Ecology, biogeography and responses to habitat degradation of a highly diverse rainforest ant community and taxonomy of Afrotropical *Pheidole* Westwood (Hymenoptera, Formicidae)

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Chapter 4:

Taxonomy of the ant genus *Pheidole* Westwood (Hymenoptera, Formicidae) in the Afrotropical zoogeographic region: definition of species groups and systematic revision of the *Pheidole pulchella* group

G. Fischer, F. Hita Garcia and M. K. Peters - Zootaxa, in review

Summary

Natural ecosystems around the world are increasingly impacted by human disturbances, the most severe being deforestation, climate change and introduction of invasive species. Yet, there is a growing scientific and public understanding of the link between our own survival and the conservation of intact environments, stable ecosystems and of biodiversity in general. Despite that knowledge and several initiatives to stop the further destruction of vulnerable species-rich habitats, the pressures of growing human populations and globalization are counteracting our best intentions. One dilemma of the scientific community is that the number of species currently existing cannot even be estimated within an order of magnitude, much less so the amount of species currently endangered or already extinguished by human activities. Still, some hope is left to protect a great proportion of the biological diversity and global conservation efforts are relatively high. The question is if they will be enough? This cