palm oil baits (see Weissflog et al., 2000) to which were attracted *Dorylus (Dichthadia) laevigatus* (Smith). Beetles were also collected from an excavated nest of this army ant using a technique devised by Berghoff (2002b). The taxonomy was done by Kistner. The capture of the specimens and the description of their behavior and interactions of the ants was done by Berghoff.

Materials and methods

The hypogaeic movements of *D. laevigatus* were monitored within an oil palm plantation via buckets baited with palm oil (Berghoff et al., 2002a). Observations were made between February

and April 2001 near Sitiawan, Perak, West Malaysia (peninsular Malaysia). Combining bait observations with trail excavations, the nest could be located (Berghoff et al., 2002a). The nest was excavated with an excavator and the colony kept in a soil-filled container. The collected nest fraction contained approximately 120,000 workers and 80,000 brood. Beetles were observed during colony emigrations through transparent plastic tubes to new containers. After several days of observation, the remainder of the colony was killed and beetles were separated from the ants and brood. The beetles found are closely associated to *D. (D.) laevigatus*, living in or very close to the nest and following emigrations. Other observations were made of beetles attracted to oil baits with *D. (D.) laevigatus* at Poring Hot Springs, Sabah, East Malaysia (on the island of Borneo).

Specimens were studied in ethyl alcohol, dried and mounted on glue boards, or cleared in KOH, dissected, and mounted on slides in Hoyer's medium. Specimens (both whole mounts and dissected parts) were photographed either with a digital camera permanently built into a binocular or transmitted light microscope or photographed on film using a Nikon F camera and a light box. Measurements were made on the electronic microscopes. Morphological terminology follows that of Blackwelder (1936) except for the male genitalia which follows Sharp (1912).

Tribe Lomechusini

Subtribe Myrmedoniina

Zyras (Rhynchodonia) praedabunda Kistner New Species

Figs. 9.1-9.3

Most closely related to *Z. (R.) soror* Cameron and *Z. (R.) persimilis* Cameron through the general body shape and color but different from both of these in that the projections from the sides of abdominal III tergites are as long as segment IV whereas the projections come from tergite IV and are slightly shorter than segment V in *Z. soror* and much shorter in *Z. persimilis*. Still other species have projections from both segments III & IV. Both *soror* and *persimilis* have impressed midlines on their pronotums while *praedabunda* does not. The sculpture of abdominal segment VII is also different.

Overall appearance of the male and the female as in Figs. 9.1A & B. Color dark reddish brown throughout with the head slightly darker than the rest of the body. Dorsal surface of the entire body smooth and shiny with very few setae scattered irregularly over the surface. There are also very few fine punctures. Antennae slightly flattened. Pronotum without an impressed midline. Pronotum with 1 macrochaeta from each anterolateral corner. Abdomen with only the smallest and thinnest of setae scattered over the tergites and sternites - virtually invisible. Abdominal tergite III of males with long posteriorly directed projections from each lateral border which are as long as segment IV. These projections are lacking in females. Tergite IV without lateral projections in both males and females. Abdominal tergite VII of male (Fig. 9.2B) with a posteriorly directed point near the posterior border and scalloped teeth on the posterior border. Abdominal tergite VII of female (Fig. 9.2A) without such a point and without the scalloped posterior border. All abdominal tergites with 4 macrochaetae; sternites with 6 macrochaetae. Note the well developed defense gland canalicules on each segment VII which terminate near the anterior border around the defense glandport. While both the male and the female have posteriorly directed teeth on tergite VIII (Figs. 9.2E & C), these are more numerous and better developed in the female than in the male. Each has 6 macrochaetae, The female has more definite coruscations on the posterior half of tergite VIII (Fig. 9.2C). Sternite VIII (Figs. 9.2D & F) are nearly identical in males and females and are without teeth but with 6 macrochaetae. Tergites II-

VI without macrochaetae. Abdominal segment IX of male and female shaped as in Figs. 9.3A-B; male with longer apodemes. Median lobe of the male genitalia shaped as in Fig. 9.3C. Lateral lobe shaped as in Fig. 9.3D. Spermatheca shaped as in Fig. 9.3E.

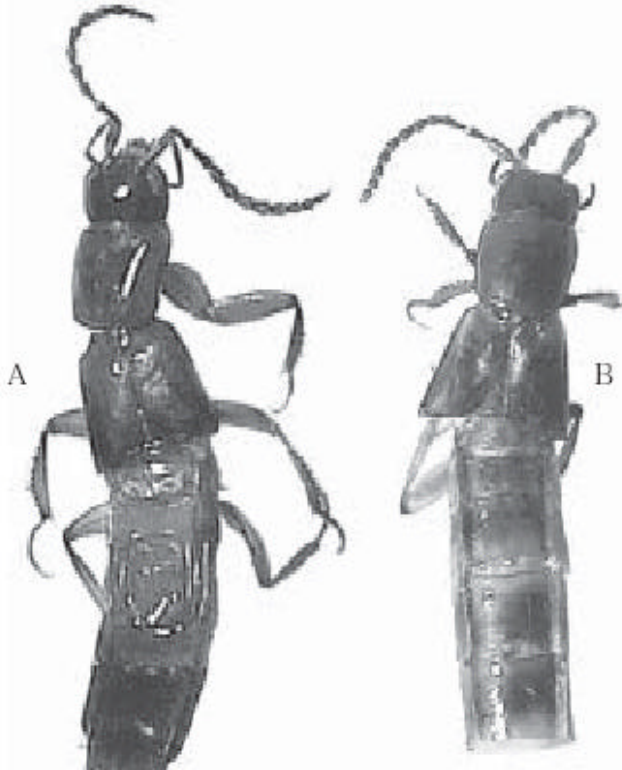


Figure 9.1. *Zyras (Rhynchodonia) praedabunda*. A: Dorsolateral view of male, B: Dorsal view of female

Measurements (in mm): (range only) Head length, 0.98-1.03; head width, 1.22-1.34; pronotum length, 1.43-1.66; pronotum width, 1.41-1.57; elytra length, 1.16-1.54. Number measured, 2. The female has the shortest measurements in the above list.

Holotype: Male, No. 20857, East Malaysia, Sabah, Poring Hot Springs, June 2000, Coll. Stefanie Berghoff, from an oil bait with *D. (Dichthadia) laevigatus* No. 1. In the collection of D.H. Kistner to be eventually deposited in the Field Museum of Natural History, Chicago.

Paratype: Female, No. 20672, same data as the holotype, (D.K.)

Notes: Both of the above specimens are partly on slides. The species name refers to the habits of the species as a predator.

Biology: This beetle was observed mainly at night on the soil surrounding baits heavily occupied by *D. laevigatus*. Here, several *Z. praedabunda* were distributed evenly around baits. The beetles darted back and forth, approaching *D. laevigatus* trails and trying to grasp ants from behind. Succeeding in catching an ant, *Z. praedabunda* dragged the ant between its legs to a hiding place in the litter. If not disturbed, the beetle reappeared after 5-15 minutes to continue hunting.

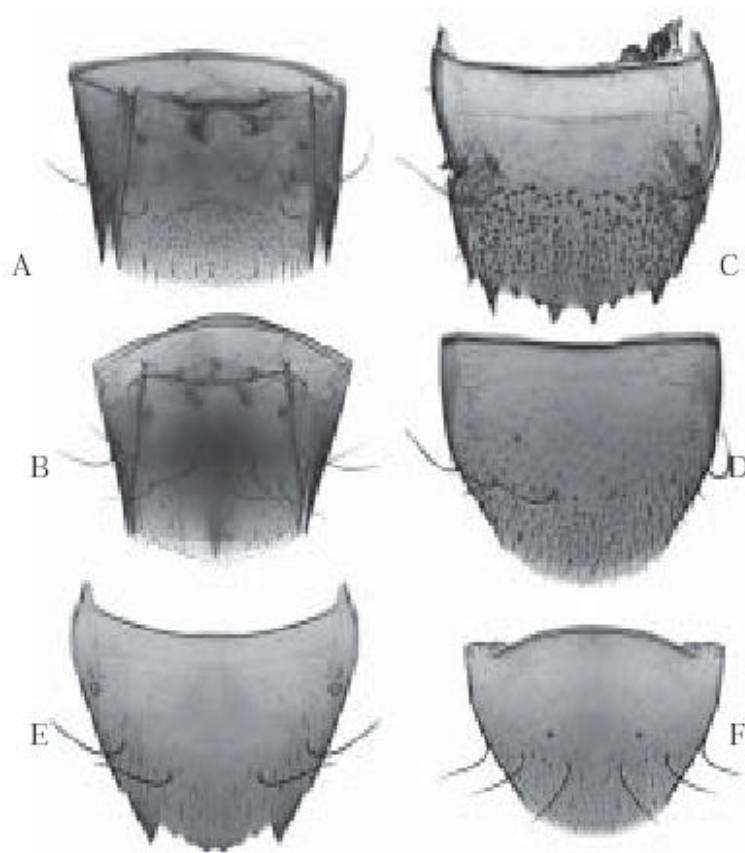


Figure 9.2. *Zyras (Rhynchodonia) praedabunda*.

A: Female abdominal segment VII,

B: Male abdominal segment VII,

C: Female abdominal tergite VIII,

D: Female abdominal sternite VIII,

E: Male abdominal tergite VIII,

F: Male abdominal sternite VIII

To further analyze the hunting behavior, 6 *Z. praedabunda* were kept in the laboratory. Beetles were confronted with *D. laevigatus* workers of different sizes in a Petri dish. Behaviors were observed with a stereo binocular microscope. Immediately after the first contact, *Z. praedabunda* started to attack an ant. This was done by darting back and forth and quickly moving its antennae over the ant's body. When *Z. praedabunda* had assumed a position behind the ant, it stood over the ant and grabbed it behind its head. The beetle moved its own head in a cutting movement and opened the ant's alitrunk between the pronotum and propleuron. The ants offered no visible resistance. Small *D. laevigatus* were quickly killed and left after a few minutes in 1 piece (n = 9), while medium ants were partially dismembered in 9 of 11 cases. It took *Z. praedabunda* considerably longer to kill large *D. laevigatus* which matched it in size (n = 7). Such ants were attacked several times, which often left them injured but not motionless. Between attacks, *Z. praedabunda* repeatedly touched the injured ant with the tip of its abdomen. Finally, *Z. praedabunda* opened the ant's body at the alitrunk or gaster, imbibing the liquids.

When additional *D. laevigatus* were in the Petri dish and came in contact with *Z. praedabunda* while it fed on an ant, the beetle immediately erected its abdomen. This effectively repelled the approaching ants.

In a similar experiment, *Z. praedabunda* was confronted with *Pheidologeton affinis* workers. Both the ants and beetles avoided each other and all were alive when the experiment ended after 2 hours.

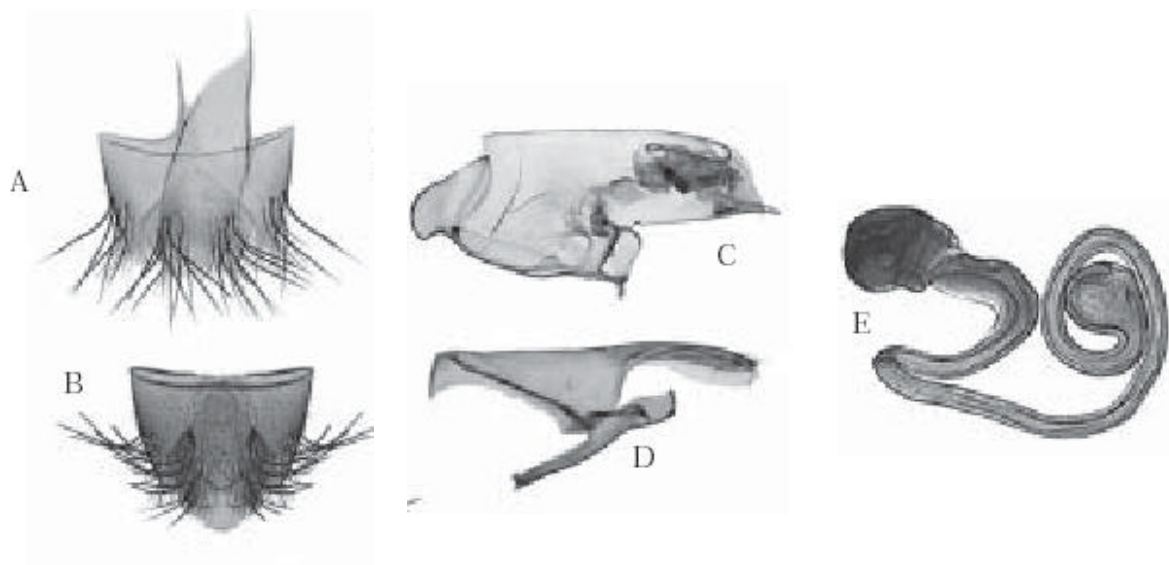


Figure 9.3. *Zyras (Rhynchodonia) praedabunda*. A: Male abdominal segment IX, B: Female abdominal segment IX, C: Median lobe of male genitalia, D: Lateral lobe of the male genitalia, E: Spermatheca

Genus Trachydonia Bernhauer

Most species of *Trachydonia* have been captured at light or by various other sampling techniques which concentrate insects indiscriminately. The virtue of all these techniques is that the presence of a species in a given area can be recorded. The downside is that nothing is known of the biology or ecology of the resulting recorded insects. Among the unknown biologies is that of the generitype of *Trachydonia*, *T. oxyteloides* Bernhauer. So far as we can tell, the first species of the genus recorded with ants was *T. anommatis* Last (1977) (Fig. 9.4A) who described the species from specimens collected by P.H. Kohl in the Congo with *Dorylus (Anomma) wilverthi* Emery (also known from Eala). We have collected similar species of the same genus in Angola, Ivory Coast, and Zambia with doryline ants but this will be explicated in a future paper. The second species recorded with ants (Fig. 9.4D) was *T. aenictophila* Kistner (Kistner et al., 1997) from Malaysia, Negeri Sembilan, with *Aenictus* sp. There are no further records with ants even though by our count 100 species have been described and there are probably more. Our purpose here is to record another species with ants. There are far fewer species described from the Orient so that determinations are much easier to do than similar determinations for African species.

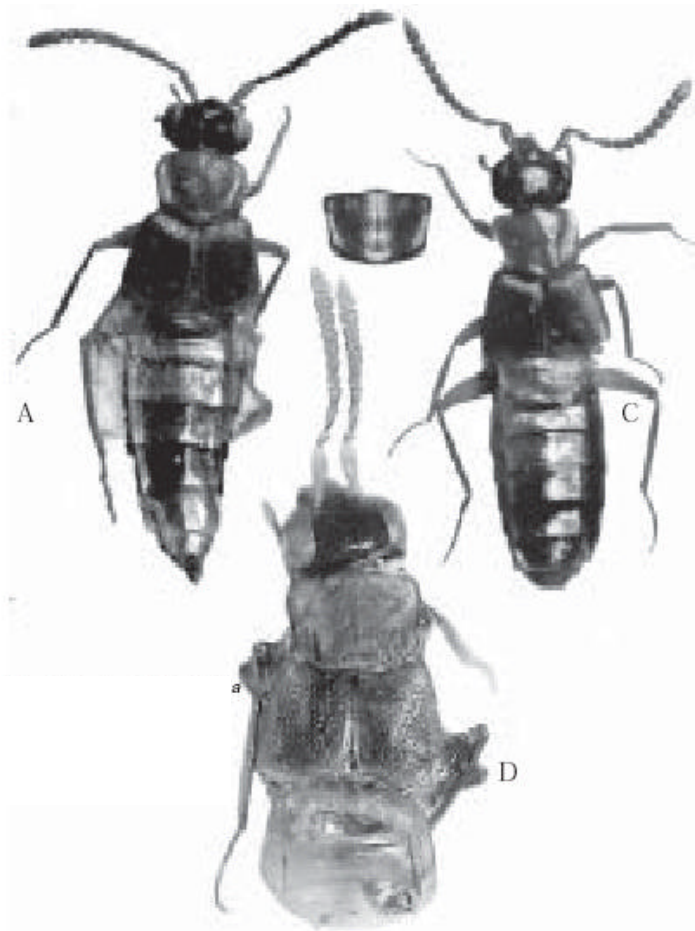


Figure 9.4.

A: *Trachydonia anommatis*,
 B,C: *T. rufoflavus* Cameron, the
 pronotum (B) is that of a female (the
 type) while the whole specimen is a
 male from Java,
 D: *T. aenictophila*

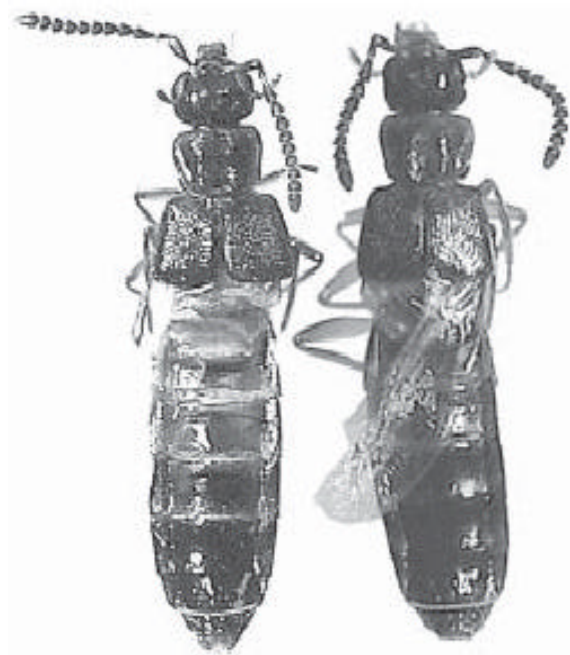


Figure 9.5. *Trachydonia dichthadiaphila*.

A: Male,
 B: Female. Part of the different appearances of
 the pronotum is caused by slightly different
 angles under the microscope.

Trachydonia dichthadiaphila Kistner New Species

Figs. 9.5-9.8

Most closely related to *T. aenictophila* and to *T. rufoflavus* Cameron (Fig. 9.4B,C) through the shapes of the head, pronotum, and elytra but distinguished there from by the somewhat different proportions of the antennal segments, a somewhat longer mesosternum and the shape of the spermatheca. Abdominal segment IX has a vestiture of setae which is less dense than in *T. aenictophila*. Males of *T. aenictophila* are unknown but when they are described, it is expected that the male genitalia will show differences.

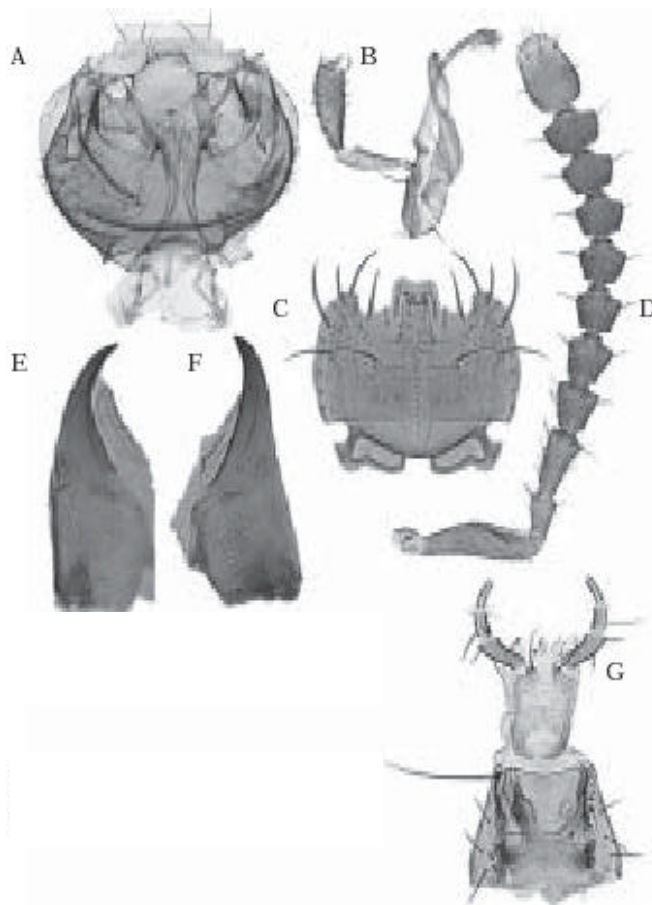


Figure 9.6. *Trachydonia dichthadiaphila*.

A. Head capsule, ventral,
 B: Maxilla,
 C: Labrum;
 D: Antenna,
 E,F: Left and right mandibles
 respectively,
 G: Mentum and labium

Overall appearance slender (Figs. 9.5A, B) similar to *T. aenictophila* (Fig. 9.4D) and *T. rufoflavus* Cameron (Figs. 9.4B,C). Color reddish brown throughout with the head and the apex of the abdomen somewhat darker. Sculpture of the dorsal surface of the head and abdomen smooth and shiny; of the pronotum and elytra roughly punctate. The ventral surface of the body and to a lesser extent the dorsal surface of the abdomen with a even vestiture of fine sparse yellow setae.

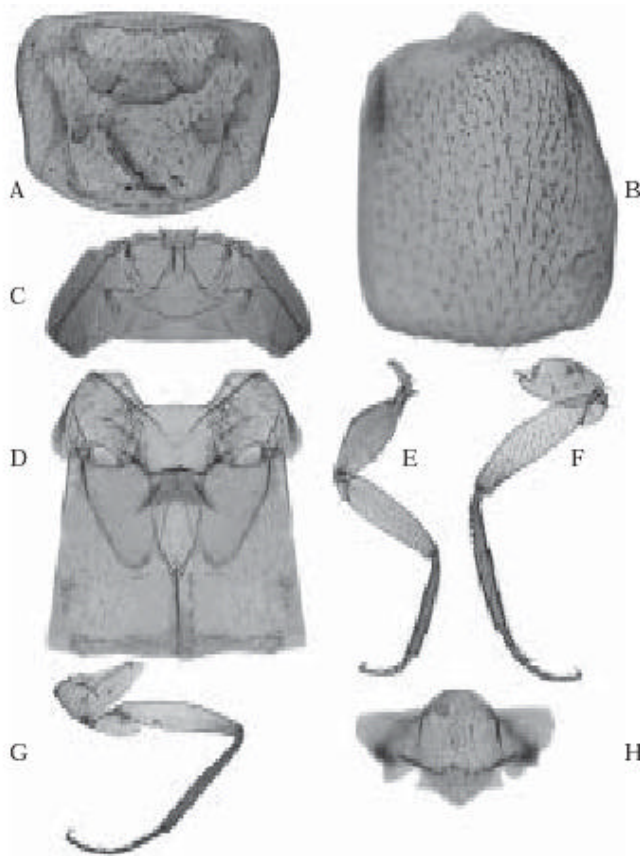


Figure 9.7. *Trachydonia dichthadiphila*.

A: Pronotum and prosternum,
 B: Elytron,
 C: Metanotum and abdominal segment I,
 D: Meso- and metasternum,
 E, F & G: Pro-, meso-, and metathoracic legs respectively,
 H: Scutellum (mesonotum)

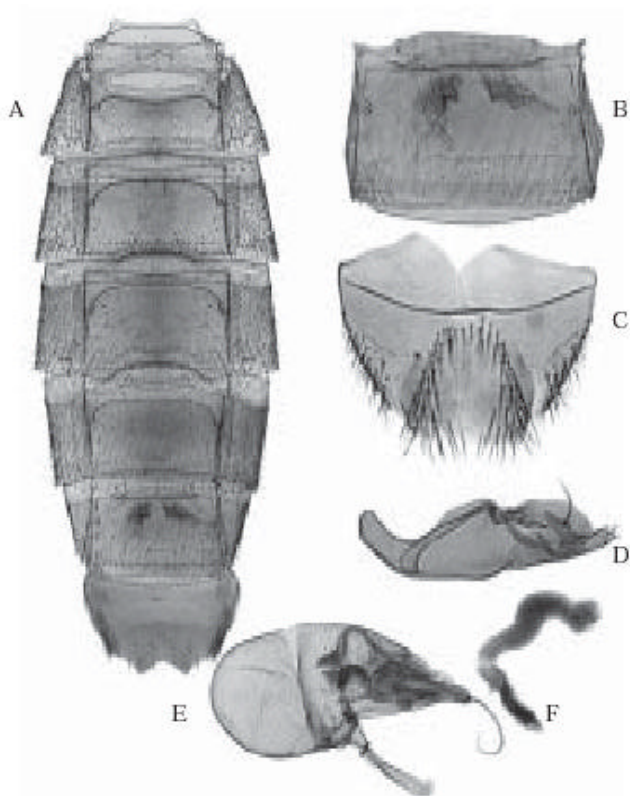


Figure 9.8. *Trachydonia dichthadiphila*.

A: Abdominal segments II-VIII, female,
 B: Enlargement of abdominal segment VII to show the 2 classes of canaliculae present to accommodate the defense glands,
 C: Abdominal segment IX of female,
 D, E: Lateral and median lobes of the male genitalia,
 F: Spermatheca

Macrochaetotaxy of abdominal tergites II-VIII: 0,4,4,4,6,6,4/8. All sternites with many very small, thin setae but no macrochaetae. Abdominal segment VIII of both males and females notched in the middle of the dorsal-posterior border (Fig. 9.8E). The notch is wider in males than in females. Abdominal segment IX of females shaped as in Fig. 9.8C; males with long apodemes at the anterior edges; chaetotaxy as shown in the Fig. 9.8C. Spermatheca shaped as in Fig. 9.8F, without an elaborate coil. Median and lateral lobes of the male genitalia shaped as in Figs. 9.8E, & D respectively.

Measurements: (in mm, given as range, mean, and standard deviation); Head length, 0.48-0.99, 0.68, 0.20; head width, 0.57-1.01, 0.75, 0.19; pronotum length, 0.57-0.91, 0.70, 0.14; pronotum width, 0.71-1.02, 0.86, 0.12; elytra length, 0.59-0.86, 0.76, 0.11. Number measured, 5.

Holotype: male, No. 20861, East Malaysia, Sabah, Poring Hot Springs, June 2000, Coll. Stefanie Berghoff, from an oil bait with *D. (Dichthadia) laevigatus* No. 1. In the collection of D.H. Kistner to be eventually deposited in the Field Museum of Natural History, Chicago.

Paratypes: 6, including 4 on slides, same data as the holotype, (D.K.)

Notes: The specific name is derived from the subgeneric name of the ant host and the phila comes from the Greek word meaning likes; thus likes *Dichthadia*. One other specimen of a different subgenus of *Zyras* was contained in the sample with the *Trachydonia* but it is represented by a single specimen and it will be studied later.

Biology: *Trachydonia dichthadiaphila* were observed at oil baits occupied by large numbers of *D. laevigatus*. Here, the beetle preyed on *D. laevigatus* by taking an ant behind the head and carrying it into the leaf litter. Beetles were observed in primary and secondary vegetation by day or night. At night, the *T. dichthadiaphila* were observed to fly to baits with large numbers of *D. laevigatus*.

Relationships among the Myrmedoniina

A phylogeny of the Myrmedoniina has never been attempted primarily because of the vast number of genera and the genus *Zyras* with its enormous number of subgenera some of which were also described as genera by various authors. What is needed is a revision of the genera and subgenera of the subtribe and then a phylogenetic study could be attempted. Of the 2 species considered here, the following comments are probably appropriate.

Zyras (Rhychodonia) is only represented in the Oriental zoogeographic region. While our catalogs are probably incomplete, we show 19 species in the Indian subcontinent, 2 (now 3) in Malaysia, 1 in Formosa, 4 in Indonesia, and 1 in China. From the earliest descriptions, they have been associated with predation, mostly of termites, while our record is most likely the first showing predation on ants. There are many subgenera in Africa with large bodies and with protrusions from various segments of the body which might serve as ancestral species. These abdominal protrusions are the source of probably many synonyms as Tottenham (1955) showed that within a given species there is considerable variation in the male secondary sexual characters. Because the majority of the species of *Zyras* are found in Africa, it is likely that *Rhychodonia* will ultimately be shown to have an African progenitor.

Trachydonia is a genus of over 100 species, most of them found in Africa so it is likely that the few *Trachydonia* in the Oriental faunal region have their origin in Africa.

In general, although the origins are not as clear as in the following tribes, there is a strong possibility that the Myrmedonnina dealt within this paper had their origins in the Ethiopian faunal region.

Tribe Dorylogastrini Wasmann

Tribe Dorylogastrini Wasmann 1916: 103, Type genus, *Dorylogaster* Wasmann; Seevers 1965: 187, considered the tribe part of the *Dorylomimus* group of the tribe Dorylomimini; Newton & Thayer 1992: 53, considered the tribe a synonym of Mimanommatini; Kistner 1993: 296, revised the status of the tribe and provided a new description.

The tribe as constituted by Kistner (loc. cit.) consisted of the single African genus *Dorylogaster* with its 12 species. The defining characteristics were: 2 coeloconic sensilla on the terminal segment of the antennae; tarsi constituted of 1 segment; absence of tarsal claws; distinctive spatulate setae on the tarsi; asymmetrical mandibles; near lyoval labrums; petiolate abdomen made up of abdominal segment II and the anterior part of abdominal segment III; and halves of abdominal segment I are separated by an extension of the metanotum.

The males of all the species of the genus *Dorylogaster* have a median sternal gland reservoir under abdominal sternite VII which is lacking in females. The genus described below agrees in all the characters above except for the male sternal gland reservoir which it lacks. The terminal segment does contain coeloconic sensilla but they are smaller and more difficult to see. The new genus represents the first Dorylogastrini known from the Orient and one of the most unique myrmecophiles we have ever seen and certainly the most highly modified of the Dorylogastrini.

KEY TO GENERA

Eyes present; fully functional wings present; abdomen not physogastric, sclerotized *Dorylogaster*
 Eyes absent; wings not present; abdomen physogastric, weakly sclerotized *Berghoffia*

For a key to the species of *Dorylogaster*, see Kistner 1993, p. 301.

Genus Berghoffia Kistner New Genus

Overall appearance as in Fig. 9.9A (see also front cover, upper right). Head shaped as in Fig. 9.9D; gula extremely short, attached to a large submentum, remainder of the so-called gular sutures formed by the joined edges of the postgenae. Eyes absent. Antennae shaped as in Fig. 9.9B, with 2 coeloconic sensilla on the terminal segment, which are small and difficult to see. Labrum with the anterior border rounded, shaped as in Fig. 9.9C. Mandibles asymmetrical, shaped as in Figs. 9.9E & F, both with many small median teeth. Maxillae shaped as in Fig. 9.9G, palpi 4-segmented. Segment 1 very short, segments 2 and 3 about equal in length. Segment 4 about 3X as long as segment 1, tapering apically. Galea much shorter than the lacinia; neither with foleose terminal setae. Labium shaped as in Fig. 9.9H, palpi 3-segmented. Segment 2 shorter than segment 1; segment 3 about equal in length to 1. Submentum distinct from the mentum.

Pronotum shaped as in Figs. 9.9A & 9.11F. Prosternum shaped as and just visible in Fig. 9.9F, mesothoracic peritremes loose, not fused to the prosternum. Large coxal cavities not closed behind, except loosely by the mesothoracic peritremes. Mesonotum (scutellum) narrow, shaped as in *Dorylogaster*. Metanotum shaped as in *Dorylogaster* with an extension that separates the 2 halves of abdominal tergite I. Meso- and metasternum extremely shortened, shaped as in *Dorylogaster*, mesocoxal cavities widely separated by an acarinate mesothoracic process; metathoracic coxal cavities also widely separated. Elytra shaped as in Fig. 9.11B. Pro-, meso-, and metathoracic legs shaped as in Figs. 9.10B-D, all with a bulbous and toothed part on the proximal end of the tibiae. Tarsal formula 1-1-1, whether this condition results from a fusion of the evolutionarily preexisting segments or to their loss cannot be determined. Pretarsus absent. Tarsi with many foleose setae different from the form of similar setae found in other tribes of the

Aleocharinae (see Kistner and Jacobson, 1977 for a complete SEM study of these kinds of setae). Wings absent.

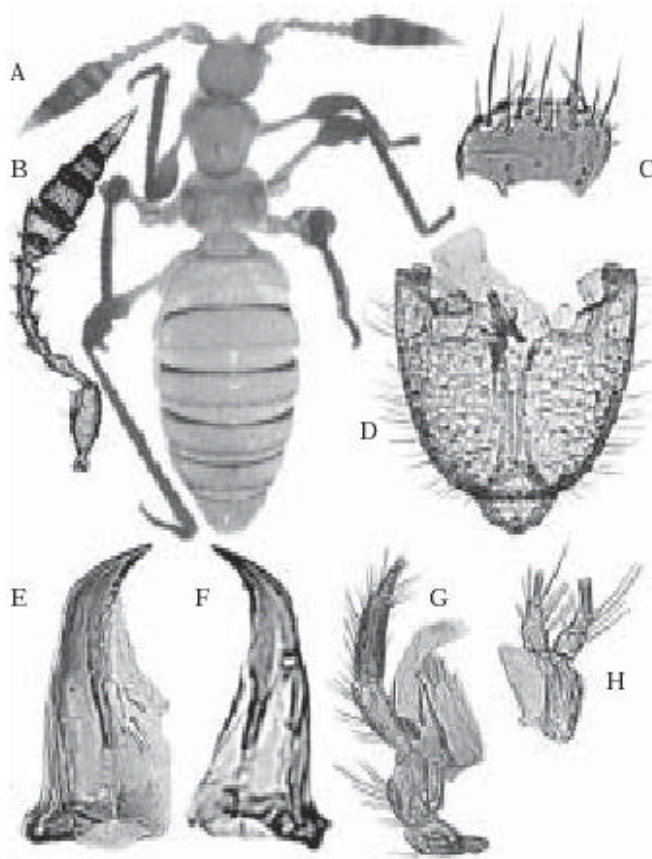


Figure 9.9. *Berghoffia spectabilis*.

A: Dorsal appearance of the entire beetle,
 B: Antenna,
 C: Labrum,
 D: Head capsule,
 E: Right mandible,
 F: Left mandible,
 G: Maxilla,
 H: Labium

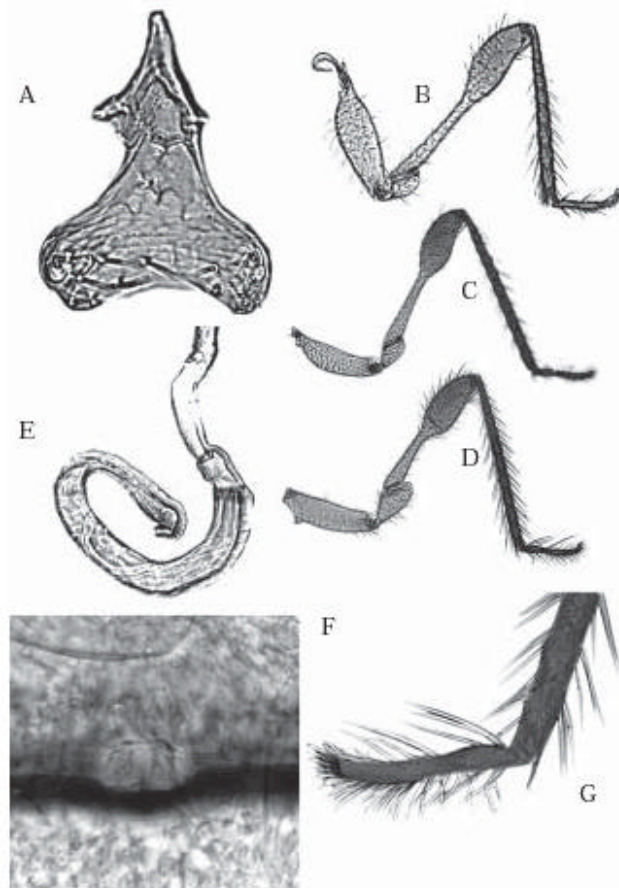
Abdomen with the tergites and sternites strongly convex, shaped as in Fig. 9.11A. Abdomen strongly constricted at the base with the constriction involving abdominal segment II and the apical half of abdominal segment III (Fig. 9.10A). All segments with no paratergites, the lines of fusion are not visible on cleared specimens so no interpretation is made here as to whether the parts are fused to the tergites and/or the sternites. Segment VII with the median opening of the defense gland on its anterior border; the actual reservoir was not found on dissected specimens. This reservoir is partially sclerotized and it has a somewhat different shape in males (Fig. 9.11E) than in females (Fig. 9.10F) and strongly resembles similar reservoirs in *Dorylogaster*. Sternite VII without an additional gland reservoir in males. Segment IX shaped as in Fig. 9.11C; with longer apodemes in males than in females. Malegenitalia bulbous; presumed variable by species. Spermatheca sclerotized, shape presumed variable by species.

Type species: *Berghoffia spectabilis* Kistner, described below.

Berghoffia spectabilis Kistner New Species

Figs. 9.9-9.11, front cover, upper right

The genus is presently monobasic so characters isolated as species specific are based on experience with other species found in other genera, particularly *Dorylogaster*.

**Figure 9.10.** *Berghoffia spectabilis*.

A: Abdominal tergite III,

B: Prothoracic leg,

C: Mesothoracic leg,

D: Metathoracic leg,

E: Spermatheca,

F: Defense gland on tergite VII (female),

G: Structure of typical tarsus

Color yellowish brown throughout; anterior borders of the abdominal tergites and sternites dark brown. Ground sculpture of the entire body shagreened. Dorsal surface of the head, pronotum, and elytra additionally punctate with fine yellow setae emerging from the punctures. Pronotum with a midline longitudinal impression extending about 0.75 mm along the median posterior half of the pronotum. Antennae long, reaching somewhat past the posterior border of the elytra. Segments 8-11 of the antennae (Fig. 9.9B) forming a large spindle shaped club, the maximum width of which is 3X the width of segment 5. All femora enlarged at the apex and bearing hooks, a little more than 3.5X as wide as at the narrowest part of segment 6. Tibia not noticeably enlarged at the apex. Spermatheca shaped as in Fig. 9.10E. Median and lateral lobes of the male genitalia shaped as in Figs. 9.11G & D.

Measurements (in mm): Head length, 0.28-0.31; head width, 0.34-0.39; pronotum length, 0.34-0.36; pronotum width, 0.35-0.40; elytra length, 0.22-0.25. Number measured, 4.

Holotype: male, No. 20853, Malaysia, Perak, near Sitiawan, March 2001, Coll. Stefanie Berghoff from a nest of *Dorylus (Dichthadia) laevigatus* Smith. In the collection of D.H. Kistner to be deposited eventually in the Field Museum of Natural History, Chicago.

Paratypes: 3 (2 on slides), same data as the holotype, (D.K.)

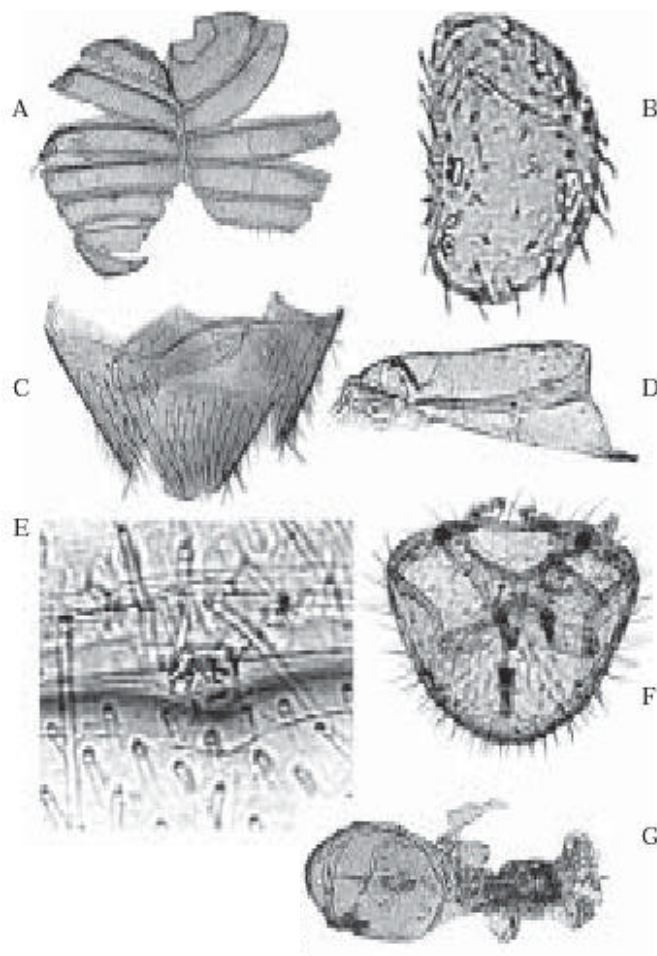


Figure 9.11. *Berghoffia spectabilis*.

A: Abdominal segments III-VIII,

B: Elytron,

C: Abdominal segment IX,

D: Lateral lobe of the male genitalia,

E: Defense gland on tergite VII (male),

F: Pronotum and prosternum,

G: Median lobe of the male genitalia

Notes: The genus is named for its collector while the species name is for its spectacular appearance.

Biology: After *D. laevigatus* had completed 2 emigrations in the laboratory, eight *B. spectabilis* were collected with the remaining colony fraction.

Relationships among the Dorylogastrini

The Dorylogastrini is an extremely specialized tribe which was formerly known only by its type genus, *Dorylogaster* Wasmann. There can be little doubt that *Berghoffia* is the most specialized of the 2 genera now included. All of the known *Dorylogaster* are found in Africa so it is highly likely that *Berghoffia*, the derived genus, had African origins. The relationship of the Dorylogastrini to other Staphylinidae is obscure.

Tribe Pygostenini Fauvel

A complete bibliography of the Pygostenini is given by Kistner and Jacobson (1975, p. 337). Some subsequent references are given by Kistner et al. (1997). The Pygostenini are primarily an African group associated with *Dorylus (Anomma)* sp. and other subgenera of *Dorylus* as well as *Aenictus* sp. and fungus growing termites. The following species are known from the Orient.

- Aenictoxenus chapmani* Seevers, 1953: 127, Philippines, with *Aenictus gracilis*; Kistner and Jacobson, 1975: 23; Jacobson and Kistner, 1975: 200.
- Aenictoxenus giganteus* Kistner (Kistner et al., 1997: 199, Figs. 57, 58e, & 61e) Malaysia with *Aenictus hottae*.
- Aenictoxenus malaysianus* Kistner (Kistner et al., 1997: 202, Figs. 59a,f,g, & 60a.) Malaysia with *Aenictus* aff. *gracilis*, probably new.
- Aenictoxenus rosciszewskii* Kistner (Kistner et al., 1997: 202, Figs. 58f, 60b, 61b,d,h,i, & j) Malaysia with *Aenictus laeviceps*.
- Aenictoxenus weissflogi* Kistner (Kistner et al., 1997: 205, Figs. 58b,d,g, 59b-e, 61a,f,g) Malaysia with *Aenictus* n.sp.
- Cephalakoxena rougemonti* Pace, 1998: 961, Figs. 197-208, Hong Kong, no host. This is most likely not a pygostenine but the single specimen known has not been examined. It is most probably a myrmecophile however.
- Delibius longicornis* Fauvel, 1899, Singapore, no host
- Deliodes duplex* Fauvel, 1899, Sumatra, no host
- Deliodes hongkongensis* (Pace) transfer from *Odontoxenus hongkongensis* Pace, 1998: 956, Figs. 195-196, Hong Kong, no host, new transfer
- Deliodes reelsi* (Pace) transfer from *Odontoxenus reelsi* Pace, 1999:682, Figs. 65-66, Hong Kong, no host, new transfer
- Deliodes rougemonti* (Pace) transfer from *Odontoxenus rougemonti* Pace, 1998: 956, Figs. 191-194, Hong Kong, no host, new transfer
- Doryloxenus groveri* Kistner and Jacobson, 1975, Malaysia with termites
- Doryloxenus hongkongensis* Pace, 1998: 956, Figs. 185-188, Hong Kong, no host.
- Doryloxenus rougemonti* Pace, 1998: 956, Figs. 189-190, Hong Kong, no host
- Mesomegaskela adesi* Pace, 1998: 953, Figs. 176-184, Hong Kong, no host. This species probably belongs to the genus *Mimocete* but the unique specimen that is the holotype has not been examined.
- Micropolemon malayensis* Kistner and Jacobson, 1975, Malaysia with termites.
- Odontoxenus* sp. many species are known from termites, mostly *Odontotermes*. All are from the Oriental Region.
- Typhloponemys khandalae* Kistner, 1958: 84 from India with *Odontotermes obesus*.
- Xenidus retractus* Rey, 1886: 254 from Sumatra, no host.
- No pygostenines associated with *Dorylus (Dichthadia)* sp. were previously known from anywhere except for 2 species which were collected adventitiously from other niches.

Genus Doryloxenus Wasmann

Doryloxenus groveri Kistner and Jacobson

Figs. 9.12-9.15

Doryloxenus groveri Kistner and Jacobson, 1975: 192, Malaysia:

Selangor, Sungai Buloh Forest Reserve, 11 July 1973; Ulu Gombak, 7 July 1973; Pahang, Taman Negara, 1 km NE of Kampsong Tehan, 21 June 1973.

The following augmented description is given because the number of specimens has been greatly increased and to provide a comparison to the blind species to be described later. In the original description, the closest relative was given as *D. hirsutus* Wasmann, an African species found with a variety of species of *Dorylus (Anomma)*. On further study, it is even closer to *Doryloxenus*

punicus Normand which is found with a more subterranean ant, *D. (Typhlopone) fulvus* Westwood.

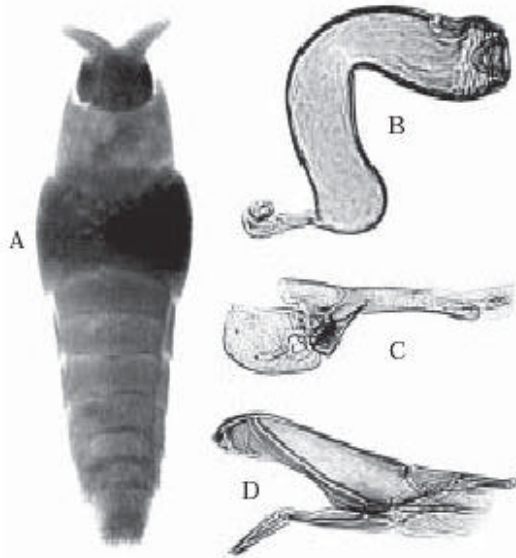


Figure 9.12. *Doryloxenus groveri*.

A: Dorsal appearance of the entire beetle,
 B: Spermatheca,
 C: Median lobe of the male genitalia,
 D: Lateral lobe of the male genitalia

Overall appearance as in Fig. 9.12A. Head shaped as in Fig. 9.13A; gula about half the length of the head, attached to a large and elongate mentum. Eyes present. Antennae shaped as in Fig. 9.13C, without coeloconic sensilla on the terminal segment. Labrum with the anterior border bisinuate, shaped as in Fig. 9.13G. Mandibles symmetrical, shaped as in Fig. 9.13B, both with very few small median teeth. Maxillae shaped as in Fig. 9.13I, palpi 4-segmented. Segment 1 very short, segment 2 about 2X the length of the first and 3 almost 3X the length of segment 2. Segment 4 about equal in length to segments 1 and 2 together, tapering apically. Galea much shorter than the lacinia; both with foleose terminal setae. Labium shaped as in Fig. 9.13D, palpi 3-segmented. Segment 2 shorter than segment 1; segment 3 about equal in length to 2. Submentum (Fig. 9.13A) distinct from the mentum. Mentum large and anteriorly, shaped as in Fig. 9.13D.

Pronotum vaulted shaped as in Figs. 9.12A & 9.13F. Prosternum shaped as in Fig. 9.13E, mesothoracic peritremes loose and weakly sclerotized, not fused to the prosternum. Large coxal cavities closed behind, except loosely by the mesothoracic peritremes. Mesonotum (scutellum) subtriangular, shaped as in Fig. 9.13H. Metanotum shaped as in Fig. 9.14F, without much noteworthy structure except that it is slightly shorter than similar structure in non-limuloid genera. Meso- and metasternum not shortened, shaped Fig. 9.14D, mesocoxal cavities narrowly separated by a carinate mesothoracic process; metathoracic coxal cavities close together and marginate (Fig. 9.14D). Elytra shaped as in Fig. 9.12A. Pro-, meso-, and metathoracic legs shaped as in Figs. 9.14B, 9.14A, & 9.14E, respectively, with the coxa of the prothoracic leg greatly enlarged as is characteristic of the limuloid genera. Tarsal formula 4-4-4, each segment with a single pair of membranous lobes. Pretarsus present but lacking in most specimens. Wings present and with the usual staphylinid venation and functional as field captures have indicated.

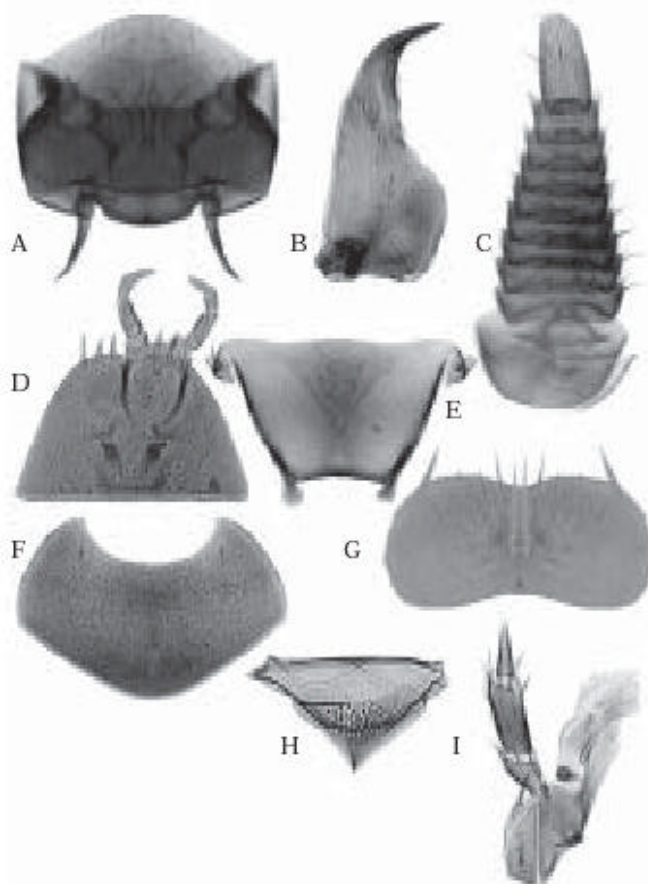


Figure 9.13. *Doryloxenus groveri*.

A: Head, ventral,
 B: Left mandible,
 C: Antenna,
 D: Labium and mentum,
 E: Prosternum,
 F: Pronotum, somewhat flattened in the slide preparation,
 G: Labrum,
 H: Scutellum,
 I: Maxilla

Abdomen with the tergites and sternites strongly convex, shaped as in Figs. 9.15A, E. Abdomen widest at the base and becoming narrower posteriorly. Segment II with a tergite only; segments II-VI each with a tergite, a sternite and 2 pairs of paratergites. Segment VII with a tergite, a sternite and 2 pairs of paratergites but the inner paratergites are much shorter than the outer ones. Tergite VII (Fig. 9.15B) with a very small opening to the tergal defense gland reservoir. Segment VIII (Fig. 9.15C) with a tergite and a sternite only. Segment IX as is typical for nearly all pygostenines, shaped as in Fig. 9.15E; with longer apodemes in males than in females. Median lobe of the male genitalia bulbous, shaped as in Fig. 9.12C. Lateral lobe of the male genitalia shaped as in Fig. 9.12D. Spermatheca sclerotized, shaped as in Fig. 9.12B.

Measurements (in mm): (Given by range and mean), Head length, 0.25-0.31, 0.27; head width, 0.36-0.48, 0.41; pronotum length, 0.47-0.57, 0.52; pronotum width, 0.64-0.76, 0.69; elytra length, 0.27-0.34, 0.31. Number measured, 6.

New material examined: 13, Malaysia, Perak, near Sitiawan, March 2001, Coll. Stefanie Berghoff from a nest of *Dorylus (Dichthadia) laevigatus* Smith, (D.K.); 1 male, East Malaysia, Sabah, Poring Hot Springs, 2 April 2002, Coll. S. Berghoff, (D.K.).

Notes: The original 6 specimens of this species were captured either flying near or actually in the nests of the following termites: *Macrotermes carbonarius* (Hagen), *Dicuspiditermes kistneri* Krishna, and *D. fissifex* Krishna. In the notes to the original description, the authors speculated that the termites were not the actual hosts but that a subterranean ant such as *Dorylus (Dorylus)* sp. might actually be found to be the host. It was a great catch for MS Berghoff to capture the

species with *Dorylus (Dichthadia) laevigatus*. These ants probably raid termite nests as such raids can be mounted in a completely subterranean environment. Some pygostenines probably get left behind as the raid ends. Since the specimen from Sabah was a male, it is not as certain an identification as if it were a female.

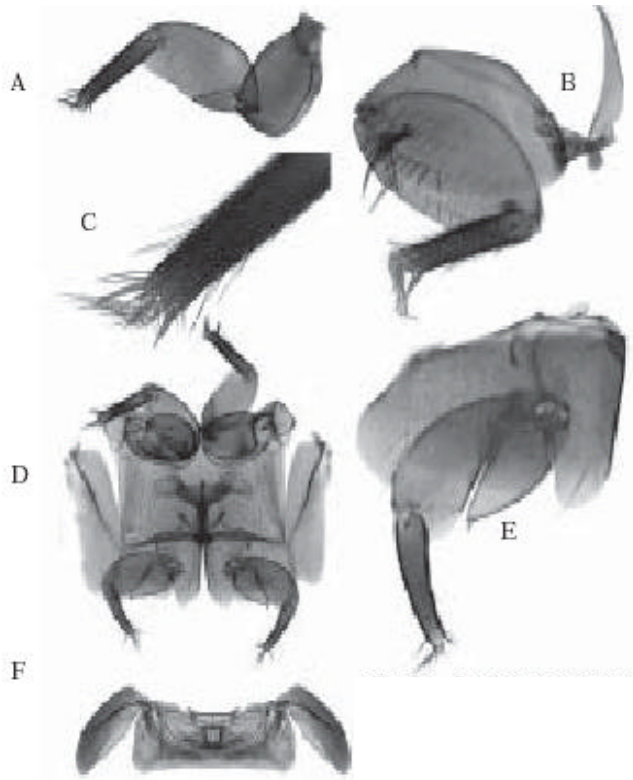


Figure 9.14. *Doryloxenus groveri*.

A: Mesothoracic leg,

B: Prothoracic leg,

C: Tip of prothoracic leg showing the structure of the tarsus,

D: Meso- and metasternum with attached legs,

E: Metathoracic leg,

F: Metanotum and abdominal segment I

Biology; *Doryloxenus groveri* was observed to run short distances in the ants' emigration columns before they jumped on the gasters of large workers. The abdomen of the beetles were raised while running or riding. While running, *D. groveri* stayed in the middle of the emigration columns with no indication of avoidance towards or from the ants. However, every opportunity was used to jump back onto an ant's gaster, independent of whether the ant was carrying brood or not. *Dorylus laevigatus* showed no visible reaction when they came in contact with the erect abdomen of the beetle.

Visible through the transparent wall of a nest box, one *D. groveri* was seen moving within a brood cluster centered in a *D. laevigatus* bivouac.

Another *D. groveri* (from Sabah) was collected from a *D. laevigatus* foraging column 30m away from the nest. The beetle was running freely in the collected worker sample but kept in constant contact with the ants, following them as they moved. Overall 34 *D. groveri* were collected from the nest and 1 from a foraging column.

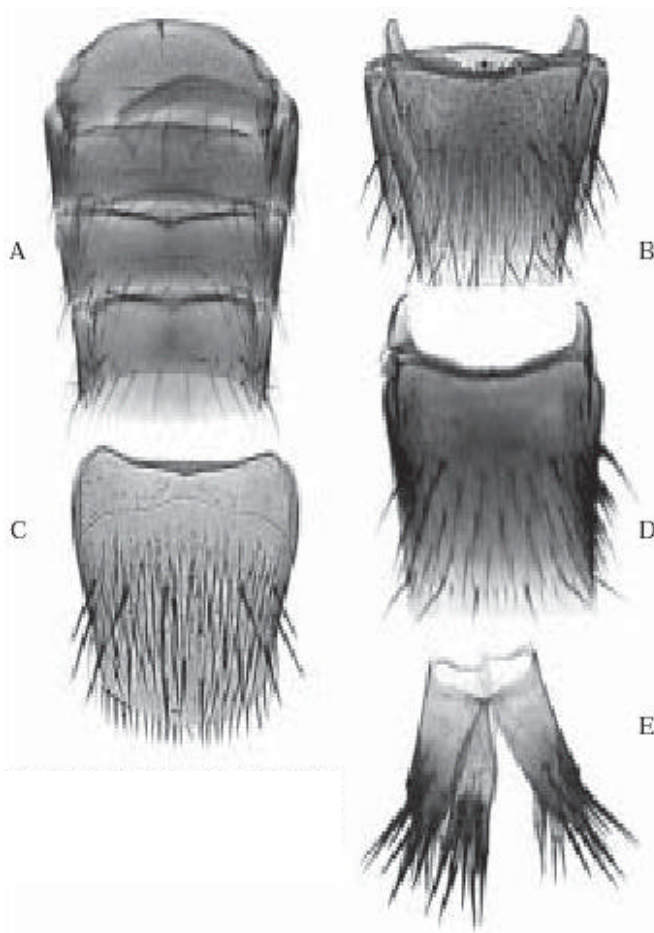


Figure 9.15. *Doryloxenus groveri*.

A: Abdominal segments II-V, the more numerous setae are found on the sternites,
 B: Abdominal segment VII,
 C: Abdominal sternite VIII,
 D: Abdominal tergite VIII,
 E: Abdominal segment IX

Doryloxenus coecus Kistner New Species

Figs. 9.16-9.18

Distinguished from *Doryloxenus groveri* by its somewhat smaller size, its slightly lighter color, and by the shapes of the male genitalia and spermatheca. It is most easily distinguished from *D. groveri* and all other *Doryloxenus* spp. by the unique characters that include eyelessness and winglessness.

Overall appearance as in *Doryloxenus groveri* (Fig. 9.12A) except that no eyes show on the lateral surface. Head shaped as in Fig. 9.16A; gula about half the length of the head, attached to a large and elongate mentum. Eyes absent. Antennae shaped as in Fig. 9.16C, without coeloconic sensilla on the terminal segment. Labrum with the anterior border bisinuate, shaped as in Fig. 9.16B. Mandibles symmetrical, shaped as in Figs. 9.16E, & F, both with very few small median teeth. Maxillae shaped as in Fig. 9.16G, palpi 4-segmented. Segment 1 very short, segment 2 about 2X the length of the first and 3 almost 3X the length of segment 2. Segment 4 about equal in length to segments 1 and 2 together, tapering apically. Galea much shorter than the lacinia; both with foliose terminal setae. Labium shaped as in Fig. 9.16D, palpi 3-segmented. Segment 2 much shorter than segment 1; segment 3 about equal in length to 2. Submentum (Fig. 9.16D) distinct from the mentum. Mentum large and narrowed anteriorly, shaped as in Fig. 9.16D.

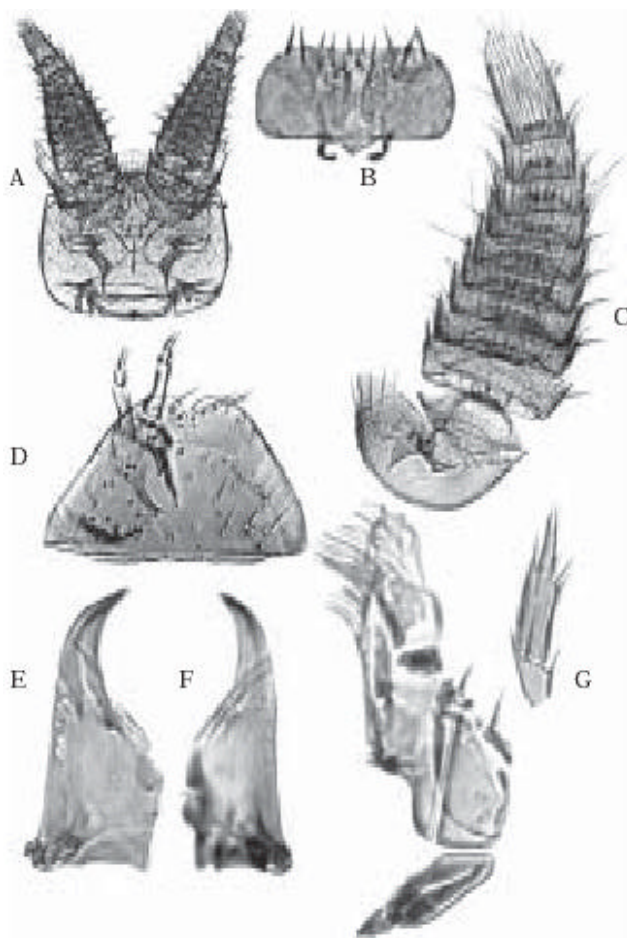


Figure 9.16. *Doryloxenus coecus*.

A: Head, ventral, note particularly the absence of eyes on the lateral anterior border,

B: Labrum,

C: Antenna,

D: Labium and mentum,

E & F: Right and left mandibles, note their symmetry and lack of significant medial teeth,

G: Maxilla, a part of the palp was lost in the dissection

Pronotum vaulted shaped as in Fig. 9.17D. Prosternum shaped as in Fig. 9.17F, mesothoracic peritremes loose and weakly sclerotized, not fused to the prosternum. Large coxal cavities loosely closed behind, by the mesothoracic peritremes. Mesonotum (scutellum) subtriangular, shaped as in *D. groveri* (Fig. 9.13H); it may also be vaguely seen in Fig. 9.17C. Metanotum shaped as in Fig. 9.17C, without much noteworthy structure except that it is much shorter than in *D. groveri* and similar structures in non-limuloid genera. Meso- and metasternum shortened, shaped Figs. 9.17A & I, mesocoxal cavities marginate and narrowly separated by a carinate mesothoracic process; metathoracic coxal cavities close together (Fig. 9.17A). Elytra short, shaped as in Fig. 9.17B. Pro-, meso-, and metathoracic legs shaped as in Figs. 9.17G, E, & H, with the coxa of the prothoracic leg greatly enlarged as is characteristic of the limuloid genera. The coxae of the metathoracic legs are also enlarged compared to non-limuloid genera. Tarsal formula 4-4-4, each segment with a single pair of membranous lobes. Pretarsus present but lacking in most specimens. Wings absent.

Abdomen with the tergites and sternites strongly convex, shaped as in Fig. 9.18A. Abdomen widest at the base and becoming narrower posteriorly. Segment II with a tergite only; segments II-VI each with a tergite, a sternite and 2 pairs of paratergites. Segment VII (Fig. 9.18E) with a tergite, a sternite and 2 pairs of paratergites but the inner paratergites are much shorter than the outer ones. Tergite VII with a very small opening to the tergal defense gland reservoir. Segment VIII (Figs. 9.18B, C) with a tergite and a sternite only. Segment IX as typical for nearly all pygostenines, shaped as in Fig. 9.18D; with longer apodemes in males than in females. Median

lobe of the male genitalia bulbous, shaped as in Fig. 9.18G. Lateral lobe of the male genitalia shaped as in Fig. 9.18H. Spermatheca sclerotized, shaped as in Fig. 9.18F.

Measurements (in mm): Given as range only, Head length, 0.20-0.26; head width, 0.30-0.31; pronotum length, 0.40-0.46; pronotum width, 0.39-0.48; elytra length, 0.13-0.16. Number measured, 4.

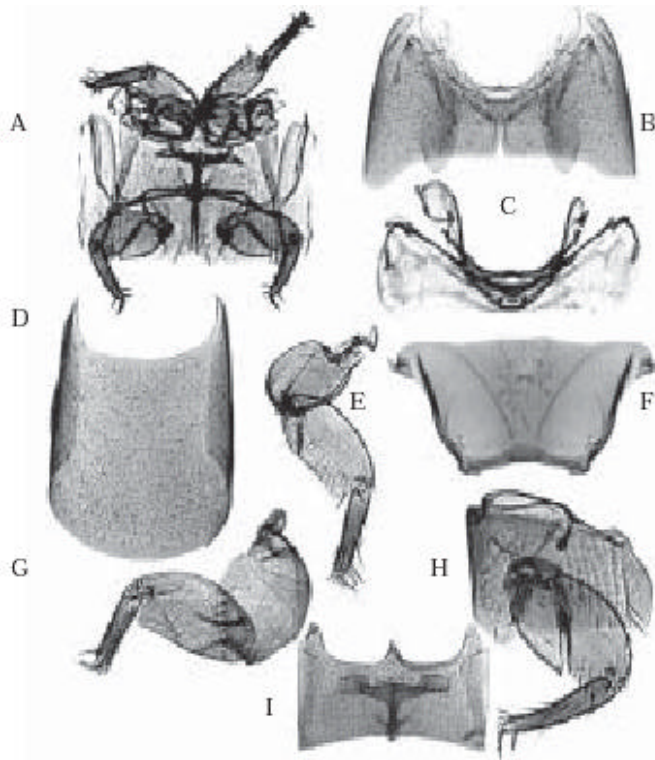


Figure 9.17. *Doryloxenus coecus*.

A: Meso- and metasternum with the legs in position,
 B: Elytra with the metasternum and abdominal segment barely showing through,
 C: Meso- and metanotum and abdominal segment I,
 D: Pronotum,
 E: Mesothoracic leg,
 F: Prosternum,
 G: Prothoracic leg,
 H: Metathoracic leg,
 I: Meso- and metasternum

Holotype: female, No. 20859, Malaysia, Perak, near Sitiawan, March 2001, Coll. Stefanie Berghoff from a nest of *Dorylus (Dichthadia) laevigatus* Smith. In the collection of D.H. Kistner to be deposited eventually in Field Museum of Natural History, Chicago.

Paratypes: 2 (including 2 on slides), same data as the holotype,(D.K.).

Notes: This species is retained in the genus *Doryloxenus* rather than placed in a new genus because the characters are very similar except for the lack of eyes and wings and the much shorter mesothorax which is related to the winglessness. It is interesting that this ant species has both an eyed and an eyeless species of *Doryloxenus*. If this occurs in other subterranean species of *Dorylus*, the shorter mesothorax might be an argument for a new genus which would unite all the eyeless and wingless species. At present this is the only such species of *Doryloxenus* known from any of the ant hosts. The species name, *coecus*, means blind.

Biology: After *D. laevigatus* had completed 2 emigrations in the laboratory, 4 *Doryloxenus coecus* were collected with the remaining colony fraction.

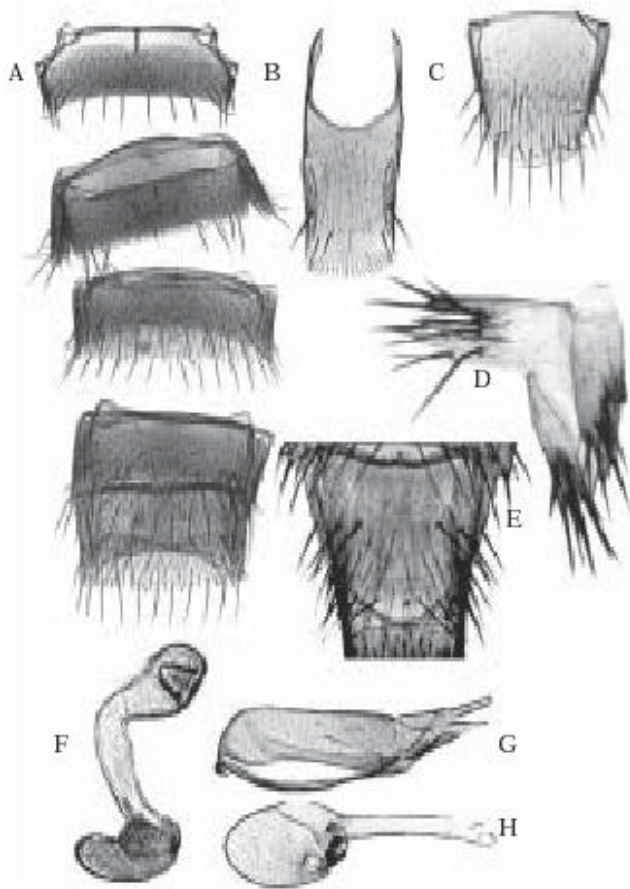


Figure 9.18. *Doryloxenus coecus*.

A: Abdominal segments II-VI,
 B: Tergite VIII,
 C: Sternite VIII,
 D: Abdominal segment IX, the left lateral lobe was twisted in the dissection,
 E: Abdominal segment VII,
 F: Spermatheca,
 G: Lateral lobe of the male genitalia,
 H: Median lobe of the male genitalia

Genus Pseudolydorus Kistner New Genus

The relationships of this genus are to *Anommatoxenus* Wasmann and *Lydorus* Normand. Superficially, it looks like *Lydorus* from Tunisia. However abdominal segment IX is trilobed and possesses the chaetae characteristic of nearly all Pygostenini whereas *Lydorus* has unique chaetotaxy (largely absent) on abdominal segment IX. However, if we assume the unique chaetotaxy of abdominal segment IX is apomorphic, then *Lydorus* is the closest relative. *Lydorus* is represented by 2 species, *L. myrmidon* associated with *Dorylus (Typhlopone) fulvus* Westwood and *L. grossii* Patrizi associated with *Aenictus* sp. from Kenya. While *L. myrmidon* has been studied from numerous specimens (Kistner, 1958, p. 102-104) repeatedly captured from *D. fulvus* by Normand, *L. grossii* has not been recaptured since the original specimen and the ant determination was labeled on the holotype as provisional by Patrizi. *D. fulvus* is a predominantly subterranean ant that emerges to the surface on occasional nocturnal raids. The easiest way to identify *Pseudolydorus* is by the arching of the body dorsoventrally (Fig. 9.19B). Additionally it differs from *Lydorus* by the following: the prosternum lacks macrochaetae from the anterior border, the procoxae lack macrosetae on the dorsolateral border, the pronotal epimerons are shorter, and as mentioned above, the median lobe of abdominal segment IX has 2 macrochaetae on the apical edge. *Anommatoxenus* differs from both of the above by the possession of eyes, a

much longer pronotum, a much longer meso- and metasternum, presence of wings, a much wider mentum and submentum, and much longer gula.

Overall appearance as in Figs. 9.19A, B, see also the front cover, upper left. Head shaped as in Fig. 9.20A; gula extremely short, attached to a large submentum, remainder of the so-called gular sutures formed by the joined edges of the postgenae. Eyes absent. Antennae shaped as in Fig. 9.20C, without coeloconic sensilla on the terminal segment. Labrum with the anterior border arcuate, shaped as in Fig. 9.20B. Mandibles almost symmetrical, shaped as in Figs. 9.20D & E, both without median teeth. Maxillae shaped as in Fig. 9.20F, palpi 4-segmented. Segment 1 very short, segments 2 and 3 about equal in length. Segment 4 about equal in length to segment 3, tapering apically. Galea much shorter than the lacinia but terminating at the same level; both with foleose terminal setae. Labium shaped as in Fig. 9.20G, palpi 3-segmented. All segments about equal in length. Mentum (Fig. 9.20G) distinct from the submentum.



Figure 9.19. *Pseudolydorus linsenmairi*. A,B: Dorsal and lateral views of the entire beetle

Pronotum shaped as in Figs. 9.19A & 9.20H. Prosternum shaped as in Fig. 9.21A, mesothoracic peritremes loose, not fused to the prosternum. Large coxal cavities not closed behind, except loosely by the mesothoracic peritremes. Mesonotum (scutellum) narrow, shaped as in *Anommatoxenus*. Metanotum reduced in length, shaped as in Fig. 9.21C. Meso- and metasternum extremely shortened, shaped as in Fig. 9.21B, mesosternum particularly reduced; mesocoxal cavities narrowly separated by a narrow acarinate mesothoracic process; metathoracic coxal cavities also narrowly separated (Fig. 9.21B) by a median process. Elytra extremely short, shaped as in Fig. 9.21C, wings also absent. Pro-, meso-, and metathoracic legs shaped as in Figs. 9.21D-F. Procoxae without large macrochaetae. Tarsal formula 4-4-4, segments 1-3 with a single pair of foleose setae on each segment; 4th segment fragile and missing on most specimens. Pretarsus

present. Tarsi with the pairs of foleose setae similar to the form of similar setae found in other limuloid genera of the Pygostenini (see Kistner and Jacobson, 1977) for a complete SEM study of these kinds of setae. Wings absent.

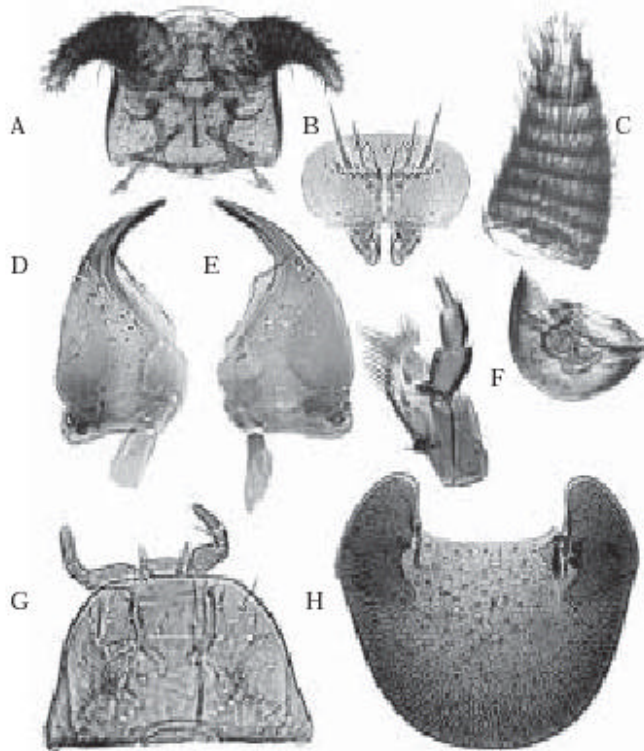


Figure 9.20. *Pseudolydorus linsenmairi*.

A: Head, ventral,

B: Labrum,

C: Antenna, segments 1 & 2 became separated from the rest of the antenna during the dissection,

D,E: Left and right mandibles,

F: Maxilla,

G: Labium and mentum,

H: Pronotum

Abdomen with the tergites and sternites somewhat convex, shaped as in Figs. 9.19A, B, & 9.22C; all tergites and sternites with scalloped posterior edges; abdomen with segment III widest and tapering to very narrow posteriorly. Segments III-VI (Fig. 9.22C) each with 2 pairs of paratergites; segment VII with 2 pairs but the inners are greatly reduced; segment VIII without paratergites. Segment VII with the median opening of the defense gland reservoir on its anterior border; the actual reservoir was not found on dissected specimens. These openings are reduced in the Pygostenini (see Shower and Kistner, 1976). Segment IX shaped as in Fig. 9.22E, with 2 macrochaetae on the apical part of the median lobe; with longer apodemes in males than in females. Male genitalia bulbous; presumed variable by species. Spermatheca sclerotized, shape presumed variable by species.

Type species: *Pseudolydorus linsenmairi* Kistner, described below.

Pseudolydorus linsenmairi Kistner New Species

Figs. 9.19-9.22, front cover, upper left

The genus is monobasic so that characters isolated as specific here are based on experience with other closely related genera such as *Anommatoxenus* and *Lydorus*.

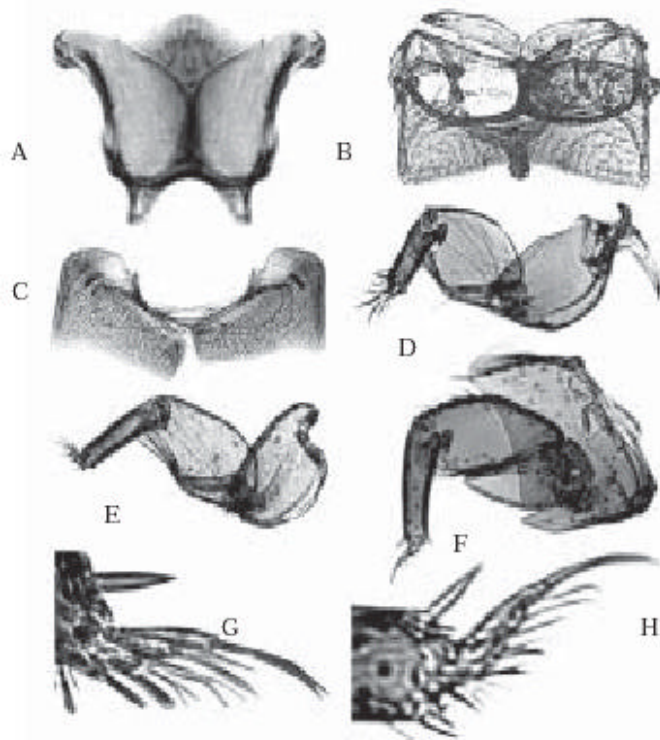


Figure 9.21. *Pseudolydorus linsenmairi*.

A: Prosternum,
 B: Meso- and metasternum,
 C: Elytra with the metanotum & abdominal segment I barely visible beneath them,
 D: Prothoracic leg,
 E: Mesothoracic leg,
 F: Metathoracic leg,
 G & H: views of different tarsi showing the placement of the modified setae

Color reddish brown throughout. Ground sculpture of the entire body smooth and shiny. Dorsal surface of the head, pronotum, and elytra additionally shallowly punctate with sparse fine yellow setae emerging from the punctures. Pronotum shaped as in Figs. 9.19A, B, & 9.20H, strongly curved dorsoventrally and covering almost the entire anterior part of the body. Lateral edges strongly recurved to broadly attach to the prosternum. Antennae short and spindle shaped (Fig. 9.20C). Macrochaetotaxy of abdominal tergites II-VIII as follows: 6,6,4,4,4,4/4,6. Spermatheca shaped as in Fig. 9.22A. Median and lateral lobes of the male genitalia shaped as in Figs. 9.22B & D.

Measurements (in mm): Head length, 0.23-0.25; head width, 0.22-0.24; pronotum length, 0.62-0.65; elytra length, 0.13-0.14. Number measured. 4.

Holotype: male, No. 20853, Malaysia, Perak, near Sitiawan, March 2001, Coll. Stefanie Berghoff from a nest of *Dorylus (Dichthadia) laevigatus* Smith. In the collection of D.H. Kistner to be deposited eventually in Field Museum of Natural History, Chicago.

Paratypes: 13 (3 on slides), same data as the holotype.

Notes: The genus is named for its similarity to *Lydorus*, the species name honors Professor Linsenmair at Universität Würzburg who has provided valuable guidance to Stefanie Berghoff.

The measurements of the body parts are extremely difficult because of overlapping and vaulting of the segments. The most accurate measurements were made from slide mounted material and the most accurate of these were made of the elytra and the heads. The pronotum is extremely vaulted and even slide mounted material cannot be measured very accurately.

Biology: Twice *P. linsenmairi* was observed in a tube with heavy ant emigration traffic. When *P. linsenmairi* was touched by an ant, it temporarily raised its abdomen. However, when a beetle was overrun by ants, it remained motionless on the floor of the tube. In each case, the ants showed no reaction to the beetles. After awhile *P. linsenmairi* moved to the side of the ant

column and eventually jumped onto an ant's gaster. When riding on the gaster, *P. linsenmairi* raised its abdomen slightly. Overall, 37 *P. linsenmairi* were collected from the nest.

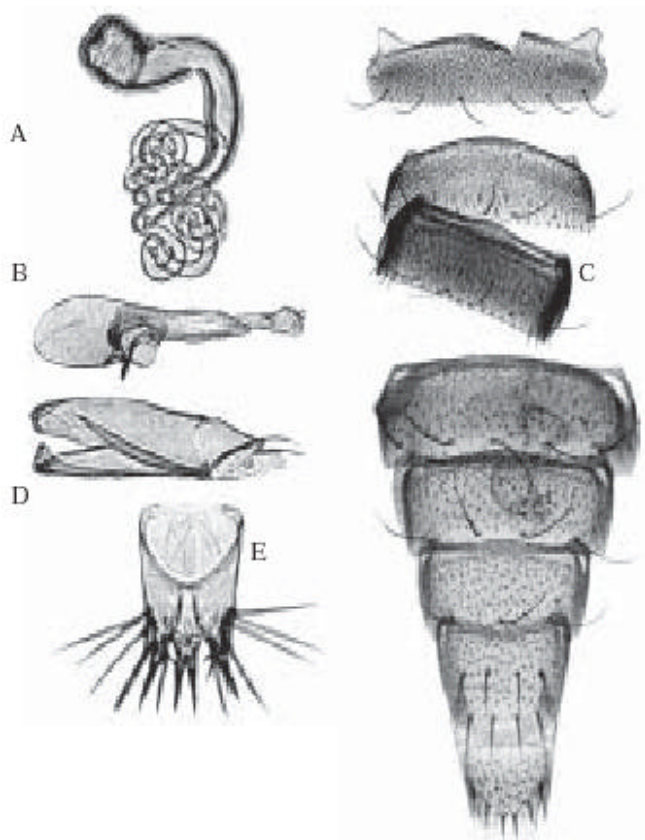


Figure 9.22. *Pseudolydorus linsenmairi*.
 A: Spermatheca,
 B: Median lobe of the male genitalia,
 C: Abdominal segments II-VIII, segments II & III became disarticulated in the dissection,
 D: Lateral lobe of the male genitalia,
 E: Abdominal segment IX of female

Genus *Pygoplanus* Kistner New Genus

This genus is most closely related to *Doryloxenus* through the overall limuloid shape, the shapes of the prosternum, the submentum, antenna, and legs. It is distinguished from *Doryloxenus* by the flattened condition of the limuloid shape, the shapes of the mandibles, the maxillae where the foleose lacinia and galea are nearly longer than the rest of maxilla, and the labrum. The flattening of the beetle, in particular the flattening of the pronotum without much change in the prosternum, has resulted in the hypomera being greatly expanded (Fig. 9.25A). The pronotum of *Doryloxenus*, which is greatly vaulted, has hypomera which are greatly reduced.

While we now have a blind and wingless species of *Doryloxenus*, this is an unusual condition in the genus and *Pygoplanus* shares with that species (*D. coecus*) the lack of eyes and wings with the correlated changes in the length of the meso- and metanotum and the metasternum with its attached abdominal segment I.

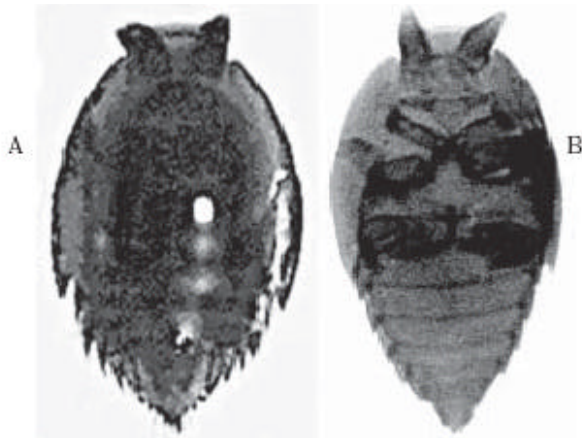


Figure 9.23. *Pygoplanus subterraneus*. A: Dorsal appearance and B: Ventral appearance of the entire beetle. (The first author apologizes of the quality of these photos but the beetles are less than 1.5 mm in total length.)

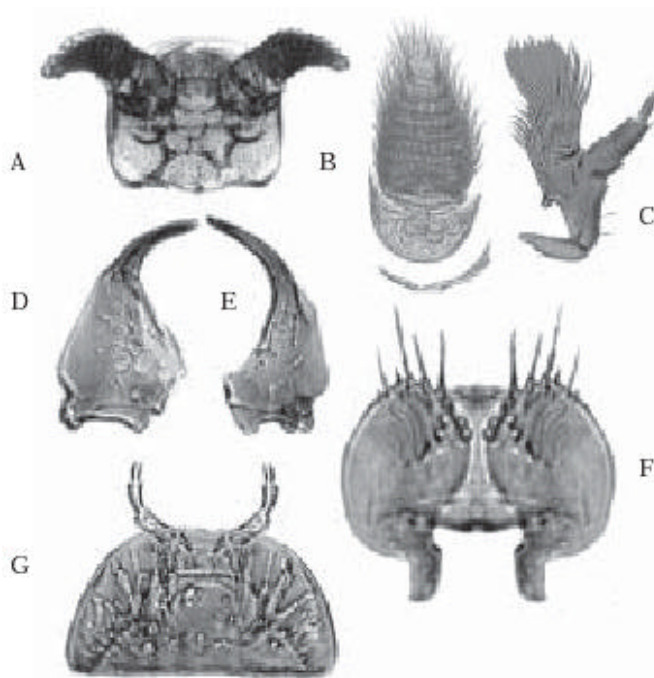


Figure 9.24. *Pygoplanus subterraneus*.
 A: Head, ventral,
 B: Antenna,
 C: Maxilla,
 D & E: Left and right mandibles respectively,
 F: Labrum,
 G: Labium and submentum

Overall appearance flattened as in Figs. 9.23A, & B, see also the front cover, lower left and right. Head shaped as in Fig. 9.24A; gula extremely short, attached to a large submentum, remainder of the so-called gular sutures formed by the joined edges of the postgenae. Eyes absent. Antennae shaped as in Fig. 9.24B, without coeloconic sensilla on the terminal segment. Labrum with the anterior border arcuate and somewhat flattened medially, shaped as in Fig. 9.24F. Mandibles not quite symmetrical, shaped as in Figs. 9.24 & E, both without median teeth and highly acicular. Maxillae shaped as in Fig. 9.24C, palpi 4 segmented. Segment 1 very short, segments 2 somewhat longer but shorter than segment 3. Segment 4 about equal in length to segment 3, about half the

width and tapering apically. Lacinia much shorter than the galea but terminating at the same level; both with foliose terminal setae; the whole lobe nearly as long as the rest of the maxilla. Labium shaped as in Fig. 9.24G, palpi 3-segmented; segment 1 almost twice the length to segment 2, segment 3 about 2/3 the length of segment 2. Mentum (Fig. 9.24G) large and distinct from the submentum.

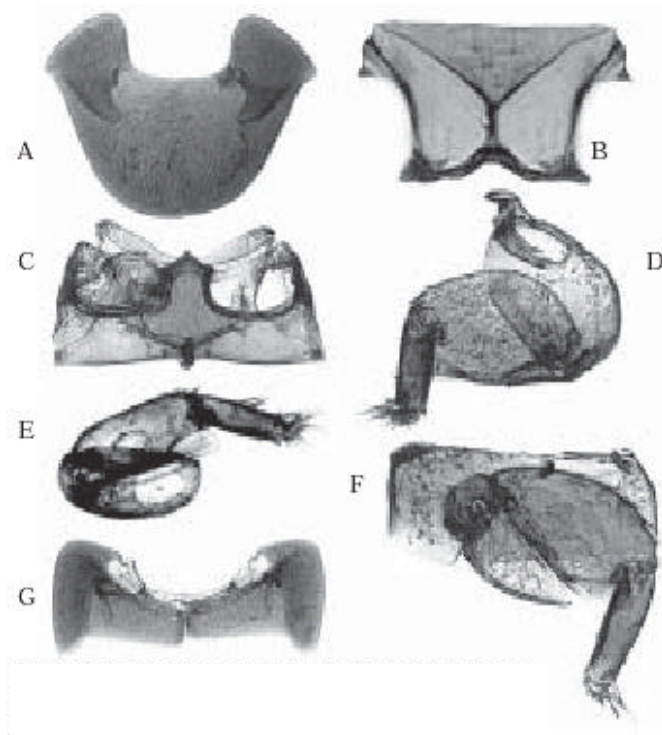


Figure 9.25. *Pygoplanus subterraneus*.

A: Pronotum,
 B: Prosternum,
 C: Meso- and metasternum, the shortened metanotum and abdominal segment I can be partially seen through the sternites,
 D: Prothoracic leg,
 E: Mesothoracic leg,
 F: Metathoracic leg,
 G: Elytra

Pronotum shaped as in Figs. 9.23A & 9.25A. Prosternum shaped as in Fig. 9.25B, mesothoracic peritremes loose, not fused to the prosternum, shaped as in Fig. 9.25C. Large procoxal cavities not closed behind, except loosely by the mesothoracic peritremes. Mesonotum (scutellum) narrow, shaped as in *Anommatoxenus*. Metanotum reduced in length, shaped as in Fig. 9.25G. Meso- and metasternum extremely shortened, shaped as in Fig. 9.25C, mesosternum particularly reduced; mesocoxal cavities widely separated by a broad a carinate mesothoracic process; metathoracic coxal cavities also narrowly separated (Fig. 9.25C) by a median process. Mesocoxal cavities marginate. Elytra short, shaped as in Fig. 9.25G. Pro-, meso-, and metathoracic legs shaped as in Figs. 9.25D-F. Procoxae without large macrochaetae. Tarsal formula 44-4, segments 1-3 with a single pair of foliose setae on each segment; 4th segment fragile and missing on most specimens. Pretarsus present. Tarsi with the pairs of foliose setae similar to the form of similar setae found in other limuloid genera of the Pygostenini (see Kistner and Jacobson, 1977) for a complete SEM study of these kinds of setae. Wings absent.

Abdomen with the tergites and sternites somewhat flattened, shaped as in Figs. 9.26A, C; all tergites and sternites without scalloped posterior edges; abdomen with segment III widest and tapering to very narrow posteriorly. Segments III-VI with 2 pairs of paratergites; segment VII with 2 pairs but the inners are greatly reduced; segment VIII (Fig. 9.26F) without paratergites. Segment VII with the median opening of the defense gland reservoir reduced but on the anterior border; the actual reservoir was not found on dissected specimens. These openings are reduced in the Pygostenini (see Shower and Kistner, 1976). Segment IX shaped as in Fig. 9.26E, with 2

macrochaetae on the deeply incised apical part of the median lobe; with longer apodemes in males than in females. All outer edges of outer paratergites have densely packed small setae shown particularly well in Fig. 9.26C. Male genitalia bulbous; too small for meaningful dissections. Spermatheca sclerotized, shape presumed variable by species.

Type species: *Pygoplanus subterraneus* Kistner described below.

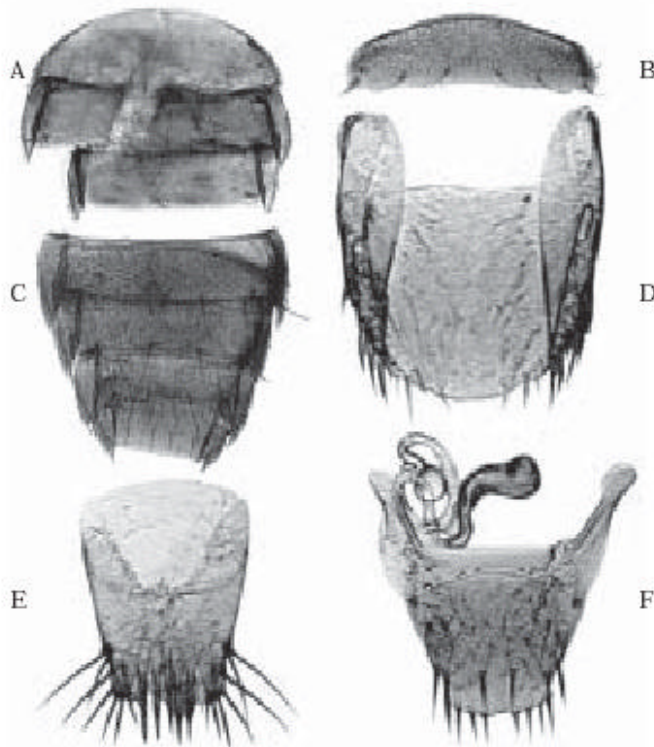


Figure 9.26 *Pygoplanus subterraneus*.

A: Abdominal segments II-IV,

B: Abdominal sternite IV,

C: Abdominal segments V-VII,

D: Abdominal sternite VII,

E: Abdominal segment IX of female,

F: Abdominal segment VIII with the spermatheca in place

Pygoplanus subterraneus Kistner new species

Figs. 9.25-9.26

The genus is monobasic so that characters isolated as specific here are based on experience with other closely related genera such as *Typhloponemys* and *Doryloxenus*.

Color reddish brown throughout. Ground sculpture of the entire body smooth and shiny. Dorsal surface of the head, pronotum, and elytra additionally shallowly punctate with virtually no fine yellow setae emerging from the punctures. Pronotum shaped as in Fig. 9.25A, flattened dorsoventrally but not covering almost the entire anterior part of the body. Antennae short and spindle shaped (Fig. 9.24B) with numerous setae which are long. Macrochaetotaxy of abdominal tergites II-VIII as follows: 0,6,6,4,4,4/4,4. Sternites with an apical row of short thin yellow setae only. Spermatheca shaped as in Fig. 9.26F. Median and lateral lobes of the male genitalia too small for meaningful dissections.

Measurements (in mm): given as range and mean, Head length, 0.23-0.26, 0.24; head width, 0.26-0.28, 0.28; pronotum length, 0.50-0.70;0.52; pronotum width, 0.50-0.72, 0.62; elytra length, 0.10-0.12, 0.11. Number measured. 4.

Holotype: male, No. 20860, Malaysia, Perak, near Sitiawan, March 2001, Coll. Stefanie Berghoff from a nest of *Dorylus (Dichthadia) laevigatus* Smith. In the collection of D.H. Kistner to be deposited eventually in Field Museum of Natural History, Chicago.

Paratypes: 3 on slides, same data as the holotype. (D.K.).

Notes: The generic name is derived from *planus* meaning flat and *Pygo* from Pygostenini or flat pygostenine. Another interpretation is that the name means flat rump and that fits the beetle also. The overall shape of this beetle resembles that of a mite and the acicular mandibles strongly suggest that the beetles feed on external secretions of the ants or that they are ectoparasites on the ants' bodies.

Biology: All beetles observed within emigration columns were riding on the gaster or the head of an ant. When riding on a worker's head *P. subterraneus* fitted to it like helmet, continuing the form and color of the head. Therefore, their detection was easiest on the heads of callow workers. Overall, 3 *P. subterraneus* were collected from the nest.

Micropolemon Wasmann

Micropolemon malayensis Kistner and Jacobson

Micropolemon malayensis Kistner and Jacobson, 1975: 195, Malaysia, Selangor, Sungai Buloh Forest Reserve, 9 July 1973, in a log with *Coptotermes* sp.

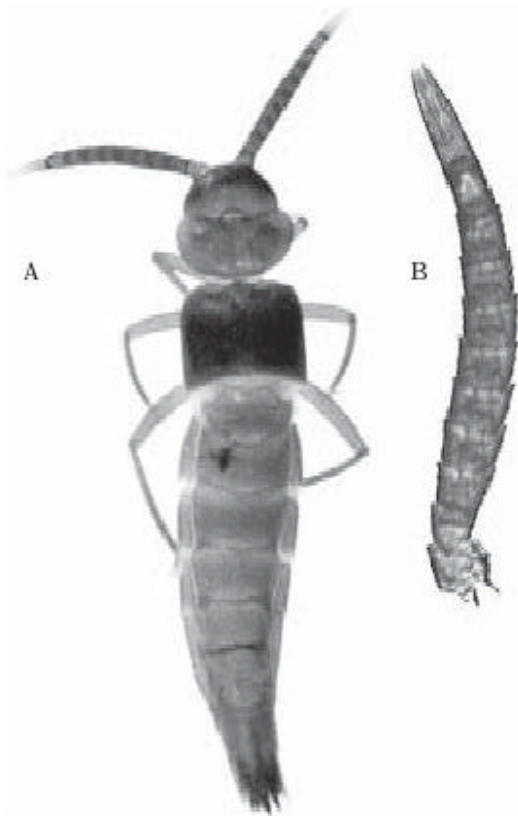


Figure 9.27. *Micropolemon malayensis*. A: Dorsal appearance of the whole beetle, B: Antenna which exhibits the typical pygostenine configuration with all the petioles covered by extensions of the sides of each segment.

Notes: In the original description notes it was stated that *Coptotermes* was not likely to be the true host of the species and that lucky collecting would probably secure the species from *Dorylus* sp. in the future. MS Berghoff brought the future to the present. The original description was based

on a single specimen so the description is expanded here. These are the first genitalia of this species described.

Overall appearance elongate as in Fig. 9.27A. Head shaped as in Fig. 9.28A; gula of normal length, attached to a subquadrate submentum, gula shaped as in Fig. 9.28A. Eyes present with forward and laterally directed facets. Antennae 11 segmented, shaped as in Fig. 9.27B, without coeloconic sensilla on the terminal segment and with the segmental petioles completely covered by extensions of the sides of the subsegments. Labrum with the anterior border arcuate and notched in the center, shaped as in Fig. 9.28B. Mandibles symmetrical, shaped as in Fig. 9.28C, both with a very small median tooth. Maxillae shaped as in Fig. 9.28D, palpi 4-segmented. Segment 1 very short, segments 2 about 3 times the length of segment 1; segment 3 about 3X the length of segment 2. Segment 4 somewhat shorter in length than segment 2, tapering apically. Galea shorter than the lacinia and terminating before that level; both with foleose terminal setae, but more on the galea. Labium shaped as in Fig. 9.28E, palpi 3-segmented. segments 3 and 1 about equal in length; segment 2 shorter than both. Mentum (Fig. 9.28E) distinct from the submentum and trapezoidal in shape.

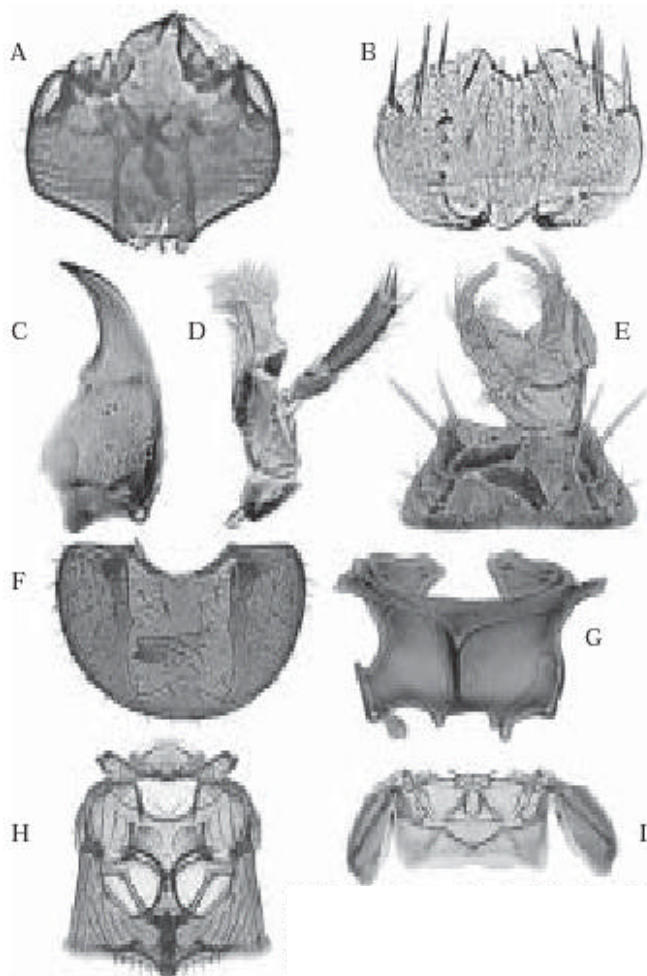


Figure 9.28. *Micropolemon malaxensis*.

- A: Head capsule,
- B: Labrum,
- C: Right mandible,
- D: Maxilla,
- E: Labium and mentum,
- F: Pronotum,
- G: Prosternum,
- H: Meso- and metasternum,
- I: Metanotum and abdominal segment I

Pronotum with the lateral borders rounded to join the posterior border seamlessly, shaped as in Figs. 9.27A and 9.28F; also with a shallow median groove. Prosternum shaped as in Fig. 9.28G and carinate, mesothoracic peritremes loose, not fused to the prosternum.

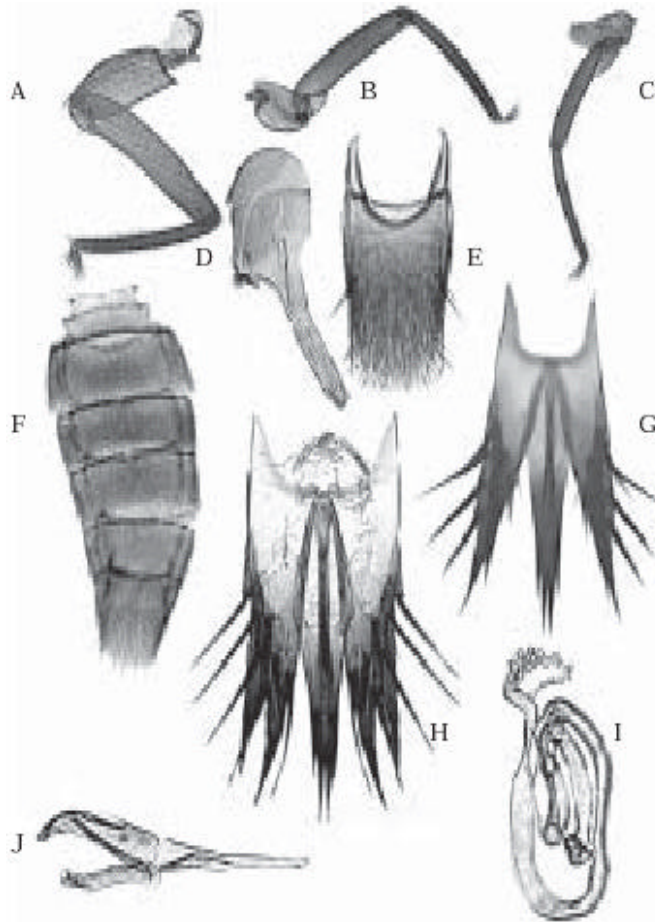


Figure 9.29. *Micropolemon malayensis*.

- A: Prothoracic leg,
- B: Mesothoracic leg,
- C: Metathoracic leg,
- D: Median lobe of the male genitalia,
- E: Abdominal segment VIII,
- F: Abdominal segments II-VII,
- G, H: Abdominal segment IX of male and female respectively,
- I: Spermatheca,
- J: Lateral lobe of the male genitalia

Coxal cavities not closed behind, except loosely by the mesothoracic peritremes. Mesonotum (scutellum) narrow, shaped as in *Anommatoxenus*. Metanotum not reduced in length, shaped as in Fig. 9.28I. Meso- and metasternum elongate, shaped as in Fig. 9.28H, mesosternum almost as long as the metasternum; mesocoxal cavities marginate, narrowly separated by a narrow slightly carinate mesothoracic process; metathoracic coxal cavities also narrowly separated (Fig. 9.28H) by an acarinate median process. Elytra long, shaped as in Fig. 9.27A; wings present and with the usual staphylinid venation. Pro-, meso-, and metathoracic legs shaped as in Figs. 9.29A-C, respectively. Procoxae with one large macrochaeta. Tarsal formula 4-4-4, segments 1-3 with many foleose setae [fora complete study of pygostenine tarsal setae (see Kistner and Jacobson, 1977)]; 4th segment fragile and missing on most specimens (all of those examined here). Pretarsus present.

Abdomen with the tergites and sternites somewhat elongate and somewhat flattened, shaped as in Figs. 9.29F; all tergites and sternites without scalloped posterior edges; abdomen with segment III widest and tapering to very narrow posteriorly. Segments III-VI with 2 pairs of paratergites; segment VII with 2 pairs but the inners are greatly reduced; segment VIII (Fig. 9.29E) without paratergites. Segment VII with the reduced median opening of the defense gland reservoir on its

anterior border; the actual reservoir was not found on dissected specimens. These openings are reduced in all of the Pygostenini (see Shower and Kistner, 1976). Abdominal tergites II-VI without macrochaetae but with numerous light yellow setae particularly on the apical border. Tergites VII and VIII with 4 black macrochaetae. Sternites lacking macrochaetae but with many fine yellow setae especially at the apical edges. Segment IX shaped as in Figs. 9.29G,H, with 2 macrochaetae on the apical part of the median lobe which is not deeply incised; with longer apodemes in males than in females. Male genitalia bulbous; variable by species. Spermatheca sclerotized, shape variable by species.

New measurements (in mm): Head length, 0.28-0.39; head width, 0.41-0.45; pronotum length, 0.25-0.29; pronotum width, 0.43-0.49; elytra length, 0.29-0.32. Number measured, 6 (including the holotype).

New material examined: 12 (including 6 on slides), Malaysia, Perak, near Sitiawan, March 2001, Coll. Stefanie Berghoff from a nest of *Dorylus (Dichthadia) laevigatus* Smith, (D.K.).

Biology: *Micropolemon malayensis* was observed in ant columns towards the end of an emigration. Here, they kept to the sides of the column and avoided contact with the ants. The beetles were never seen to lower their abdomens nor to ride on workers. When traffic became heavier, *M. malayensis* would wait at the sides of the column for more space to continue moving. Overall, 23 *M. malayensis* were collected from the nest.

Micropolemon sabahensis Kistner New species

Fig. 9.30

Most closely related to *M. malayensis* through the pronotum shape with its median groove but easily distinguished from it by the shape of the spermatheca. In gross aspect, it can be distinguished from it by the wider pronotum in proportion to the head (Fig. 9.30A).

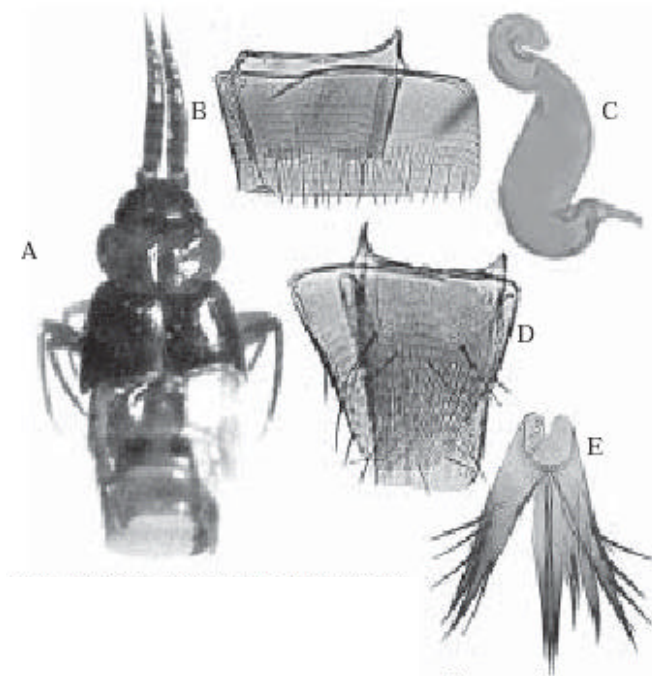


Figure 9.30. *Micropolemon sabahensis*.

A: Dorsal view of the head, pronotum, elytra, and abdominal segments II-V,
 B: Abdominal segment VI,
 C: Spermatheca,
 D: Abdominal segment VII,
 E: Abdominal segment IX

Color dark reddish brown throughout, abdomen somewhat lighter. Dorsal surface of the head, pronotum, and elytra smooth and shiny with setae emerging at sparse intervals from shallow,

barely perceptible punctures. Pronotum with only 1 furrow in the midline, lateral borders with only 2 lateral striae, shaped as in Fig. 9.30A. Abdominal tergites II-VI without macrochaetae. Tergites VII & VIII with 4 macrochaetae each as well as numerous light yellow setae. Spermatheca shaped as in Fig. 9.30C. Male unknown.

Measurements (in mm): Head length, 0.31; head width, 0.43; pronotum length, 0.27; pronotum width, 0.48; elytra length, 0.30. Number measured, 1.

Holotype: female, No. 20856, East Malaysia, Sabah, Poring Hot Springs, 24.IV.2000, Coll. Stefanie Berghoff, at oil bait with *D. (Dichthadia) laevigatus*. In the collection of D.H. Kistner to be eventually deposited in the Field Museum of Natural History, Chicago.

Notes: The species name means simply from Sabah.

The relationships of the Pygostenine genera

The phylogeny of the Pygostenini is better known than practically any other tribe of the Aleocharinae and it has been approached by a variety of methods. The first method (Kistner, 1958) was a traditional taxonomic approach characteristic of the time. Most recently the genera were examined by a variety of numerical methods (Jacobson and Kistner, 1980) and these produced cladograms or phylogenetic trees which varied somewhat but were remarkably similar regardless of the method. We have run the same data (Table 9.1 for the characters and Table 9.2 for the coding) through the PAUP program (Swofford, 2002) and the best tree produced for the previously known genera is given here (Fig. 9.31). No outgroup was selected and we rooted the tree instead to the genus *Typhlopone*, the member of the in group which has the most plesiomorphic characters and is found with the most subgenera of *Dorylus*. Of the previously derived trees, the presently derived one matches best the one derived by traditional taxonomic methods. Those interested in comparing the various trees can read Jacobson and Kistner's (1980) paper.

What interests us most here is how the 2 new genera fit into the phylogeny. The 2 genera are the first known from *Dorylus (Dichthadia)*, while all the rest are known from species of *Dorylus (Dorylus)*, *D. (Anomma)*, *D. (Typhlopone)*, or *Aenictus* and 1 genus with *Odontotermes*.

The characters of the new genera were accordingly scored for the same 31 characters previously used and these are presented in Table 9.1 and the coding in Table 9.2. Putting the data through the PAUP program produced the tree in Fig. 9.32. The most interesting part of the tree is that the blind new genera branched out as ancestral to several genera with eyes. It is unreasonable to conclude that genera with eyes evolved from eyeless genera at this phylogenetic level. We therefore ran the data through the program again, eliminating eyelessness from the list of characters and the best tree came out the same.

Table 9.1. List of characters used to investigate the phylogeny of the Pygostenini by Jacobson and Kistner (1980). Characters were coded 0 for plesiomorphic and 1 for apomorphic. Codings are given in Table 9.2.

	Plesiomorphic	Apomorphic
01	Antennae long	Antennae compressed
02	Antennae 11-segmented	Antennae with less than 11 segments
03	Eyes present	Eyes absent
04	Eyes of normal size	Eyes large or reduces
05	Eyes with anterior and laterally facing facets	Eyes with only laterally facing facets
06	Head without a shield	Head with a shield
07	Labial palpi 4-segmented	Labial palpi 3-segmented
08	Maxillary palpi with 8-10 finger-like projections	Maxillary palpi with more than 12 finger-like projections
09	Head transverse	Head quadrate or elongate
10	Pronotum with equal to or less than twice the length	Pronotum with greater than twice the length
11	Lateral margin of the pronotum straight	Lateral margin of the pronotum curved
12	Pronotum length less than twice the elytra length	Pronotum length equal to or greater than twice the elytra length
13	Lateral margin of the pronotum does not extend below the head capsule	Lateral margin of the pronotum extends below the head capsule
14	Dorsal surface of the pronotum convex	Dorsal surface of the pronotum flat (not necessarily smooth)
15	Anterior margin of the pronotum not overlapping the head	Anterior margin of the pronotum overlapping the head
16	Lateral margins of the pronotum forming a continuous margins of the pronotum and line with the lateral margins of the elytra	A gap is present between the lateral margins of the pronotum and elytra
17	Lateral margins of the elytra curved	Lateral margins of the elytra straight
18	Dorsal surface of the elytra convex	Dorsal surface of the elytra flat (not necessarily smooth)
19	Mesosternal intercoxal process acute	Mesosternal intercoxal process blunt
20	Mesosternal intercoxal process carinate	Mesosternal intercoxal process blunt
21	Mesocoxal acetabulae circular or elliptical	Mesocoxal acetabulae rectangular
22	Length of the mesosternum less than 1.5 X the length of the of metasternum	Length of the mesosternum equal to or greater than 1.5 X the length the metasternum
23	Wings normal	Wings reduced or absent
24	Dorsal surface of elytra smooth	Dorsal surface of elytra with grooves
25	Tarsal formula 4-5-5	Tarsal formula not 4-5-5
26	Procoxa does not cover the prothoracic leg in repose	Procoxa expanded so as to cover the prothoracic leg in repose
27	Tarsi elongate	Tarsi short, compressed
28	Tarsi with few spatulate setae	Tarsi with many spatulate setae
29	Procoxa without macro chaetae	Procoxa with macrochaetae
30	Posterior margins of abdominal tergites smooth	Posterior margins of abdominal tergites notched
31	Abdomen not fusiform	Abdomen fusiform
32	Pronotum without a medial groove	Pronotum with a medial groove
33	Abdominal tergite III is the widest tergite	Abdominal tergite III not the widest tergite

Table 9.2. Coding of the characters given in Table 9.1, characters 1-33 place from left to right. *Aenictoxenus* was left out because it is such an aberrant genus.

Genus	Characters
<i>Typhloponemys</i>	00000000000000000000000000000000
<i>Dorylotyphlus</i>	001??0000001000000000010000000000
<i>Pogostenus</i>	000000000100000100000000000000000
<i>Pegestenus</i>	000000000101000100000000000000010
<i>Eupygostenus</i>	000000000101000100000010000000010
<i>Pygostenus</i>	00000000000000000000000000010000000
<i>Mandera</i>	001??0000000100000001110010000000
<i>Anommatoxenus</i>	110011010001101000001100011010100
<i>Lydorus</i>	111111010001101000001100011010100
<i>Odontoxenus</i>	000001010000101000000100111000100
<i>Doryloxenus</i>	100011010000101000001100111010100
<i>Mimocete</i>	100011110000101000001100111010100
<i>Neopygostenus</i>	000100000000000100100000000000000
<i>Delibius</i>	000100000100000100110000000000000
<i>Xenidus</i>	000100000100000100110000100100000
<i>Anommatophilus</i>	000000000010010100110000000000001
<i>Prodeliodes</i>	000000000110010100110000000100001
<i>Deliodes</i>	000000000000010110010000100101001
<i>Micropolemon</i>	000000010010010110110000100101011
<i>Typhlopoemon</i>	001??0010000010110110010100101011
<i>Sympolemon</i>	000000011010010111110101100101001
<i>Pseudolydorus</i>	101??0000001100000000010111000100
<i>Pygoplanus</i>	101??1000001111001110110111001101

It therefore seems reasonable to conclude that the 2 new genera (*Pseudolydorus* and *Pygoplanus*) have retained enough plesiomorphic characters to represent the ancestors to the generic cluster containing *Odontoxenus*, *Anommatoxenus*, *Lydorus*, *Doryloxenus*, and *Mimocete* while losing their eyes due to non-selection in an underground environment. Species of previously known genera (*Doryloxenus* and *Micropolemon*) with eyes are known from the nest and associated foraging columns of *D. (Dichthadia) laevigatus* and these are the only species captured at the foraging columns attracted to the oil baits. Of interest also is the recording of the first and only blind species of *Doryloxenus*. While the eyed species (*D. groveri*) have been collected in many niches, the eyeless species (*D. coecus*) has only been captured in the nest sample. Other blind genera have evolved with other hypogean subgenera of *Dorylus*, while eyeless species have never shown up in epigeal species of ants. Table 9.3 presents a summary of the host data at the generic or subgeneric level for each of the genera of Pygostenini.

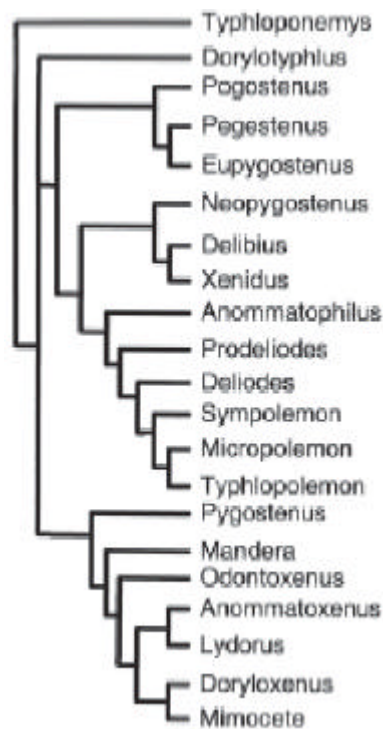


Figure 9.31. Cladogram of the Pygostenini derived from the data published by Jacobson and Kistner (1980)

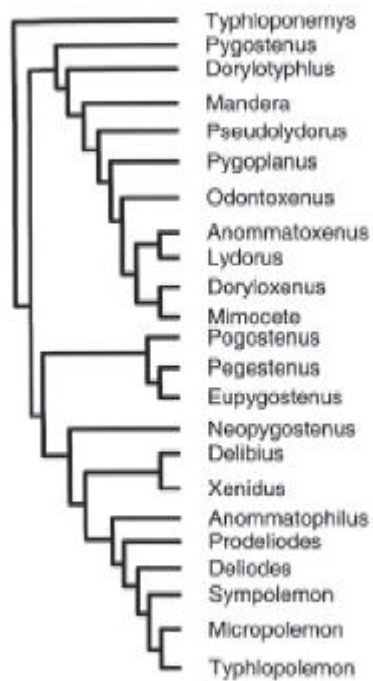


Figure 9.32. Cladogram of the Pygostenini using the same characters but incorporating the two new genera.

Table 9.3. Pygostenini genera together with their hosts at the subgeneric level. (el-eyeless)

Pygostenine genus	Doryline genus and or subgenus
<i>Typhloponemys</i>	<i>D. (Anomma)</i> , <i>D. (Dorylus)</i> , <i>D. (Typhlopone)</i> , <i>Aenictus</i> , <i>Odontotermes</i> , <i>Cubitermes</i> .
<i>Dorylotyphlus</i> – el	<i>D. (Dorylus)</i>
<i>Pogostenus</i>	<i>D. (Anomma)</i>
<i>Pegestenus</i>	Unknown
<i>Eupygostenus</i>	<i>D. (Dorylus)</i>
<i>Pygostenus</i>	Unknown
<i>Mandera</i> – el	<i>D. (Anomma)</i> , <i>D. (Dorylus) anommatoxenus</i> <i>D. (Anomma)</i>
<i>Lydorus</i> – el	<i>D. (Typhlopone)</i>
<i>Odontoxenus</i>	<i>Odontotermes</i> , <i>Hypotermes</i> , <i>Trinervitermes</i> (doubtful)
<i>Doryloxenus</i> - 1 el	<i>D. (Anomma)</i> , <i>D. (Typhlopone)</i> , <i>D. (Dichthadia)</i>
<i>Mimocete</i>	<i>D. (Anomma)</i>
<i>Neopygostenus</i>	<i>Aenictus</i>
<i>Delibius</i>	Unknown
<i>Xenidus</i>	Unknown
<i>Anommatophilus</i>	<i>D. (Anomma)</i>
<i>Prodeliodes</i>	Unknown
<i>Deliodes</i>	Unknown
<i>Micropolemon</i>	<i>D. (Anomma)</i> , <i>D. (Dichthadia)</i>
<i>Typhlpolemon</i> – el	<i>D. (Anomma)</i> , <i>D. (Dorylus)</i>
<i>Sympolemon</i>	<i>D. (Anomma)</i>
<i>Pseudolydorus</i>	<i>D. (Dichthadia)</i>
<i>Pygoplanus</i> – el	<i>D. (Dichthadia)</i>
<i>Aenictoxenus</i> – el	<i>Aenictus</i>

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Chapter 10

General discussion

Despite their probable importance in tropical ecosystems and our profound knowledge about epigaeic species, hypogaeic army ants were scientifically treated only marginally. At a time, when close to nothing was known about army ants, Savage (1849) noted for *Dorylus nigricans* "Newly expressed oils are also favorite articles of food, especially the vegetable, that obtained from the fruit of the *Elais guiniensis* – the Palm oil of commerce." Despite this early knowledge about oil-feeding, the habit was brought back to mind only recently, when it was suggested as a potential method to study hypogaeic army ants (Weissflog et al., 2000). Contrary to the general assumptions of army ant behavior, *Dorylus laevigatus* recruited predictably and in high numbers to oil baits in Malaysia. Perceiving the potentials of the method, I further developed the oil-baiting method, testing its suitability for the first detailed study of a hypogaeic army ant, i.e. *D. laevigatus*, and other hypogaeic ant species.

In the following, I discuss the results of my study, combining respective parts of different chapters and supplementing them with data, which had to be omitted in the manuscripts. Since all results base at least to some extend on the oil-baiting method, I will discuss the pros and cons of this method first. Subsequently, the reader will find a discussion of *D. laevigatus*' general sociobiology and interactions with its environment. In conclusion, I remark on the observed differences to known epigaeic species and the potential ecological importance of *D. laevigatus*.

Methodology

Central to all my investigations was a grid containing evenly spaced oil baits. Baits were regularly supplied with 50 ml palm oil, preventing a depletion of the oil (Chapter 4). Such comparatively large amounts of oil do not occur naturally and may thus influence the observed behaviors. Due to its high energy content, oil should be an attractive food source. However, only few species actually fed on oil (Chapter 7, Brinkman et al., 2001). To a few species, on the other hand, oil baits were highly attractive. Especially Dorylinae and some Ecitoninae army ants showed to have an affinity to oil. I recorded *Dorylus* species of the subgenera *Dichthadia*, *Alaopone*, and *Typhlopone* at baits (Chapter 6, Appendix A). Likewise, species of the remaining four *Dorylus* subgenera (i.e. *Anomma*, *Rhogmus*, and *Dorylus*) recruited to oil baits in Africa (C. Schöning, pers. comm.), while in the Neotropics, *Labidus* and *Neivamyrmex* species recruited to palm oil baits (Rabeling and Verhaag, 2002). Oil baits thus represent a good method to record the occurrence of these army ants, which were previously collected predominately by chance. The ready use of oil points to natural lipid sources in these species' diets. A possible source could be the commonly preyed-on arthropod larvae, many of which are rich in lipids (Inaoka et al., 1999). Another source may be plant material such as oil-rich seeds and fruits (Jordano, 2000), which *D. laevigatus* (Chapter 6), *D. orientalis* (Roonwal, 1972), *Labidus coecus* (Rettenmeyer, 1963), and possibly other army ant species include in their diet. Similar to these army ants, two mass raiding *Pheidologeton* species also recruited in large numbers to oil baits (Chapter 7). Curiously, species of the other two army ant genera occurring in the study area, i.e. *Aenictus* and *Leptogenys*, were occasionally found at oil baits during a check, but were never observed to feed on the oil (Chapter 8).

Assumed to have only limited capacity of trophallaxis (Eisner, 1957), and due to the larvae's need of protein, Weissflog and co-workers (2000) assumed *D. laevigatus* to forage and emigrate naturally despite the presence of oil baits. However, my study indicated *D. laevigatus* to feed oil to their larvae (Chapter 5). On the other hand, *D. cf. vishnui* left well

occupied baits before depleting the oil (Chapter 6). This indicates that, similar to epigeaic species (Pullen, 1963; Rettenmeyer, 1963), *D. cf. vishnui* can not be restrained to a certain area simply by providing a large enough food source. Likewise, the recorded fights at baits (Chapters 6 and 7) could have been facilitated by the presence of the unusual large food source. However, laboratory and field observations point to aggressive interactions also under natural conditions (Chapters 6 and 7). Overall, the possible influence of oil baits on the behavior of *D. laevigatus* needs to be further investigated. Nevertheless, keeping these uncertainties in mind, oil baits represent an effective, and up to now the only tool finally enabling an insight into the occurrence and some behaviors of hypogaeic (army) ants.

To study different aspects of the species' hypogaeic foraging, I tested a variety of baiting containers (Chapter 3). A researcher will profit from the easy establishment of soil baits by quickly gaining a general overview of occurring abundant hypogaeic ants. However, a bait check always represented a major disturbance, destroying the foraging trails of occurring species. This probably caused some ants to prematurely desert a bait. To minimize these disturbances, I employed oil-baited "sieve buckets" (Fig. 3.4), enabling quick bait checks without the destruction of foraging tunnels (Chapter 4). Most data could be collected within a quick glance, enabling the detection also of species with few individuals, which would otherwise retreat into the soil before being detected. The advantage of sieve buckets over soil baits is illustrated by the following example. Weissflog and co-workers (2000) recorded at 271 soil baits checked over three months in West-Malaysia seven ant species. Sampling at 12 sieve buckets for 8 days in the same area, I could collect already 12 species. The effectiveness of sieve buckets was also demonstrated by their employment in Poring Hot Springs, where I recorded 85 ant species at palm oil baits (Chapter 8). Of these species, 48% were not collected despite previous extensive sampling within the same area (Brühl, 1996). Representing mostly chance encounters using conventional study methods, my study showed hypogaeicly foraging ant species to be often undersampled and the abundance of some species to be underestimated by other methods (see Mohamed, 1994; Malsch, 2002).

Two further baiting containers were tested in the field (Chapter 3). Sieve cavities (Fig. 3.5) enabled direct observations of usually concealed hypogaeic foragers. However, *D. laevigatus* as well as *D. cf. vishnui* quickly filled the cavities with excavated soil (Chapter 4), often limiting the observations to a maximum of 48 hours, if the soil was not manually removed. Furthermore, the small sieve buckets contained in the open spaces of the sieve cavities usually began to mold within a week and were generally less frequented by ants compared to sieve buckets. Bucket baits (Fig. 3.6) allowed to restrict the bait access to workers foraging at or below a given depth. In this way, *D. laevigatus* was shown to forage still in depths of more than 1 m. However, at such depths, a container needed to be either relatively wide or observations and ant collections would be limited. Similar to sieve cavities, the establishment of bucket baits was rather laborious and not practicable in some soils.

Overall, with some limitations, the combination of the different methods to apply palm oil baits provided a good insight into the behavior of several hypogaeicly foraging species, including two sympatric *Dorylus* species. Sieve buckets showed to be especially suited for the application of oil baits. Therefore, I suggest the supplementary use of a sieve bucket grid to finally record the occurrence and approximate abundance of these cryptic species in studies of ground ant diversity.

Sociobiology of *D. laevigatus*

In Chapter 2, I presented the main biological characteristics of army ants – derived from the study of epigeaic species. Roughly following the outline of this chapter and the main questions asked in Chapter 1, I will discuss the hypogaeic behavior of *D. laevigatus* and indicate how it differed from expectation.

Occurrence and abundance

Dorylus laevigatus has been reported from most South-East Asian countries (Fig. A.27). Besides its wide distribution, I could show *D. laevigatus* to be very common and highly abundant in West-Malaysia and on Borneo. Recruiting to baits of all 15 study plots, the species occurred in habitats ranging from plantations over secondary forests to primary and montane rainforests (Table 3.1). The detected significant differences in abundances between the study plots (Chapter 4) could be related to differences in habitat, but also to taxonomic differences – if *D. laevigatus* in fact proves to be a species complex containing multiple cryptic species (Chapter 6). On average, *D. laevigatus* located 77% of the baits of a study plot (Chapters 4 and 6). The time period until the first bait was located was very short (e.g. avg. 4.6 days \pm 3.24 SD, Chapter 6), and ant abundances at baits could exceed 5000 ants per liter baited soil (Chapters 4 and 6). These data point to very high colony and forager densities within the study areas.

Along the altitudinal transect of the East Ridge of Mount Kinabalu, 74 % of litter ant species were restricted to a narrow altitudinal range (Brühl et al., 1999). Contrary, I demonstrated *D. laevigatus* to recruit to baits between 500 and 1280 m at the East Ridge and in West-Malaysia at 0 m and 250 m a.s.l. (Chapters 4 and 8). The significant change in soil composition (Malsch, 2002) and in soil moisture and temperature (unpubl. data) probably prevented an occurrence of *D. laevigatus* above the recorded altitude at the East Ridge. However, a collection of a male at 1500 m (Chapter 3) implies a possible elevated occurrence at other sites. Correspondingly, *D. nigricans* var. *molestus* was recorded at altitudes of 1828 m (Gotwald and Cunningham-van Someren, 1990) and 3000 m (C. Schöning, pers. comm.) at Mount Kenya in Africa.

The occurrence of *D. laevigatus* in diverse habitats can possibly be linked to its hypogaeic lifestyle. Within the soil, ants should be better protected from sudden changes in temperature and moisture, possibly enabling an occurrence in habitats too harsh for epigaeicly active species. Whether hypogaeic *Dorylus* species are generally able to use a wider variety of habitats than epigaeic species remains to be shown once a revision will allow the assortment of distribution data to specific species. Overall, the occurrence and abundance of *D. laevigatus* in habitats of a wide geographical and altitudinal range, varying in soil texture, moisture, and temperature (Tab. 4.1), point to the good adaptability and ecological success of the species.

Foraging behavior

Mass raids are one of the key characteristics of army ant behavior (Gotwald, 1982). Epigaeicly active species raid either in form of a column or a swarm (Schneirla, 1933, 1934, 1938), patterns, believed to be species specific (Gotwald, 1982). Generally, the reuse of old raiding trails is avoided (Franks, 1982a) and prey too large to consume or transport during a day's raid event is deserted (Pullen, 1963; Rettenmeyer, 1963). Because of this, raids of epigaeic army ants are characterized by a very localized and temporary but strong impact in a foraging area. Although some hypogaeic species occasionally come to the ground surface, where they behaved similar to predominately epigaeicly raiding species (Pullen, 1963; Rettenmeyer, 1963; Rettenmeyer et al., 1980), the hypogaeic foraging strategies of these species remained unknown. In Chapter 4, I presented the first detailed analysis of the foraging behavior of a hypogaeic army ant. Never demonstrated for epigaeic species, *D. laevigatus* established stable hypogaeic trunk trail systems, providing the ant with quick access to all regions of its foraging area. The near omnipresence *D. laevigatus* attained through this system within its foraging area was demonstrated by the high percentage of localized baits and its often predictable recruitment order to baits (Chapter 6). These observations would be unlikely if baits would have been placed in an area cropped by a few migrating colonies alternating

their raiding directions, as seen in epigaeic *Dorylus* species. Demonstrating a flexible raiding structure, *D. laevigatus* could conduct hypogaeic as well as partially epigaeic column and swarm raids (Chapter 4). Contrary to epigaeic species (Gotwald, 1982), the column raids of *D. laevigatus* were caste specific, with minor workers following existent cracks within the soil. Larger workers were recruited only when prey was located. Further differentiating it from epigaeic species, *D. laevigatus* could exploit bulky food sources, e.g. a termite mound, in a sustainable way over long periods of time. These foraging traits strongly diverge from the common view of a large mass of ants killing "almost any invertebrate that the ants can find and overcome" (Schneirla and Reyes, 1966). The use of trunk trail and long-term cropping of large food sources relate the foraging system of *D. laevigatus* to that of e.g. leaf-cutter and harvester ants (Shepherd, 1982; Howard, 2001). Only because of these "special" foraging traits could the oil-baiting method be employed this successfully. If *D. laevigatus* would forage more like epigaeic species, data additional to the species' occurrence would have been much harder to obtain; as was partially seen for the sympatric *D. cf. vishnui* (Chapter 6). The recruitment patterns and length of stay at baits within a grid can thus already tell something about the foraging strategies of other *Dorylus* species. Overall, the foraging of *D. laevigatus* implies that the spectacular raids of epigaeic species have at least partially evolved as an adaptation to their "new" habitat.

Migrating behavior

Army ants are still defined as exhibiting a unique combination of mass raiding and emigrations (Gotwald, 1995). Regular migrations were first described for epigaeically nesting, foraging, and emigrating neotropical army ant species (Schneirla, 1934, 1938). African Dorylinae, which partially raid and emigrate epigaeically but have hypogaeic nests, emigrate irregularly and much less frequently. Their stationary phases can last from a few days to several months (Raignier and Van Boven, 1955; Leroux, 1982; Gotwald and Cunningham-van Someren, 1990). Emigration frequencies of the predominately hypogaeic *Dorylus* species remain unknown. Because of the necessity to observe concealed behavior at a specific site during a very narrow time frame, emigrations of hypogaeic species have to be predicted predominately from circumstantial evidence.

By disturbing and later excavating a monitored colony, I was able to anticipate emigrations of *D. laevigatus* in the field and laboratory (Chapter 5). Soil was shifted within the soil stratum, providing no external signs of emigrations. Although *D. laevigatus* thus demonstrated its ability to move to new nesting sites when forced to do so, other colonies could stay for at least 132 days within a foraging area (Chapter 6). The high colony densities and rather stationary foraging strategy of *D. laevigatus* as well as its non-phasic brood production (Chapter 5), infer an absent or irregular emigration rhythm with long stationary periods. Considering the rather low emigration frequencies of hypogaeic and partially epigaeic army ants and the ability of numerous other ant species to emigrate recurrently (Smallwood, 1982; Maschwitz and Hänel, 1985; Byrne, 1994), the ability to emigrate does not seem to be a key characteristic of army ant behavior.

Nesting habits

As discussed in Chapter 2, nests of epigaeic as well as hypogaeic army ants are referred to as bivouacs, despite the fact that hypogaeic nests do not fit the original definition. In Chapter 5, I showed that the hypogaeic nests of *D. laevigatus* were formed by workers clinging together in a typical bivouac formation, which was suspended from a soil cavity. Since epigaeic bivouacs are also suspended and supported by objects in their environment (Gotwald, 1982) and 'bivouac' describes more a state of the colony than a particular place (Schneirla, 1971), bivouac seems to be the appropriate term also for some hypogaeic *D. laevigatus* nests.

However, being able to alter the nest form and number of cavities with local conditions, a *D. laevigatus* colony could also be dispersed onto several cavities (Chapter 5). Whether each of these cavities, containing a number of clustering workers and brood, or the compilation of cavities of a colony should be termed bivouac, remains open for discussion.

The colony and its castes

Although *D. laevigatus* is scientifically known for almost 150 years and is locally very abundant, nothing was known about colony size and composition, or worker polymorphism for this or any other hypogaecic *Dorylus* species prior to my work. With an estimated colony size of 325,000 workers, the excavated colony was much smaller than those reported for epigaeically foraging species (Vosseler, 1905; Raignier and Van Boven, 1955). Although the single excavated colony might have been young or exceptionally small due to some environmental factors, much larger colonies do not seem reasonable. With its confined hypogaecic habitat, small-scale raids, long-term use of a foraging area, and dense colony distributions, extreme colony sizes may never have gained adaptive value for *D. laevigatus*.

The morphological measurements I conducted (Chapters 5 and 6) showed small workers to be more common and to conduct more tasks in *D. laevigatus* colonies than in epigaeic species (Raignier et al., 1974; Franks, 1985). This again could be linked to *D. laevigatus*' hypogaecic habitat and foraging strategy, where small workers were able to use existent cracks and tunnels in the soil, saving the energy larger workers would need to spend on digging (Chapter 4).

Gerstäcker (1863) was the first to describe a "strange Hymenoptera", which he supposed to be a *Dorylus* queen. Although no further information about this queen or associated workers were available, Emery (1895) assumed it to be the queen of *D. laevigatus*. The queen I excavated with the *D. laevigatus* colony (Chapter 5) in fact fitted the original description of Gerstäcker (1863) and its unity with *D. laevigatus* was thus finally confirmed. Similar to the queen, the relationship between *Dorylus* males collected at light traps and *D. laevigatus* was never actually proven, but treated as if verified (Bolton, 1995). By conducting a genetic analysis, a male collected at a light trap in Sabah was shown to belong to *D. laevigatus* (Chapter 6). Finally confirmed, *D. laevigatus* is now one of five *Dorylus* species (out of a total of 61), for which all castes are known (Bolton, 1995).

Interactions of *D. laevigatus*

Closely linked to their extraordinary lifestyle, army ants interact with organisms in their environment in numerous ways. Since mass raids were believed to have a strong impact on arthropod communities (e.g. Otis et al., 1986), it is of interest which mass raiding species share a habitat, and how these species interact. Only if the prey spectrum of an army ant and its potential effect on prey communities is known can assumptions be made about its influence on local diversities. However, an army ant colony itself resembles a highly diverse organism, providing food and suitable habitats for a wide array of guests and predators (Kistner, 1979). These different levels of army ant interactions will be discussed in the following.

Interspecific army ant interactions

Dorylus laevigatus was believed to overlap in its distribution only marginally with the other three known Asian *Dorylus* species (Wilson, 1964), sharing its habitat on Borneo with *Aenictus* and *Leptogenys* army ants and mass raiding *Pheidologeton* species. Although *Aenictus* and *Leptogenys* were occasionally recorded at baits, raiding trails of *Aenictus* merely crossed a bait, while *Leptogenys* used the baiting containers as nesting sites (Chapter 8).

Fights between these species and *D. laevigatus* were never recorded. However, whenever *D. laevigatus* met with one of the two sympatric mass raiding *Pheidologeton* species at a bait or in experimental worker introductions close to a nest, interspecific fights ensued (Chapter 7). This strong reaction indicates 'enemy specification' (Hölldobler, 1977), pointing to competitive relations between the species also aside the experimental conditions. Likewise, *D. laevigatus* reacted highly aggressive toward the sympatric *Dorylus* (*Alaopone*) cf. *vishnui*, which I newly detected on Borneo (Chapter 6). Although army ants were reported to generally avoid conflicts with other army ants (e.g. Chapman, 1964), interspecific fights between the two *Dorylus* species were anticipated at baits as well as in the laboratory. By analyzing biological aspects of *D. cf. vishnui*, I showed it to be comparable to *D. laevigatus* in foraging stratum, habitat, and possibly some prey. For epigaeic species, which will emigrate to new nesting sites in the foreseeable future, it is probably energetically more efficient to avoid an aggressive conflict when occasionally meeting another army ant colony. For *D. laevigatus*, on the other hand, with its long-term use of a foraging area and high colony densities, the aggressive expulsion of a competing species from the foraging area probably has more value. Possibly reducing the competition between the two species to some extent, *D. cf. vishnui* was more likely to come to the soil surface than *D. laevigatus* (Chapter 7). These differences in stratification also fit the evolutionary implications. The ancestor of today's army ants was most likely a hypogaeicly foraging species (Gotwald, 1978). *Dorylus laevigatus*, a probably relative old *Dorylus* species (Wilson, 1964), has probably retained this hypogaeic affinity. On the other hand, *D. cf. vishnui* belongs to the more derived subgenus *Alaopone*, which might have already adapted a little more to epigaeic life.

Prey

Hypogaeic army ants were generally assumed to raid in columns and related to this, to be rather specialized predators, preying on other social insects (Gotwald, 1982). However, *D. laevigatus* had a broad food spectrum, accepting besides a wide range of invertebrates also oil, tuna, cookies, boiled rice, peanut butter, and bananas (Chapters 4, 5, and 6). Although not known to cause any crop damage, *D. laevigatus* seems likely to feed on sugar and oil-containing plant products, further increasing its interaction potentials with its environment.

The mass raids of some epigaeicly active species were shown to influence the community composition and densities of their prey species (Franks, 1982b; Franks and Bossert, 1983). Contrary, although *D. laevigatus* was shown to conduct raids in the vicinity of occupied baits (Chapter 4), its presence had only little effect on bait-surrounding arthropod communities (Chapter 7). *Dorylus laevigatus* could co-occupy a bait for several days in close vicinity to most other recorded ant species without displacing any of these species. Furthermore, the five most common ground foraging ant species demonstrated the ability to effectively avoid, kill, or even to prey on *D. laevigatus* (Chapter 7). The presence of *D. laevigatus* elicited only moderate aggressive behavior when confronted with these ants (Chapter 7), which further indicates *D. laevigatus* to be not as ferocious a predator as epigaeic species and further emphasize a decreased occurrence of similar sudden and devastating raid events.

Predators

Despite being fierce predators, epigaeic army ants are known to fall prey to a wide range of animals. These include many ant species, opportunistically overwhelming ants injured during a raid, *Oecophylla* species selectively preying on workers of a by-passing raid, and numerous amphibians, birds, and mammals (see Gotwald, 1995 for more details). Possibly to ward off this array of attackers, epigaeic army ants have some very large workers with powerful mandibles, which are predominately engaged in defensive activities (Schneirla, 1971). The absence of these large majors in *D. laevigatus* (Chapter 5) could point to the decreased

necessity to defend their hypogaeic trails from large predators. However, similar to epigaeic species, injured *D. laevigatus* workers were killed and retreated by opportunistic ant species such as *Lophomyrmex bedoti*, *Anoplolepis longipes*, and two *Pheidole* species. Since *D. laevigatus* did not leave the ground surface (Chapter 4), interactions with the mainly arboreal *Oecophylla smaragdina* are probably rare. However, similar to *Oecophylla* species (Gotwald, 1995), *Odontoponera denticulata* and *O. transversa* actively preyed on *D. laevigatus* at baits (Chapter 7). Likewise, I recorded two beetle species (*Zyras (Rhynchodonia) praedabunda* and *Trachydonia dichthadiaphila*) effectively preying on *D. laevigatus* (Chapter 9). All predations were observed at highly occupied baits or at night on epigaeic foraging trails. Since the nest locations and most foraging trails were not epigaeically apparent (Chapter 5), visually oriented predators were probably restricted to chance encounters of *D. laevigatus*, leading rather to facultative predation. Which hypogaeically foraging species commonly prey on *D. laevigatus* remains to be investigated.

Intranidal guests

Army ant nests and lifestyles provide favorable habitats for many species, resulting in a high diversity of guests and associates. The raids and middens of epigaeically active species have numerous extranidal associates (see Gotwald, 1995). Due to the difficult observations of the predominately hypogaeic trails and middens of *D. laevigatus*, I will focus the following discussion on intranidal associates. The most diverse intranidal associates of army ants are certainly mites (Acarina, Rettenmeyer, 1962) and beetles (Coleoptera: Staphylinidae, Akre and Rettenmeyer, 1968). Besides these groups, a large and diverse array of species was found, including snakes (Watkins et al., 1967) and a snail (Witte et al., 2002), just to name the most unusual. Mites were commonly associated with *D. laevigatus* in West-Malaysia and on Borneo, riding on the worker bodies or attached to brood in the nest. Unfortunately, no taxonomist works any more on myrmecophilous mites, rendering the identification of the collected mites impossible. Besides mites, seven beetle species were found to be associated with *D. laevigatus*. Six of these species, including five new species and three new genera, were associated with the excavated *D. laevigatus* nest (Chapter 9). Laboratory observations of five species demonstrated them to differ in their level of integration. The limuloid species, i.e. *Pseudolydorus linsenmairi* and *Pygoplanus subterraneus*, were most closely integrated into the colony, riding on workers during emigration peaks, causing no apparent reactions of the ants. The more elongated *Doryloxenus groveri*, and probably *D. coecus*, rode as well as walked during emigrations, partially appeasing *D. laevigatus* with their raised abdomens. The former species was also found to follow raiding columns. Laboratory observations of *Micropolemon malayensis* showed this species to be even less integrated, following an emigration column only towards its end, when traffic was light, and staying out of the ant's reach as much as possible. *Micropolemon sabahna* was not found in the excavated nest in West-Malaysia, but was detected together with *D. laevigatus* at an oil bait in Poring Hot Springs. No predatory behavior of the beetle was observed. The detection of the related *M. malayensis* in the nest implies the possibility of *M. sabahna* to be associated with a *D. laevigatus* colony as well, following its foraging columns to the bait.

Of the associated beetles, only *D. groveri* was found in West-Malaysia as well as on Borneo. However, a nest excavation on Borneo would probably reveal other species conformities. Overall, the diversity of intranidal guests found associated with *D. laevigatus* was rather low when compared to epigaeically foraging species (see Gotwald, 1995 for references). The observed higher guest diversity in epigaeic species could be related to the following circumstances:

- 1) Epigaeic trails and migrating movements increase the exposure of epigaeic colonies to potential guests, and thus their probability to enter a colony in due time (Gotwald, 1995).
- 2) Larger *Dorylus* colonies should be able to host more guests.
- 3) The extinction probability of a guest population should be smaller in larger colonies (Wilson, 1971).
- 4) The easier guest sampling from epigaeic foraging trails resulted in a larger sample size of guests, collected from different colonies and different regions.
- 5) A more careful excavation of a *D. laevigatus* nest will probably reveal additional guest species, since the conducted excavation method probably collected mainly species which stayed spatially close to the bivouac center.

Conclusions

Overall, I demonstrated that the designed baiting containers represented an effective method, finally enabling the investigation of hypogaeic ant species. A new *Dorylus* species was detected and described and several other hypogaeic species were shown to be more common than anticipated. Their role in tropical ecosystems is now open for investigation.

Throughout my study, I showed *D. laevigatus* to be a very common and abundant ant species in Malaysia. Investigating its sociobiology, I revealed that *D. laevigatus* differs in several aspects from epigaeicly foraging species and thus from the behavioral pattern predicted for army ants in general. Aside from variations expectable when comparing different species, *D. laevigatus* showed several significant differences to epigaeic species and the assumed behavior of hypogaeic ants. All of these differences could be related to some extent to the hypogaeic environment of the species. Summarizing the observed peculiarities of *D. laevigatus*, the established definition of "typical" army ant behavior and traits needs to be changed in order to be suitable also for the hypogaeic species majority.

The first insights my study permitted into the behavior of *D. laevigatus* clearly indicated its apparent importance in tropical habitats due to the following traits:

1. Its ability to quickly locate prey objects even on the soil surface, and to transfer, relocate, and eventually consume them in the ground, should essentially aid the nutrient cycling in tropical soils.
2. With its broad diet, including species with high ecological importance such as termites and earthworms (Fragoso and Lavelle, 1995; Reddy, 1995), *D. laevigatus* should influence a wide variety of soil fauna, possibly controlling population levels of tropical soils.
3. Due to its large (although for army ants rather small) colonies and high densities, the digging activities and tunnel establishment conducted by numerous foragers should substantially aerate the soil and thus further enhance nutrient cycling.

Future investigations on this and other hypogaeic (army) ant species will thus enhance our overall perception of tropical ecosystems.

Chapter 11

Possible future methods to study hypogaecic (army) ants

Oil baits applied in sieve buckets proved to be a valuable tool to study occurrence and abundance of hypogaecic ants. Supplementing this method with a variety of other methods (Chapter 3), I was able to gain first insights into numerous details of *D. laevigatus*' sociobiology. Nevertheless, especially questions concerning colony migration had to rely to a certain extent on circumstantial evidence. A method enabling to mark a number of ants large enough to recapture and, even better, to follow them, would be highly useful for future studies of hypogaecic ants. In attempting this, I conducted numerous experiments trying to mark ants at baits with different, fast-drying paints. However, even when applied as a fine mist with an air-brush pistol, the delicate joints of too many ants would have been pasted over, rendering this method neither useful nor justifiable. Furthermore, even if applied manually, which is not practicable for the large number of ants needed, every external marking of an ant quickly disappeared due to the emery paper effect of the soil. Internal marking by feeding the ants oil dyed with food colorings (red and black), were similarly futile for the use in the field. Medium and major workers were often simply too dark in color to see the dye in their gasters. Also, the presence of other food in an ant's crop could influence the color of the dye and thus impeded its identification. Only for laboratory studies, where single ants of manageable number could be observed close by, under good light conditions, and without other food in their crop, provided these internal markings a good method to assign ants to a certain sample (Chapter 6).

In trying to overcome these difficulties in marking and following hypogaecic army ants, I found radioactive labeling of the ants to be a promising method. Already successfully employed to study ants hidden from view in tree trunks (Kloft and Hölldobler, 1964; Kloft et al., 1965), I conducted some preliminary experiments to investigate the method's suitability to study hypogaecic ants. First of all, an appropriate marker for *D. laevigatus* would need to meet the following requirements:

1. Be mixable with oil and be ingestible by the ants.
2. Have an emission strong enough to detect a highly frequented ant trail through at least 10 cm of soil.
3. To be selectively detectable with a hand-held detector.
4. Not to be lethal to the ants.
5. To have a short half-life, removing it from the environment as quickly as possible.

¹³¹Iodine met all these requirements. In cooperation with the Clinic for Nuclear Medicine of the University of Würzburg, I fed sunflower oil marked with ¹³¹I to 50 *Lasius flavus* workers, which readily ingested the oil. Within an hour, a group of workers which had fed on the oil was clearly discernible in the artificial nest from another group which was not yet radioactively labeled. After 24 hours, all ants emitted β -radiation, detectable with a Mini-Monitor (Wellhöfer). Except for 13 ants, all ants were still alive after four weeks, when the radiation had fallen below the critical level. Inserting different materials between the marked ants and the detector indicated that the radiation emitted by even a few ants should be strong enough to penetrate 10 cm of soil. These encouraging results combined with the high numbers of *D. laevigatus* available for markings at baits, enable me to propose a possible experimental design (based on the experience gained through my study):

A grid containing sieve buckets with 10 m distances should be established within a study area of at least 1 ha. Baiting each sieve bucket with 20 ml palm oil and checking the baits daily should allow an approximation of *D. laevigatus*' occurrence and foraging movements within

the study area. Eventually, when the oil begins to be depleted, one of the best occupied baits at a strategic point should be selected and exchanged with a sieve bucket containing 30 ml oil mixed with 20 mCi fresh ^{131}I Iodine. This bucket should then be completely covered with a lead plate. Similar to a normal bait check, occurring *D. laevigatus* should quickly resume to feed at this bucket, starting the experiment without delay. The experimenter should now be able to follow ant trails leading away from the bait in the average depth of 10 – 15 cm by using a portable Mini-Monitor. The detector should have been coated with an extra layer of lead, except for the tip of the detection rod, to focus the absorption of α -radiation. Even if trails will be lost at some point, the accumulation of ^{131}I in the nest should render it detectable after two to three days with some searching activity.

Due to the difficulties in keeping army ant colonies in the laboratory (Chadap and Rettenmeyer, 1975), field studies are the ultimate choice when investigating these species. Taking the necessary precautions and following the legal terms, I esteem radioactive labeling with ^{131}I an elegant and effective method to come as close to direct observations of hypogaecic army ants as possible.

Chapter 12

References

- AKRE, R.D. and C.W. Rettenmeyer, 1968. Trail-following by guests of army ants (Hymenoptera: Formicidae: Ecitonini). *J. Kansas Entomol. Soc.* 41: 165-174.
- ANDERSEN, A.N., 1986. Patterns of community organization in mesic southeastern Australia. *Austr. J. Ecol.* 11: 87-97.
- BALDRIDGE, R.S., C.W. Rettenmeyer and J.F. Watkins, 1980. Seasonal, nocturnal and diurnal flight periodicities of Nearctic army ant males (Hymenoptera: Formicidae). *J. Kansas Entomol. Soc.* 53: 189-204.
- BARR, D. and W.H. Gotwald, Jr., 1982. Phenetic affinities of males of the army ant genus *Dorylus* (Hymenoptera: Formicidae: Dorylinae). *Can. J. Zool.* 60: 2652-2658.
- BARR, D., J. van Boven and W.H. Gotwald, Jr., 1985. Phenetic studies of African army ant queens of the genus *Dorylus* (Hymenoptera: Formicidae). *Syst. Entomol.* 10: 1-10.
- BASU, P., 1997. Seasonal and spatial patterns in ground foraging ants in a rain forest in the Western Ghats, India. *Biotropica* 29: 489-450.
- BECKERS, R., S. Goss, J.L. Deneubourg and J.M. Pasteels, 1989. Colony size, communication and ant foraging strategy. *Psyche* 96: 239-256.
- BEEBE, W., 1919. The home of the army ants. *Atlantic Monthly* 124: 454-464.
- BERGHOFF, S.M., A. Weissflog, K.E. Linsenmair, R. Hashim and U. Maschwitz, 2002a. Foraging of a hypogaeic army ant: a long neglected majority. *Insectes soc.* 49: 133-141.
- BERGHOFF, S.M., A. Weissflog, K.E. Linsenmair, M. Mohamed and U. Maschwitz, 2002b. Nesting habits and colony composition of the hypogaeic army ant *Dorylus (Dichthadia) laevigatus* Fr. Smith. *Insectes soc.* 49: 380-387.
- BESTELMEYER, B.T., D. Agosti, L.E. Alonso, C.R.F. Brandao, W.L. Brown, Jr., J.H.C. Delabie and R. Silvestre, 2000. Field techniques for the study of ground-dwelling ants. An overview, description, and evaluation. In: *Ants. Standard Methods for Measuring and Monitoring Biodiversity* (D. Agosti, J.D. Majer, L.E. Alonso and T.R. Schultz, Eds.), Smithsonian Institution Press, Washington and London. pp 122-144.
- BINGHAM, C.T., 1903. *The Fauna of British India, including Ceylon and Burma. Hymenoptera. Ants and Cuckoo-Wasps.* Taylor & Francis, London. 506 pp.
- BLACKWELDER, R.E., 1936. Morphology of the coleopterous family Staphylinidae. *Smithsonian Miscellaneous Collection* 13: 1-102.
- BOLTON, B., 1990. Army ants reassessed: the phylogeny and classification of the doryline section (Hymenoptera, Formicidae). *J. Nat. Hist.* 24: 1339-1364.
- BOLTON, B., 1994. *Identification Guide to the Ant Genera of the World.* Harvard University Press, London. 222 pp.
- BOLTON, B., 1995. *A New General Catalogue of the Ants of the World.* Harvard University Press, Cambridge, London. 504 pp.
- BORGMEIER, T., 1955. Die Wanderameisen der Neotropischen Region. *Stud. Ent.* 3: 1-717.
- BOSWELL, G.P., N.R. Franks and N.F. Britton, 2001. Arms races and the evolution of big fierce societies. *Proc. R. Soc. Lond. B* 268: 1723-1730.
- BRADAO, C.R.F., M. Verhaag and J.L.M. Diniz, 2002. A new ant subfamily from central Amazon soil samples. In: Proc. 14th Int. Congr. IUSSI, Sapporo, Hokkaido University. p. 159.
- BRADY, S.G., 2002. The phylogeny and biogeography of army ants (Hymenoptera: Formicidae: Aenictinae, Dorylinae, Ecitoninae). In: Proc. 14 Int. Congr. IUSSI, Sapporo, Hokkaido University. p. 156.
- BRADY, G., J. Gadau and P.S. Ward, 2000. Systematics of the ant genus *Camponotus* (Hymenoptera: Formicidae). A preliminary analysis using data from the mitochondrial gene cytochrom oxidase I. In: *Hymenoptera: Evolution, Diversity and Biological Control* (A. Austin and M. Dowton, Eds.), CSIRO Publishing, Canberra. pp. 131-139.
- BRAUNS-WILLOWMORE, J., 1901. Über die Lebensweise von *Dorylus* und *Aenictus* (Hym.). *Z. Syst. Hymenopt. Dipterol.* 1: 1-4.
- BRINKMAN, M.A., W.A. Gardner, R.M. Ipser and S.K. Diffie, 2001. Ground-dwelling ant species attracted to four food baits in Georgia. *J. Entomol. Sci.* 36: 461-463.
- BROSSET, A., 1988. Le peuplement de mammifères insectivores des forêts du Nord-Est du Gabon. *Rev. Ecol. (Terre Vie)* 43: 23-46.
- BROWN, W.L., Jr., 1973. A comparison of the Hylean and Congo-West African rain forest ant faunas. In: *Tropical Forest Ecosystems in Africa and South America: A Comparative Review* (B.J. Meggers, E.S. Ayensu and W.D. Duckworth, Eds.), Smithsonian Institution Press, Washington D.C. pp. 161-185.
- BRÜHL, C., 1996. Ameisenzönosen in einem Primärwaldgradienten am Mount Kinabalu, Borneo: Höhenverbreitung und Stratifizierung. Thesis. Würzburg, Julius-Maximilian University.

- BRÜHL, C.A., G. Gunsalam and K.E. Linsenmair, 1998. Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. *J. Trop. Ecol.* 14: 285-297.
- BRÜHL, C.A., M. Mohamed and K.E. Linsenmair, 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *J. Trop. Ecol.* 15: 265-277.
- BRÜHL, C.A., 2001. Leaf litter ant communities in tropical forests in Sabah, Malaysia: effects of disturbance and fragmentation. Thesis. Würzburg, Julius-Maximilian University. 168 pp.
- BURTON, J.L. and N.R. Franks, 1985. The foraging ecology of the army ant *Eciton rapax*: an ergonomic enigma? *Ecol. Entomol.* 10: 131-141.
- BYRNE, M.M., 1994. Ecology of twig-dwelling ants in a wet lowland tropical forest. *Biotropica* 26: 61-72.
- CAMPIONE, B.M., J.A. Novak and W.H. Gotwald, Jr., 1983. Taxonomy and morphology of the West African army ant, *Aenictus asantei* n. sp. (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* 76: 873-883.
- CHADAP, R. and C.O. Rettenmeyer, 1975. Mass recruitment by army ants. *Science* 188: 1124-1125.
- CHAPMAN, J.W., 1964. Studies on the ecology of the army ants of the Philippines genus *Aenictus* Schuckard (Hymenoptera: Formicidae). *Philippine J. Sci.* 93: 551-592.
- DARLINGTON, J.P.E.C., 1985. Attacks by doryline ants and termite nest defense (Hymenoptera; Formicidae; Isoptera; Termitidae). *Sociobiology* 11: 189-200.
- DELABIE, J.H.C., B.L. Fisher, J.D. Majer and I.W. Wright, 2000. Sampling effort and choice of methods. In: *Ants. Standard Methods for Measuring and Monitoring Biodiversity* (D. Agosti, J.D. Majer, L.E. Alonso and T.R. Schultz, Eds.), Smithsonian Institution Press Washington and London. pp. 145-154.
- DELABIE, J.H.C. and H.G. Fowler, 1990. Cryptic species assemblages in tropical and temperate latitudes. In: *Proc. 11th Int. Congr. IUSSI: Social Insects and the Environment*. Oxford & IBH Publ. Co. Pvt. Ltd, New Delhi. pp. 695-696.
- DELABIE, J.H.C. and H.G. Fowler, 1995. Soil litter and cryptic ant assemblages of Bahian cocoa plantations. *Pedobiologia* 39: 423-433.
- DROUAL, R., 1984. Anti-predator behavior in the ant *Pheidole desertorum*: the importance of multiple nests. *Anim. Behav.* 32: 1054-1058.
- EISNER, T., 1957. A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). *Bull. Mus. Comp. Zool.* 116: 437-490.
- EMERY, C., 1887a. Catalogo delle Formiche esistenti nelle collezioni del Museo Civico di Genova. *Ann. Mus. Civ. Genova* 5: 427-473.
- EMERY, C., 1887b. Le tre forme sessuali del *Dorylus helvolus* L. e degli altri Dorilidi. *Boll. Soc. Entomol. Ital.* 19: 344-351.
- EMERY, C., 1895a. Viaggio di Leonardo Fea in Birmania e regioni vicine. *Ann. Mus. Civ. Stor. Nat. Genova* 14: 450-483.
- EMERY, C., 1895b. Die Gattung *Dorylus* Fab. und die systematische Eintheilung der Formiciden. *Zool. Jahrbücher. Abt. Syst., Geogr. Biol. Tiere* 8: 685-778.
- EMERY, C., 1901a. Studi sul polimorfismo e la metamorfosi del genere *Dorylus*. *Mem. R. Accad. Sci. Inst. Bologna* 5: 183-201.
- EMERY, C., 1901b. Formiciden von Celebes. *Zool. Jahrbücher Abt. Syst. Geogr. Biol. Tiere* 14: 565-580.
- FAUVEL, A., 1899. Genres et espèces de Staphylinides nouveaux d'Afrique. III. Sur une Tribu nouvelle Staphylinides (Pygostenini) et descriptions de genres et espèces. *Rev. Entomol.* 18: 1-44.
- FINKE, M.D., 2002. Complete nutrient composition of commercially raised invertebrate used as food for insectivores. *Zoo Biology* 21: 269-285.
- FLOREN, A. and K.E. Linsenmair, 1997. Diversity and recolonization dynamics of selected arthropod groups on different tree species in a lowland rainforest in Sabah, Malaysia with special reference to Formicidae. In: *Canopy Arthropods* (N.E. Stork, J. Adis and R.K. Didham, Eds.), Chapman & Hall, London. pp. 344-381.
- FOREL, A., 1901. Les Formicides de L'empire des Indes et de Ceylan. *J. Bombay Nat. Hist. Soc.* 13: 462-477.
- FOREL, A., 1909. Ameisen aus Java und Krakatau. Beobachtet und gesammelt von Herrn Edward Jacobson – Systematischer Theil. *Notes Leyden Mus.* 31: 221-232.
- FOREL, A., 1914. Wissenschaftliche Ergebnisse einer Forschungsreise nach Ostindien, ausgeführt im Auftrag der Kgl. Preuß Akademie der Wissenschaften zu Berlin von H. v. Buttel-Reepen. II Ameisen aus Sumatra, Java, Malacca und Ceylon. *Zool. Jahrbücher Abt. Syst. Geogr. Biol. Tiere* 36: 1-148.
- FOWLER, H.G., 1979. Notes on *Labidus praedator* (Fr. Smith) in Paraguay (Hymenoptera: Formicidae: Dorylinae: Ecitonini). *J. Nat. Hist.* 13: 3-10.
- FRAGOSO, C. and P. Lavelle, 1995. Are earthworms important in the decomposition of tropical litter? In: *Soil Organisms and Litter Decomposition in the Tropics* (M.V. Reddy, Ed.), Westview Press, Boulder, San Francisco, Oxford. pp. 103-112.
- FRANKS, N., 1982a. Ecology and population regulation in the army ant *Eciton burchelli*. In: *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes* (E.G. Leigh, A.S. Rand and D.M. Windsor, Eds.), Smithsonian Institution Press, Washington D.C. pp. 389-395.

- FRANKS, N.R., 1982b. Social Insects in the aftermath of swarm raids of the army ant *Eciton burchelli*. In: *The Biology of Social Insects* (M.D. Breed, C.D. Michener and H.E. Evans, Eds.), Westview Press, Boulder, Colorado. pp. 275-279.
- FRANKS, N.R., 1985. Reproduction, foraging efficiency and worker polymorphism in army ants. In: *Sinauer Associates Experimental Behavioral Ecology and Sociobiology: in Memoriam Karl von Frisch, 1886-1982* (B. Hölldobler and M. Lindauer, Eds.), G. Fischer Verlag, Sunderland, Stuttgart. pp. 91-107.
- FRANKS, N.R., 1989. Thermoregulation in army ant bivouacs. *Physiol. Entomol.* 14: 397-404.
- FRANKS, N.R. and W.H. Bossert, 1983. The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. In: *Tropical Rain Forest: Ecology and Management* (N.R. Franks and W.H. Bossert, Eds.), Blackwell, Oxford. pp. 151-163.
- FRANKS, N.R. and C.R. Fletcher, 1983. Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behav. Ecol. Sociobiol.* 12: 261-270.
- FRANKS, N.R., N. Gomez, S. Goss and J.L. Deneubourg, 1991. The blind leading the blind in army ant raid patterns: testing a model of self-organization (Hymenoptera: Formicidae). *J. Insect Behav.* 4: 583-607.
- GADAU, J., J. Heinze, B. Hölldobler and M. Schmid, 1996. Population and colony structure of the carpenter ant, *Camponotus floridanus*. *Mol. Ecol.* 5: 785-792.
- GERSTÄCKER, A., 1863. Ueber ein merkwürdiges neues Hymenopteron aus der Abteilung der Aculeata. *Entomol. Z.* 24: 76-93.
- GOTWALD, W.H., 1974a. Foraging behavior of *Anomma* driver ants in Ghana cocoa farms (Hymenoptera: Formicidae). *Bull. de l'I. F. A. N.* 36: 705-713.
- GOTWALD, W.H., 1974b. Predatory behavior and food preferences of driver ants in selected African habitats. *Ann. Entomol. Soc. Am.* 67: 877-886.
- GOTWALD, W.H., Jr., 1977. The origins and dispersal of army ants of the subfamily Dorylinae. In: Proc. Int. Congr. IUSI (H.H.W. Velthuis and J.T. Wiebes, Eds.), Centre for Agricultural Publishing and Documentation, Wageningen. pp. 126-127.
- GOTWALD, W.H., Jr., 1978a. Emigration behavior of the East African driver ant: *Dorylus (Anomma) molesta* Gerstaecker (Hymenoptera: Formicidae: Dorylinae). *J. N.Y. Entomol. Soc.* 86: 290.
- GOTWALD, W.H., Jr., 1978b. Trophic ecology and adaptation in tropical old world ants of the subfamily Dorylinae (Hymenoptera: Formicidae). *Biotropica* 10: 161-169.
- GOTWALD, W.H., Jr., 1979. Phylogenetic implications of army ant zoogeography (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* 72: 462-467.
- GOTWALD, W.H., Jr., 1982. Army ants. In: *Social Insects*. Volume 4 (W.H. Gotwald, Jr., Ed.), Academic Press, New York. pp. 157-254.
- GOTWALD, W.H., Jr., 1995. *Army ants: the biology of social predation*. Ithaca, Cornell University Press / Comstock Press.
- GOTWALD, W.H., Jr., 2002. Taxonomic revision of the army ant genus *Dorylus*: the subgenera - to be or not to be? In: Proc. 14 Int. Congr. IUSI, Sapporo, Hokkaido University. p. 169.
- GOTWALD, W.H., Jr. and G.R. Cunningham-Van Someren, 1976. Taxonomic and behavioral notes on the African ant, *Aenictus eugenii*, Emery, with a description of the queen (Hymenoptera: Formicidae). *J. N.Y. Entomol. Soc.* 84: 182-188.
- GRANT, S. and V.C. Moran, 1986. The effects of foraging ants on arboreal insect herbivores in an undisturbed woodland savanna. *Ecol. Entomol.* 11: 83-93.
- GREENSLADE, P.J.M., 1973. Sampling ants with pitfall traps: digging-in effects. *Insectes soc.* 20: 343-353.
- HADDOW, A.J., I.H.H. Yarrow, G.A. Lancaster and P.S. Corbet, 1966. Nocturnal flight cycle in the males of African doryline ants (Hymenoptera: Formicidae). *Proc. R. Ent. Soc. Lond. (A)* 41: 103-106.
- HIROSAWA, H., S. Higashi and M. Mohamed, 2000. Food habits of *Aenictus* army ants and their effects on the ant community in a rain forest of Borneo. *Insectes soc.* 47: 42-49.
- HÖLLDOBLER, B., 1974. Home range orientation and territoriality in harvesting ants. *Proc. Nat. Acad. Sci.* 71: 3274-3277.
- HÖLLDOBLER, B., 1979. Territories of the African weaver ant (*Oecophylla longinoda* [Latreille]). *Z. Tierpsychol.* 51: 201-213.
- HÖLLDOBLER, B., 1986. Konkurrenzverhalten und Territorialität in Ameisenpopulationen. In: *Chemische Ökologie Territorialität Gegenseitige Verständigung* (Information Processing in Animals), (T. Eisner, B. Hölldobler and M. Lindauer, Eds.), Gustav Fischer Verlag, New York. pp. 25-70.
- HÖLLDOBLER, B. and E.O. Wilson, 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge. 732 pp.
- HOLLINGSWORTH, M.J., 1960. Studies on the polymorphic workers of the army ant *Dorylus (Anomma) nigricans* Illiger. *Insectes soc.* 7: 17-37.
- HOWARD, J., 2001. Costs of trail construction and maintenance in the leaf-cutting ant *Atta columbica*. *Behav. Ecol. Sociobiol.* 49: 348-356.

- INAOKA T., G. Okubo, M. Yokota and M. Takemasa, 1999. Nutritive value of house fly larvae and pupae fed on chicken feces as food sources for poultry. *Japan. Poultry Sci.* 36: 174-180.
- ITO F., S. Yamane, K. Eguchi, W.A. Noerdjito, S. Kahono, K. Tsuji, K. Ohkawara, K. Yamauchi, T. Nishida and K. Nakamura, 2001. Ant species diversity in the Bogor Botanic Garden, West Java, Indonesia, with descriptions of two new species of the genus *Leptanilla* (Hymenoptera, Formicidae). *Tropics* 10: 379-404.
- JACKSON, W.B., 1957. Microclimatic patterns in the army ant bivouac. *Ecology* 38: 276-285.
- JACOBSON, H.R. and D.H. Kistner, 1975. The natural history of the myrmecophilous tribe Pygostenini (Coleoptera: Staphylinidae). Section 11. New species and new records of Pygostenini. *Sociobiology* 1: 163-200.
- JACOBSON, H.R. and D.H. Kistner, 1980. The natural history of the myrmecophilous tribe Pygostenini (Coleoptera: Staphylinidae) Section 8. The phylogeny of the Pygostenini. *Sociobiology* 5: 307-324.
- JORDANO, P., 2000. Fruits and Frugivory. In: *Seeds. The Ecology and Regeneration in Plant Communities* (M. Fenner, Ed.), CABI Publishing, New York. pp. 125-165.
- KISTNER, D.H., 1958. The evolution of the Pygostenini (Coleoptera Staphylinidae). *Ann. Mus. R. Congo Belge* 68: 1-198.
- KISTNER, D.H., 1975. A review of the myrmecophiles associated with *Aenictus* in Africa and the Orient (Coleoptera; Hymenoptera: Formicidae) with notes on their behavior and glands. *Sociobiology* 1: 20-73.
- KISTNER, D.H., 1979. Social and evolutionary significance of social insect symbionts. In: *Social Insects* Vol. 1 (H.R. Hermann, Ed.) Academic Press, New York. pp. 339-413.
- KISTNER, D.H., 1993. Cladistic analysis, taxonomic restructuring and revision of the Old World genera formerly classified as Dorylomimini with comments on their evolution and behavior. *Sociobiology* 22: 147-383.
- KISTNER, D.H. and H.R. Jacobson, 1977. The natural history of the myrmecophilous tribe Pygostenini (Coleoptera: Staphylinidae). Section 5. Ultrastructure of the Pygostenini. *Sociobiology* 3: 39-66.
- KISTNER, D.H., A. Weissflog, K. Rosciszewski and U. Maschwitz, 1997. New species, new genera, and new records of myrmecophiles associated with army ants (*Aenictus* sp.) with the description of a new subtribe of Staphylinidae (Coleoptera; Formicidae: Aenictinae). *Sociobiology* 29:121-221.
- KITAYAMA, K., 1992. An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetation* 102: 149-171.
- KITAYAMA, K., 1996. Climate of the summit region of Mount Kinabalu (Borneo) in 1992, an El Nino year. *Mountain Res. Develop.* 16: 65-75.
- KLOFT, W. and B. Hölldobler, 1964. Untersuchungen zur forstlichen Bedeutung der holzerstörenden Roßameise unter Verwendung der Tracer-Methode. *Anz. Schädlingskunde* 37: 163-169.
- KLOFT, W., B. Hölldobler and A. Haisch, 1965. Traceruntersuchungen zur Abgrenzung von Nestarealen holzerstörender Rossameisen (*Camponotus herculeanus* L. und *C. ligniperda* Latr.). *Ent. Exp. Appl.* 8: 20-26.
- KÖHLER, W., G. Schachtel and P. Voleske, 1996. *Biostatistik - Einführung in die Biometrie für Biologen und Agrarwissenschaftler*. Springer Verlag, Berlin. 285 pp.
- KORB, J. and K.E. Linsenmair, 1999. Reproductive success of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) in two neighbouring habitats. *Oecologia* 118: 183-191.
- LAMON, B. and H. Topoff, 1981. Avoiding predation by army ants: defensive behaviours of three ant species of the genus *Camponotus*. *Anim. Behav.* 29: 1070-1081.
- LAST, H., 1977. New species of *Zyras* from Africa. *Rev. Zool. Afric.* 91: 913-954.
- LEROUX, J.R., 1977. Densité des colonies et observations sur les nids des dorylines *Anomma nigricans* Illiger (Hym. Formicidae) dans la région de Lamto (Cote d'Ivoire). *Bull. Soc. Zool. France* 102: 51-62.
- LEROUX, J.M., 1979. Sur quelques modalités de disparition des colonies d'*Anomma nigricans* Illiger (Formicidae Dorylinae) dans la région de Lamto (Cote D'Ivoire). *Insectes soc.* 26: 93-100.
- LEROUX, J.M., 1982. Ecologie des populations de dorylines *Anomma nigricans* Illiger (Hym. Formicidae) dans la région de Lamto (Cote d'Ivoire). Paris, Ecole Normale Supérieure.
- MALSCH A.K.F. 2002. Kausale Faktoren für die Abnahme der Artenvielfalt von Ameisen - Untersuchung entlang eines Höhengradienten am Mt. Kinabalu, Sabah, Malaysia. Thesis. Frankfurt, Johann Wolfgang Goethe University.
- MARCEVIZ, S., 1979. Some consequences of Fisher's sex ratio principle for social Hymenoptera that reproduce by colony fission. *Am. Nat.* 113: 363-371.
- MASCHWITZ, U. and H. Hänel, 1985. The migrating herdsman *Dolichoderus (Diabolus) cuspidatus*: an ant with a novel mode of life. *Behav. Ecol. Sociobiol.* 17: 174-184.
- MASCHWITZ, U., S. Steghaus-Kovac, R. Gaube and H.H. Hänel, 1989. A South East Asian ponerine ant of the genus *Leptogenys* (Hym., Form.) with army ant life habits. *Behav. Ecol. Sociobiol.* 24: 305-316.
- MASUKO, K., 1987. *Leptanilla japonica*: the first bionomic information on the enigmatic ant subfamily Leptanillinae. In: *Chemistry and Biology of Social Insects* (J. Eder and H. Rembold, Eds.), Peperny Verlag, Munich. pp. 597-598.
- MENOZZI, C., 1927. Zur Kenntnis des Weibchens von *Dorylus (Anomma) nigricans* var. *molesta* Gerst. (Hymenoptera-Formicidae). *Zool. Anz.* 70: 263-266.

- MIRENDA, J.T., D.G. Eakins, K. Gravelle and H. Topoff, 1980. Predatory behavior and prey selection by army ants in a desert-grassland habitat. *Behav. Ecol. Sociobiol.* 7: 119-127.
- MOFFETT, M.W., 1984. Swarm raiding in a myrmicine ant. *Naturwissenschaften* 71: 588-590.
- MOFFETT, M.W., 1986. Marauders of the jungle floor. *National Geographic* 170: 273-286.
- MOFFETT, M.W., 1987. Ants that go with the flow: a new method of orientation by mass communication. *Naturwissenschaften* 74: 551-553.
- MOFFETT, M.W., 1988a. Foraging behavior in the Malayan swarm-raiding ant *Pheidologeton silenus* (Hymenoptera: Formicidae: Myrmicinae). *Ann. Entomol. Soc. Am.* 81: 356-361.
- MOFFETT, M.W., 1988b. Foraging dynamics in the group-hunting myrmicine ant, *Pheidologeton diversus*. *J. Insect Behav.* 1: 309-331.
- MOHAMED M., A. Hussein and A. Kadri, 1996. Terrestrial ants (Formicidae: Hymenoptera) of Poring, Kinabalu Park, Sabah. In: *Tropical Rainforest Research - Current Issues* (D.S. Edwards, W. E. Booth and S.C. Choy, Eds.), Kluwer Academic Press, Netherlands. pp. 117-123.
- NEWTON, A.F. and M.K. Thayer, 1992. Current classification and family-group names in Staphyliniformia (Coleoptera). *Fieldiana: Zoology* 67: iv +1-92.
- OLSON, D.M., 1991. A comparison of the efficacy of litter sifting and pitfall traps for sampling leaf litter ants (Hymenoptera, Formicidae) in a tropical wet forest, Costa Rica. *Biotropica* 23: 166-172.
- OTIS, G.W., E.C. Santana, D.L. Crawford and M.L. Higgins, 1986. The effect of foraging army ants on leaf-litter arthropods. *Biotropica* 18: 56-61.
- PACE, R., 1998. Aleocharinae della Cina: Parte IV (Coleoptera, Staphylinidae). *Rev. Suisse Zool.* 105: 911-982.
- PACE, R. 1999. Aleocharinae di Hong Kong (Coleoptera, Staphylinidae) (151° contributo alla conoscenza delle Aleocharinae). *Rev. Suisse Zool.* 106: 663-689.
- PERFECTO, I., 1992. Observations of a *Labidus coecus* (Latreille) underground raid in the central highlands of Costa Rica. *Psyche* 99: 214-220.
- PETAL, J., 1978. The role of ants in ecosystems. In: *Production Ecology of Ants and Termites* (V. Brian, Eds.), Cambridge University Press, Cambridge. pp. 293-321.
- PULLEN, B.E., 1963. Termitophagy, myrmecophagy, and the evolution of the Dorylinae (Hymenoptera, Formicidae). *Studia Ent.* 6: 405-414.
- QUINET, Y., J.C. de Biseau and J.M. Pasteels, 1997. Food recruitment as a component of the trunk-trail foraging behavior of *Lasius fuliginosus* (Hymenoptera: Formicidae). *Behav. Proc.* 40: 75-83.
- QUIROZ-ROBLEDO, L. and J. Valenzuela-González, 1995. A comparison of ground ant communities in a tropical rainforest and adjacent grassland in Los Tuxtlas, Veracruz, Mexico. *Southwestern Entomologist* 20: 203-213.
- RABELING, C. and M. Verhaag, 2002. Erste Erfahrungen mit Palmöl als Köder zum Fang bodenbewohnender Ameisen in Amazonien (Formicidae). In: *Beitr. Hymenopt.-Tagung, Stuttgart*. pp. 58-59.
- RAIGNIER, A., 1972. Sur l'origine des nouvelles sociétés des fourmis voyageuses Africaines (Hymenopteres Formicidae, Dorylinae). *Insectes soc.* 19: 153-170.
- RAIGNIER, A. and J. van Boven 1955. Étude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera Formicidae). *Ann. Mus. R. Congo Belge* 2: 1-284.
- RAIGNIER, A., J.K.A. van Boven and R. Ceusters, 1974. Der Polymorphismus der afrikanischen Wanderameisen unter biometrischen und biologischen Gesichtspunkten. In: *Sozialpolymorphismus bei Insekten* (G.H. Schmidt, Ed.), Wissenschaftliche Verlagsgesellschaft MBH., Stuttgart. pp. 668-693.
- REDDY, M.V., 1995. Litter arthropods. In: *Soil Organisms and Litter Decomposition in the Tropics* (M.V. Reddy, Ed.), Westview Press, Boulder, San Francisco, Oxford. pp. 113-140.
- RETTENMEYER, C.W., 1962. The diversity of arthropods found with Neotropical army ants and observations on the behavior of representative species. *Proc. Entomol. Soc. Am. N. Cent. Br.* 17: 14-15.
- RETTENMEYER, C.W., 1963. Behavioral studies of army ants. *Univ. Kansas Sci. Bull.* 44: 281-465.
- RETTENMEYER, C.W., R. Chadab-Crepet, M.G. Naumann and L. Morales, 1980. Comparative foraging by Neotropical army ants. In: *Social Insects in the Tropics* (P. Jaisson, Ed.), Université Paris-Nord, Cocoyoc, Morelos. pp. 59-73.
- RETTENMEYER, C.W., H. Topoff and J. Mirenda, 1978. Queen retinues of army ants. *Ann. Entomol. Soc. Am.* 71: 519-528.
- REY, Claudius 1886. Description de deux genres nouveaux de Tachyporiens. *Rev. Entomol.* 5: 252-256.
- ROBERTS, D.L., R.J. Cooper and L.J. Petit, 2000. Use of premontane moist forest and shade coffee agroecosystems by army ants in western Panama. *Conserv. Biol.* 14: 192-199.
- ROONWAL, M.L., 1972. Plant-pest status of root-eating ant, *Dorylus orientalis*, with notes on taxonomy, distribution and habits (Insecta: Hymenoptera). *J. Bombay Nat. Hist. Soc.* 72: 305-313.
- ROSCISZEWSKI, K., 1995. Die Ameisenfauna eines tropischen Tieflandregenwaldes in Südostasien: Eine faunistisch-ökologische Bestandsaufnahme. Thesis. Frankfurt, Johann Wolfgang Goethe University.
- ROSCISZEWSKI, K. and U. Maschwitz, 1994. Prey specialization of army ants of the genus *Aenictus* in Malaysia. *Andrias* 13: 179-187.

- SAVAGE, T.S., 1847. On the habits of “drivers” or visiting ants of West Africa. *Trans. Entomol. Soc. London* 5: 1-15.
- SAVAGE, T.S., 1849. The driver ants of Western Africa. *Proc. Acad. Nat. Sci. Philadelphia* 4: 195-200.
- SCHNEIRLA, T.C., 1933. Studies on army ants in Panama. *J. Comp. Psychol.* 15: 267-299.
- SCHNEIRLA, T.C., 1934. Raiding and other outstanding phenomena in the behavior of army ants. *Proc. Natl. Acad. Sci. U.S.A.* 20: 316-321.
- SCHNEIRLA, T.C., 1938. A theory of army-ant behavior based upon the analysis of activities in a representative species. *J. Comp. Psychol.* 25: 51-90.
- SCHNEIRLA, T.C., 1945. The army-ant behavior pattern: nomad-statory relations in the swarmers and the problem of migration. *Biol. Bull.* 88: 166-193.
- SCHNEIRLA, T.C., 1957. Theoretical considerations of cyclic processes in Doryline ants. *Proc. Am. Phil. Soc.* 101: 106-133.
- SCHNEIRLA, T.C., 1958. The behavior and biology of certain Nearctic army ants last part of the functional season Southeastern Arizona. *Insectes soc.* 5: 215-255.
- SCHNEIRLA, T.C., 1963. The behaviour and biology of certain nearctic army ants: springtime resurgence of cyclic function - southeastern Arizona. *Anim. Behav.* 11: 583-595.
- SCHNEIRLA, T.C., 1971. *Army Ants. A Study in Social Organization*. W.H. Freeman, San Francisco. 349 pp.
- SCHNEIRLA, T.C., R.Z. Brown and F.C. Brown, 1954. The bivouac or temporary nest as an adaptive factor in certain terrestrial species of army ants. *Ecol. Monographs* 24: 269-296.
- SCHNEIRLA, T.C. and A.Y. Reyes, 1966. Raiding and related behaviour in two surface-adapted species of the old world doryline ant, *Aenictus*. *Anim. Behav.* 14: 132-148.
- SCHNEIRLA, T.C. and A.Y. Reyes, 1969. Emigrations and related behaviour in two surface-adapted species of the old-world doryline ant *Aenictus*. *Anim. Behav.* 17: 87-103.
- SEEVERS, C.H., 1953. Two new genera of myrmecophilous Staphylinidae from the Philippines. *Philippine J. Sci.* 81: 125-132.
- SHARP, D. and F. Muir, 1912. The comparative anatomy of the male genital tube in Coleoptera. *Trans. Entomol. Soc. London Part III (December)*, reprinted by the *Entomol. Soc. Am.* 1969.
- SHEPHERD, J.D., 1982. Trunk trails and the searching strategy of a leaf-cutter ant, *Atta colombica*. *Behav. Ecol. Sociobiol.* 11: 77-84.
- SHOWER, J.A. and D.H. Kistner, 1976. The natural history of the myrmecophilous tribe Pygostenini (Coleoptera: Staphylinidae). Section 4. Glandular anatomy of the Pygostenini. *Sociobiology* 2: 305-321.
- SHUCKHARD, 1840. Appendix to Mr. Shuckhard’s monograph of the Dorylidae, containing a description of two new species of *Labidus*. *Ann. Nat. Hist.* 5: 396-398.
- SIMON, C., F. Frati, A. Bechenbach, B. Crespi, H. Liu and P. Flook, 1994. Evolution, weighting, and the phylogenetic utility of mitochondrial gene sequences and a compilation of conserved chain reaction primers. *Ann. Entomol. Soc. Am.* 87: 651-701.
- SMALLWOOD, J., 1982. Nest relocation in ants. *Insectes soc.* 29: 138-147.
- SMITH, F., 1857. Catalogue of the Hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A.R. Wallace. *J. Linn. Soc. London* 2: 42-89.
- STRASBURGER E., F. Noll, H. Schenk and A.F.W. Schimper, 1991. *Lehrbuch der Botanik für Hochschulen*. Gustav Fischer Verlag, Stuttgart, Jena, New York. 1030 pp.
- SWOFFORD, D.L., 2002. “PAUP”, *Phylogenetic Analysis Using Parsimony (and Other Methods)*, Version 4.0b10”. Sinauer Associates, Sunderland, Massachusetts.
- TAFURI, J.F., 1955. Growth and polymorphism in the larva of the army ant (*Eciton (E.) hamatum* Fabricius) *J. N.Y. Entomol. Soc.* 63: 21-41.
- TAYLOR, R.W., 1965. A monographic revision of the rare tropicopolitan ant genus *Probolomyrmex* Mayr (Hymenoptera: Formicidae). *Trans. R. Entomol. Soc. London* 117: 345-365.
- TOBIN, J.E., 1995. Ecology and diversity of tropical forest canopy ants. In: *Forest Canopies* (M.D. Lowman and N.M. Nadkari, Eds.), Academic Press Inc., San Diego. pp. 129-147.
- TOPOFF, H., 1971. Polymorphism in army ants related to division of labor and colony cyclic behavior. *Am. Naturalist* 105: 529-548.
- TOPOFF, H. and J. Mirenda, 1980. Army ants do not eat and run: influence on food supply on emigration behaviour in *Neivamyrmex nigrescens*. *Anim. Behav.* 28: 1040-1045.
- TOPOFF, H., H. Mirenda, R. Droual and S. Herrick, 1980. Behavioral ecology of mass recruitment in the army ant *Neivamyrmex nigrescens*. *Anim. Behav.* 28: 779-789.
- TOTTENHAM, C.E., 1955. Variation in the male secondary characters of three African species of *Zyras* Stephens (Coleoptera: Staphylinidae). *Proc. R. Entomol. Soc. London* 30: 151-154.
- VERHAAGH, M., 1990. The Formicidae of the rain forest in Panguana, Peru: The most diverse local ant fauna ever recorded. Proc. 11th Int. Congr. IUSSI: *Social insects and the environment*. Oxford & IBH Publishing, New Delhi. pp. 217-218.

- VORIS, H.K., 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *J. Biogeography* 27: 1153-1167.
- VOSELER, J., 1905. Die ostafrikanische Treiberameise (Siafu). *Der Pflanze* 19: 289-302.
- WASMANN, E., 1916. Neue dorylophile Staphyliniden Afrikas (Col.). *Entomol. Mitteilungen* 5: 92-109, 134-147, + 1 plate.
- WATKINS, J.F. II, F.R. Gehlbach and R.S. Baldrige, 1967. Ability of the blind snake, *Leptotyphlops dulcis*, to follow pheromone trails of army ants, *Neivamyrmex nigrescens* and *N. opacithorax*. *Southwest Naturalist* 12: 455-462.
- WEISSFLOG, A., E. Sternheim, W.H.O. Dorow, S. Berghoff and U. Maschwitz, 2000. How to study subterranean army ants: a novel method for locating and monitoring field populations in the South East Asian army ant *Dorylus (Dichthadia) laevigatus* Smith, 1857 (Formicidae, Dorylinae) with observations on their ecology. *Insectes soc.* 47: 317-324.
- WESTWOOD, J.O., 1835. *Proc. Zool. Soc. Lond.* 3: 72.
- WHEELER, G.C. and J. Wheeler, 1986a. Ten-year supplement to "ant larvae: review and synthesis". *Proc. Entomol. Soc. Wash.* 88: 684-702.
- WHEELER, G.C., 1943. The larvae of army ants. *Ann. Entomol. Soc. Am.* 36: 319-332.
- WHEELER, G.C. and J. Wheeler, 1964. The ant larvae of the subfamily Dorylinae: supplement *Proc. Entomol. Soc. Wash.* 66: 129-137.
- WHEELER, G.C. and J. Wheeler, 1974. Ant larvae of the subfamily Dorylinae: second supplement (Hymenoptera: Formicidae). *J. Kansas Entomol. Soc.* 47: 166-172.
- WHEELER, G.C. and J. Wheeler, 1984. The larvae of the army ants (Hymenoptera: Formicidae): a revision. *J. Kansas Entomol. Soc.* 57: 263-275.
- WHEELER, G.C. and J. Wheeler, 1986b. Young larvae of *Eciton* (Hymenoptera: Formicidae: Dorylinae). *Psyche* 93: 341-349.
- WHEELER, W.M., 1913. Zoological records of the Arbor expedition, 1911-12. Hymenoptera, II: ants (Formicidae). *Rec. Indian Mus.* 9: 233-237.
- WILSON, E.O., 1953. The origin and evolution of polymorphism in ants. *Q. Rev. Biol.* 28: 136-156.
- WILSON, E.O., 1958. The beginnings of nomadic and group-predatory behavior in ponerine ants. *Evolution* 12: 24-36.
- WILSON, E.O., 1964. The true army ants of the Indo-Australian area (Hymenoptera: Formicidae: Dorylinae). *Pacific Insects* 6: 427-483.
- WILSON, E.O., 1971. *The insect societies*. The Belknap Press of Harvard University, Cambridge, Mass. 548 pp.
- WILSON, E.O., 1975. Enemy specification in the alarm-recruitment system of an ant. *Science* 190: 798-800.
- WITTE, V., 2001. Organisation und Steuerung des Treiberameisenverhaltens bei südostasiatischen Ponerinen der Gattung *Leptogenys*. Biologie und Informatik. Frankfurt, Johann Wolfgang Goethe Universität Frankfurt am Main. 239 pp.
- WITTE, V. and U. Maschwitz, 2000. Raiding and emigration dynamics in the ponerine army ant *Leptogenys distinguenda* (Hymenoptera, Formicidae). *Insectes soc.* 47: 76-83.
- WITTE, V., R. Janssen, A. Eppenstein and U. Maschwitz, 2002. *Allopeas myrmekophilos* (Gastropoda, Pulmonata), the first myrmecophilous mollusc living in colonies of the Ponerine army ant *Leptogenys distinguenda* (Formicidae, Ponerinae). *Insectes soc.* 49: 301-305.
- XU, Z., T. Liu, Y. He and G. Zeng, 1999. A comparative study on the ant communities in primeval and secondary forests of four vegetation subtypes in Xishuangbanna of China. *Zool. Research* 20: 360-364.

Appendix A

Asian Dorylinae – a guide to morphology and distribution

The Dorylinae subfamily being in the strong need of a taxonomic revision, even the most common *Dorylus* species can not be identified unequivocally (see Chapter 6). Of the 61 described *Dorylus* species (Bolton, 1995), a species key exist only for the four Asian species (Wilson, 1964). These species, i.e. *D. (Alaopone) vishnui*, *D. (A.) orientalis*, *D. (Typhlopone) labiatus*, and *D. (Dichthadia) laevigatus*, represent three of the six *Dorylus* subgenera. A species' allocation to a certain subgenus, five of which will probably be elevated to genus level (Gotwald, 2002), is relatively easy (e.g. with the key of Gotwald, 1982). However, for species identifications Wilson's key (1964) showed to be futile due to the following reasons:

1. A main key characteristic is the number of antennal segments (AS). *Dorylus laevigatus* workers are stated to have 10 to 12 AS. However, I could show that *D. laevigatus* range in AS between 8 and 12 (Chapter 5). Furthermore, the number of AS varies for *D. vishnui* between the original description (Wheeler, 1913) and Wilson's key (i.e. eight to nine segments) – although both base on the analysis of the same individuals.
2. The description of morphological characters are partially incomplete in the key and, for *D. vishnui*, based on only a single collection of a dozen workers. Since the characteristic morphological traits can vary greatly with worker size, species identifications should focus on major workers, guaranteeing a comparable analyses. Large worker samples are thus needed to estimate worker size variability and to collect major workers.
3. Distribution ranges are given for each species. However, the detection of *D. cf. vishnui* on Borneo and the expected discovery of other hypogaecic species by employing the oil-baiting method, obscure the believed distribution patterns. Likewise, the difficult species identifications most probably resulted in numerous wrong species denominations.

To omit the difficulties caused by the variation in AS and the size-related change of prominent morphological characters, I propose to collect large worker samples to obtain an estimation of size variability and to call upon only the largest workers for species identifications. The number of collected workers and the main body measurements (Chapters 5 and 6) of the analyzed specimen used to characterize the species should be given to allow comparisons of other authors.

Following this proposition, I provide the requested data for the two study species, i.e. *D. (D.) laevigatus* and *D. (A.) cf. vishnui* in the following. Supplementary to Chapter 5, I present some additional data for the castes of the *D. laevigatus* colony. To relate the study species to the third Asian subgenus (or probably third genus, according to Gotwald, 2002), I included the corresponding description of *D. (T.) labiatus*, collected with the same method in Jordanian. Furthermore, for comparative reasons, some biological data and approximate distribution maps are provided for all four Asian *Dorylus* species. Distribution maps were derived by noting a species' detection from the literature and extrapolating the vegetation information of these locations to a possible overall occurrence map.

Abbreviations of body measurements are as defined in Chapter 5, the morphological terminology follows Bolton (1995).

Dorylus (Dichthadia) laevigatus

Dorylus laevigatus Smith (1857). *J. Linn. Soc. Lond.* 2: 70, worker. Type locality: Sarawak, Borneo.

Overall, I analyzed morphological traits of 520 *D. laevigatus* workers collected from West-Malaysia and Sabah. Workers were collected from a nest, six different baits (= different colonies), and five raiding trails. An overview of morphological ranges is given in Chapters 5 and 6. General morphology of the castes are represented by Figures A.1 – A.5 (major worker), A.6 – A.8 (minor worker), A.9 – A.11 (queen), A.12 – A.14 (male), and A.15 – A.17 (brood sample).

Workers were highly polymorphic (see Chapter 5). Mandibular dentition and number of antennal segments varied between heaviest and lightest worker. However, by sorting according to these traits, workers could be arranged in a continuous series.

DIAGNOSIS OF HEAVIEST (DW) WORKER (Code: 9)

DW: 5.754 mg, L: 9.30 mm, HW: 1.95 mm, HL: 1.80 mm, HTL: 1.35 mm, PnW: 1.20 mm, AtL: 2.30 mm, PtW: 0.85 mm, AS: 12.

Few stout hairs are found on the anterior clypeal margin, mandibles, petiole, subpetiolar process, sternites, and last two tergites (Fig. A.1 – A.5). Pubescence fine, short, and not very abundant. Petiole trapezoid in dorsal view (Fig. A.1) and approximately round in profile (Fig. A.2 and A.3). Subpetiolar process pointed posteriorly, and with acute angle at anterior margin (Fig. A.3). Mandibles linear, without subapical teeth (Fig. A.4). Frontal lobes closely approximate but do not reach the anterior clypeal margin, which is concave (Fig. A.4). Head approximately square, with a slightly concave occipital margin (Fig. A.5). Pygidial impression without well defined margins, with a single spine on each side. Color reddish-brown.



1 mm

Fig. A.1 *D. laevigatus* major worker



1 mm

Fig. A.2. Major worker side view



1 mm

Fig. A.3. Petiole of major worker



1 mm

Fig. A.4. Frontal lobes



1 mm

Fig. A. 5. Head of major worker

DIAGNOSIS OF LIGHTEST (DW) WORKER (Code: 88)

Due to the variation of morphological characters with worker size, *Dorylus* minor workers can not be assigned unequivocally to different species according to their morphology. Only general features of a *D. laevigatus* minor worker are thus given in Figures A.6 – A.8 to

illustrate the worker variability within the species. For this reason, data corresponding to the major worker are provided for the smallest worker in the following.

DW: 0.048 mg, L: 2.25 mm, HW: 0.48 mm, HL: 0.58 mm, HTL: 0.35 mm, PnW: 0.33 mm, AtL: 0.65 mm, PtW: 0.23 mm, AS: 8.

The whole body covered with short hairs (Fig. A.6 – A.8). Pubescence fine and short. Petiole oval in dorsal view (Fig. A.6) and round in profile (Fig. A.7). Subpetiolar process slender, without protruding angles. Mandibles elongated with two subapical teeth. Intercalary found between first and second subapical tooth and the basal margin of mandible. Frontal lobes do not reach the anterior clypeal margin, which is strongly convex. Head approximately square, with a slightly concave occipital margin (Fig. A.8). Pygidial impression without well defined margins, with a single spine on each side. Color yellowish.



Fig. A.6. *D. laevigatus* minor worker



Fig. A.7. Minor worker side view

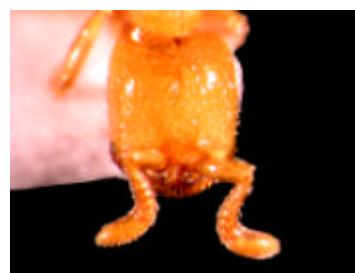


Fig. A.8. Head of minor worker

DIAGNOSIS OF QUEEN

DW: 71.7 mg, L: 28.00 mm, HW: 4.60 mm, HL: 4.05 mm, HTL: 2.05 mm, PnW: 2.50 mm, AtL: 5.15 mm, PtW: 4.10 mm, AS: 12.

Few hairs are found only on the anterior clypeal margin and the mandibles. Pubescence absent. Petiole as in Fig. 5.3 and A.9. Mandibles linear, without subapical teeth. Frontal lobes far apart, lining the posterior clypeal margin, which is approximately straight. Head near square, with a strong median impression, connecting the concave occipital margin of the head and the posterior clypeus margin (Fig. A.11). Color reddish-brown.



Fig. A.9. *D. laevigatus* queen



Fig. A.10. Queen side view

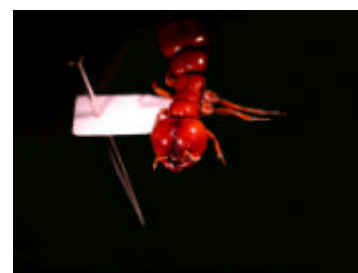


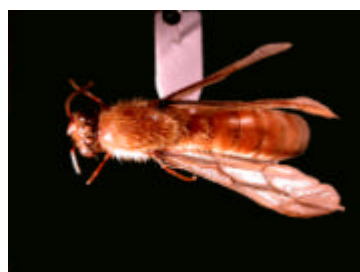
Fig. A.11. Head of queen

DIAGNOSIS OF MALES

Although males are stated as known for *D. laevigatus* (Bolton, 1995), a male was never collected together with workers. The association of *Dorylus* males collected at light traps within the Sunda Shelf and *D. laevigatus* was based merely on the fact that no other *Dorylus* species was known from the region. The discovery of *D. cf. vishnui* on Borneo made this assumption uncertain. Conducting a genetic analysis, we finally verified the assumed association (Chapter 6).

L: 24.65 mm, HW: 4.30 mm, HL: 1.90 mm, HTL: 2.40 mm, PnW: 3.30 mm, AtL: 6.35 mm, PtW: 2.45 mm, AS: 13.

Compared to the workers, the queen and male are similar in size. Although a little smaller than the queen, the alitrunk of the male is larger, probably due to the contained muscles of the wings. Its whole body is densely covered with hair (Fig. A.12 and A.13). Compared to the body, the legs look rather feeble (Fig. A.13) and seem not well suited to walk long distances. In comparison to the queen, the head of the male is rather small. The large compound eyes make up about half of its head (Fig. A.14). Three ocelli are found on the top of the head. The mandibles have a single subapical tooth and curved inward (Fig. A.14).



10 mm
Fig. A.12. *D. laevigatus* male



10 mm
Fig. A.13. Male side view

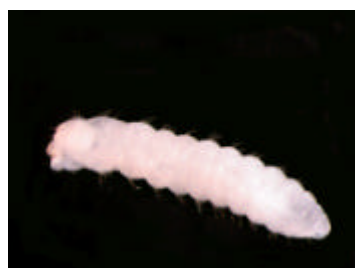


10 mm
Fig. A.14. Head of male

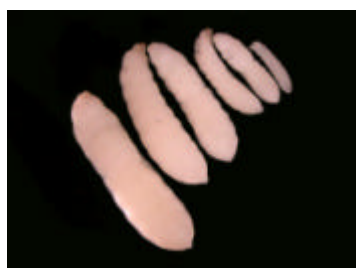
Males resemble the night-active wasp *Provespa nocturna*, which is very common in Malaysia and feared for its powerful sting. Further increasing this resemblance, *D. laevigatus* males move their abdomen when caught as if trying to sting (J.Beck, pers. comm.). Only an experienced biologist will not let go of a male at this time. This possible mimicry could provide some protection for males from nocturnal predators.

DIAGNOSIS OF BROOD

Excavated together with the nest (Chapter 5), brood was reported for the first time for *D. laevigatus*. Brood of all developmental stages occurred simultaneously (Fig. A.16 and A.17), pointing to a non-phasic brood production. Larvae were discernible by their distinct segmentation and protruding setae (Fig. A.15). Due to the lack of a cocoon in *Dorylus* army ants, old larvae were often difficult to discriminate from young pupae – Figure A.16 shows from top right to lower left alternating a larva and a pupa. The strong variation in worker and thus in brood sizes rendered the allocation of larval sizes to a certain developmental stage impossible.



1 mm
Fig. A.15. Young larva



1 mm
Fig. A.16. Larvae and young pupae of different subcastes and ages



1 mm
Fig. A.17. Pupae

RELATIONSHIPS AND BIOGEOGRAPHY

Dorylus laevigatus is the only known member of the subgenus *Dichthadia*, which probably will be elevated to genus status (Gotwald, 2002). Due to the primitive number of antennal segments in large workers (i.e. 12), and lacking other prominent apomorph traits, Wilson (1964) assumed it to be a relatively primitively *Dorylus* species. Combined with its distribution (Fig. A.18), this might hint to an early immigration into Asia (20 Ma), a colonization of the islands of the Sunda Shelf during the glacial periods of the Quaternary,

and a displacement from the rest of Asia possibly by on-following *Dorylus* species or climatic changes during the Quaternary.



Figure A.18. Proposed distribution of *D. laevigatus*. Black circles represent literature and own collection sites. The shaded area encompasses a proposed distributional area, derived from the extrapolation of vegetation data. The question-mark on Sulawesi indicates the uncertain site allocation (refer to text for more information).

Dorylus laevigatus has been reported from Myanmar, Thailand, Malaysia (Peninsular Malaysia and Borneo), Indonesia (Java, Sumatra, and Sulawesi) (Fig. A.18). The single worker collection from Sulawesi (Emery, 1901), is marked with a question-mark in Figure A.18, since even the most recent studies of Quaternary sea levels did not indicate the existence of a past land-connection between Sulawesi and Borneo or Java (Voris, 2000). Due to the distributional limitations of Dorylinae, i.e. the need of a wingless (hypogaecic) queen to move along with a large number of associated workers, render already small rivers impassable barriers (Brown, 1973). A verification of the Sulawesi collection would therefore strongly point to a past land-connection between Sulawesi and the Sunda Shelf.

Dorylus (Alaopone) cf. vishnui

Dorylus vishnui Wheeler (1913). *Rec. Ind. Mus.* 9: 233, worker. Type locality: Mulmein, lower Myanmar.

Dorylus vishnui was only once collected (Wheeler, 1913). Due to the imprecision of the species key discussed above, the species I detected on Borneo was termed *D. cf. vishnui* until a revision elucidates its status.

Overall, I measured morphological traits of 54 *D. cf. vishnui* workers collected in Poring Hot Springs, Sabah. Workers were collected from five different baits (= different colonies). An overview of morphological ranges is given in Chapter 6. Figures A.19 – A.23 illustrate the morphology of a major worker.

Workers varied continuously in size. Mandibular dentition varied only slightly and number of antennal segments not at all between the heaviest and lightest worker.

DIAGNOSIS OF HEAVIEST (DW) WORKER (Code: 565)

DW: 5.117 mg, L: 9.45 mm, HW: 2.05 mm, HL: 2.45 mm, HTL: 1.80 mm, PnW: 1.15 mm, AtL: 2.70 mm, PtW: 0.75 mm, AS: 9.

Few stout hairs are found on the anterior clypeal margin, mandibles, petiole, subpetiolar process, sternites, and last tergite (Fig. A.19 – A.23). Pubescence fine, short, and not very abundant. Petiole rectangular in dorsal view and profile (Fig. A.19 – A.21). Subpetiolar process bulged antero-ventrally, with a pointed anterior and translucent ventral margin (Fig.

A.21). Mandibles elongated with two subapical teeth (Fig. A.22). A diastema found between apical and first subapical tooth, four denticles between the first and second subapical teeth. Frontal lobes do not reach the anterior clypeal margin, which is slightly concave (Fig. A.22). Head rectangular, with a strongly concave occipital margin (Fig. A.23). Pygidial impression with well defined margins, with a pair of spines on each side. Color reddish-brown.



Fig. A.19. *D. cf. vishnui*



Fig. A.20. Major worker side view



Fig. A.21. Petiole of major worker



Fig. A.22. Frontal lobes



Fig. A.23. Head of major worker

DIAGNOSIS OF LIGHTEST (DW) WORKER (Code: 492)

For the same reasons given for the description of the small *D. laevigatus* worker, the lightest *D. cf. vishnui* worker will be characterized in the following.

DW: 0.148 mg, L: 3.10 mm, HW: 0.65 mm, HL: 0.75 mm, HTL: 0.50 mm, PnW: 0.38 mm, AtL: 0.80 mm, PtW: 0.25 mm, AS: 9.

The whole body covered with short hairs. Pubescence fine and short. Petiole rectangular in dorsal view and approximately round in profile. Subpetiolar process slender, elongated, and rectangular, with a slightly crenulated ventral margin. Mandibles elongated with one subapical tooth and a final denticle. Intercalary found between the subapical tooth and the denticle. Frontal lobes do not reach the anterior clypeal margin, which is approximately straight. Head slightly rectangular, with a slightly concave occipital margin. Pygidial impression with well defined margins, with a simple spine on each side. Color reddish-brown.

OTHER CASTES

The queen, males, and brood of *D. vishnui* remain undetected.

RELATIONSHIPS AND BIOGEOGRAPHY

Dorylus vishnui has retained some ancestral morphological traits and might represent a relict of an early *Alaopone* invasion into Asia (Wilson, 1964). Similar to *D. laevigatus*, *D. cf. vishnui* probably colonized Borneo during the glacial periods of the Quaternary.

Due to the uncertain relationship between *D. vishnui* and *D. cf. vishnui*, the collection site of the former species is marked with a question-mark in Figure A.24. *Dorylus cf. vishnui* was collected on Borneo; from Poring Hot Springs, Sabah (own collection) and from the Bako National Park, Sarawak by W. Dorow (Fig. A.24). If it is identical with *D. vishnui*, it should have a distribution similar to *D. laevigatus* (Fig. A.18).

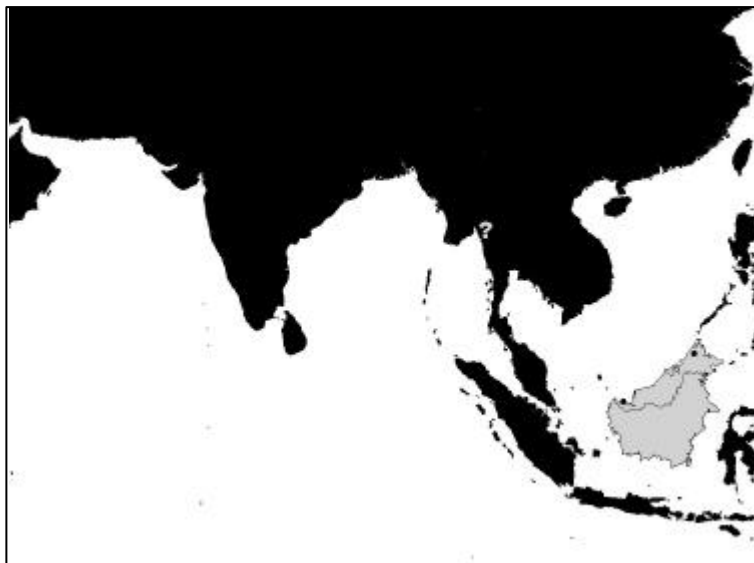


Figure A.24. Proposed distribution of *D. cf. vishnui*. Black circles represent the collection sites of W. Dorow and myself. The question-mark in Myanmar indicates the collection site of the original species, i.e. *D. vishnui*. The shaded area encompasses a proposed distributional area, of *D. cf. vishnui*, derived from the extrapolation of vegetation data.

Dorylus (Typhlopone) labiatus

Dorylus labiatus Schuckhard (1840). *Ann. Mag. Nat. Hist.* 5: 319, male. Type locality: India. Forel, (1901). *J. Bombay Nat. Hist. Soc.* 13: 464, worker.

Employing the palm oil baiting method described in this thesis, my student helper N. Karbek distributed 10 soil baits (Fig. 3.3) in a date palm plantation near Amman, Jordanian. Already within the first 24 hours, *D. labiatus* recruited to two of these baits. Out of a collection of 78 workers, I selected and measured the heaviest (DW 4.110 mg) and the lightest worker (DW 0.220 mg). For the reasons discussed above, only the measures of the heaviest worker are provided in the following (Fig. A.25 – A.29).

No disjunction in worker sizes was perceivable in the collected sample. Mandibular dentition varied only slightly and number of antennal segments not at all between the heaviest and the lightest worker.

DIAGNOSIS OF HEAVIEST (DW) WORKER (Code: 576)

DW: 4.110 mg, L: 8.55 mm, HW: 1.65 mm, HL: 2.10 mm, HTL: 1.35 mm, PnW: 1.10 mm, AtL: 2.15 mm, PtW: 0.63 mm, AS: 11.

Few stout hairs are found on the anterior clypeal margin, mandibles, subpetiolar process, sternites, and last tergite (Fig. A.25 – A.29). Pubescence fine, short, and more dense than in the previous species. Petiole trapezoid in dorsal view (Fig. A.25) and approximately square in profile (Fig. A.26 and A.27). Subpetiolar process wedge-shaped, with a translucent ventral margin (Fig. A.27). Mandibles elongated with a subapical tooth and one denticle (Fig. A.28). Frontal lobes overhang the anterior clypeal margin, which is approximately straight (Fig. A.28). Head rectangular, with a nearly straight occipital margin (Fig. A.29). Pygidial impression without well defined margins, with a single spine on each side. Color reddish-brown.



1 mm
Fig. A.25. *D. cf. labiatus*



1 mm
Fig. A.26. Major worker side view



1 mm
Fig. A.27. Petiole of major worker



1 mm
Fig. A.28. Frontal lobes



1 mm
Fig. A.29. Head of major worker

OTHER CASTES

The queen and brood of *D. labiatus* remain unknown. Since no *D. labiatus* nest has ever been excavated, nor have males been collected together with workers, the association of collected males remain uncertain.

RELATIONSHIPS AND BIOGEOGRAPHY

Dorylus labiatus is very similar and probably identical to *D. fulvus* (Wilson, 1964), which has been collected from Africa, the middle East, and some Mediterranean countries (Bolton, 1995). If this identity is confirmed, *D. labiatus* would represent a connecting link between the Asian and African *Dorylus* populations. Aside from our Jordanian collection, *D. labiatus* has been collected throughout most of India (Fig. A.30). Possibly occurring in Asia only as far westward as India, it might have emigrated rather recently from Africa to Asia, possibly partially displacing the earlier immigrated *D. laevigatus* and *D. vishnui*.



Figure A.30. Proposed distribution of *D. labiatus*. Black circles represent collection sites from the literature. The shaded area encompasses a proposed distributional area, derived from the extrapolation of vegetation data.

Dorylus (Alaopone) orientalis

Dorylus orientalis Westwood (1835). *Proc. Zool. Soc. Lond.* 3: 72, male. Type locality: India. Forel, (1901). *J. Bombay Nat. Hist. Soc.* 13: 463, worker.

Of the four known Asian *Dorylus* species, *D. orientalis* is the only species noted recurrently in the literature, due to its habit of regularly including plants into its diet, rendering it a serious crop pest in some areas (e.g. Roonwal, 1972). Nevertheless, despite the high attention *D. orientalis* has obtained in comparison to other hypogaecic Asian *Dorylus* species, the biology of this species is as little known as of *D. laevigatus* and *D. cf. vishnui* prior to my work. No nest excavation has been reported and queen and brood remain unknown. Likewise, males were never collected together with workers, rendering their association with *D. orientalis* uncertain.

RELATIONSHIPS AND BIOGEOGRAPHY

Showing more derived morphological characters than the other known Asian *Alaopone* species, i.e. *D. vishnui*, *D. orientalis* might have immigrated later into Asia than *D. vishnui* (Wilson, 1964). A later immigration could also explain the absence of *D. orientalis* from the sundaic region (Fig. A.31), the islands of which could have been reached only during the glacial periods of the Quaternary. Being the most widespread Asian *Dorylus* species, *D. orientalis* was reported from China, Nepal, north to central India, Sri Lanka, and south-west as far as lower Myanmar (Fig. A.31).

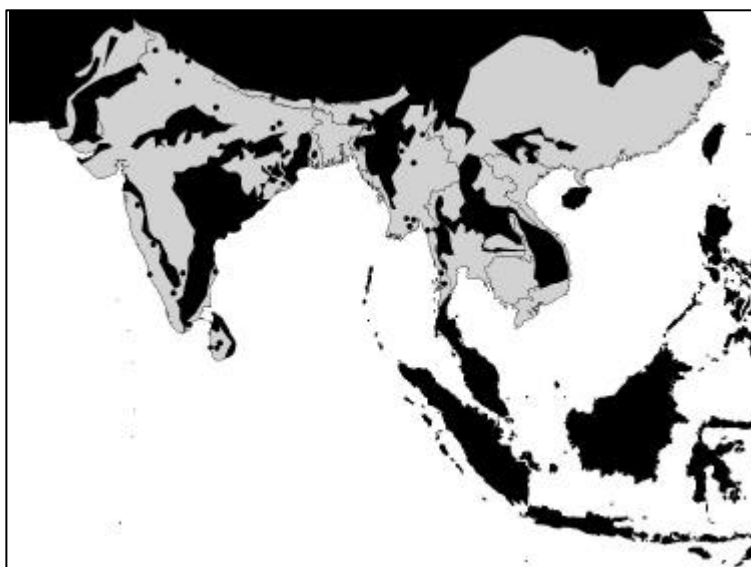


Figure A. 31. Proposed distribution of *D. orientalis*. Black circles represent collection sites from the literature. The shaded area encompasses a proposed distributional area, derived from the extrapolation of vegetation data.

Appendix B

Curriculum vitae

Personal Data

NAME Stefanie Maria Berghoff
 DATE OF BIRTH March 09. 1973
 PLACE OF BIRTH Heessen (Westf.), Germany
 CITIZENSHIP German

Education

School

08/1979 – 01/1980 Johannes-Schule Soest
 02/1980 – 06/1983 Grundschule Aurich-Sandhorst
 08/1983 – 07/1985 Orientierungsstufe Sandhorst, Aurich
 08/1985 – 06/1988 Realschule Aurich
 10/1988 – 07/1990 Irvin High School, El Paso, Texas (USA)
 07/1990 High School Diploma
 08/1990 – 05/1992 Undergraduate student at the University of Texas at El Paso (USA)
 05/1992 German Abitur

University

10/1992 – 03/1995 Undergraduate student at the University of Giessen
 03/1995 'Pre-diploma' in General Biology
 05/1995 – 03/1998 Undergraduate student at the University of Wuerzburg
 03/1998 M.Sc. in Biology (Majors: Tropical Zoology, Biochemistry, Biological
 Pharmaceutics)
 THESIS TITLE: 'Structuring mechanisms of an arboreal ant community in
 Sabah, Malaysia, Borneo'.

Graduate studies

07/1998 – 08/1999 Research project of the University of Wuerzburg and the Smithsonian
 Tropical Research Institute in Wuerzburg and BCI (Panama)
 RESEARCH TITLE: 'The influence of the myrmecophytic epiphyte
Caularthron bilamellatum (Orchidaceae) on the arboreal ant
 communities of *Annona glabra* (Annonaceae) in Panama'.

Ph.D. studies

11/1999 – Ph.D. student at the University of Wuerzburg
 THESIS TITLE: 'Sociobiology of the hypogaeic army ant *Dorylus*
(Dichthadia) laevigatus Fr. Smith'.

List of publications

WEISSFLOG, A., E. Sternheim, W.H.O. Dorow, S. Berghoff and U. Maschwitz, 2000. How to study subterranean army ants: a novel method for locating and monitoring field populations in the South East Asian army ant *Dorylus (Dichthadia) laevigatus* Smith, 1857 (Formicidae, Dorylinae) with observations on their biology. *Insectes sociaux* 47: 317-324.

BERGHOFF, S.M., A. Weissflog, K.E. Linsenmair and U. Maschwitz, 2001. How to solve the enigma of subterranean ants: Foraging movements and trail systems of a hypogaeic army ant. In: Proceedings of the 2001 Berlin Meeting of the European Sections of IUSSI (R. Menzel & E. Rademacher, Eds.), IUSSI. pp. 6.

BERGHOFF, S.M., A. Weissflog, K.E. Linsenmair and U. Maschwitz, 2002. Foraging of a hypogaeic army ant: a long neglected majority. *Insectes sociaux* 49: 133-141.

BERGHOFF, S.M., A. Weissflog, K.E. Linsenmair and U. Maschwitz, 2002. Nesting habits and colony composition of the hypogaeic army ant *Dorylus (Dichthadia) laevigatus* Fr. Smith. *Insectes sociaux* 49: 380-387.

KISTNER, D.H., S.M. Berghoff and U. Maschwitz, 2003. Myrmecophilous Staphylinidae (Coleoptera) associated with *Dorylus (Dichthadia) laevigatus* (Hymenoptera: Formicidae) in Malaysia with studies of their behavior. *Sociobiology* 41: 209-264.

BERGHOFF, S.M., J. Gadau, T. Winter, K.E. Linsenmair and U. Maschwitz (in press - *Insectes sociaux* 50). Sociobiology of hypogaeic army ants: characterization of two sympatric *Dorylus* species on Borneo and their colony conflicts.

BERGHOFF, S.M., U. Maschwitz and K.E. Linsenmair 2003. Influence of the hypogaeic army ant *Dorylus (Dichthadia) laevigatus* on tropical arthropod communities. *Oecologia* 135: 149-157.

BERGHOFF, S.M., U. Maschwitz and K.E. Linsenmair (submitted - *Tropical zoology*). Baited sieve buckets: an easy method to include hypogaeic ant species into ground ant diversity studies.

BERGHOFF, S.M., G. Zotz and K.E. Linsenmair (submitted - *Journal of Tropical Ecology*). The ant community on *Annona glabra*: its composition and interactions with an epiphytic orchid.

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Erklärung

gemäß § 4 Abs. 3 Ziff. 3, 5 und 8
der Promotionsordnung der Fakultät für Biologie der
Bayerischen Julius-Maximilians-Universität Würzburg

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation selbstständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Die Dissertation wurde bisher weder vollständig noch teilweise einer anderen Hochschule mit dem Ziel, einen akademischen Grad zu erwerben, vorgelegt.

Am 13. März 1998 wurde mir von der Universität Würzburg der akademische Grad "Diplom-Biologin Univ." verliehen. Weitere akademische Grade habe ich weder erworben noch versucht zu erwerben.

Würzburg, den 12. Dezember 2002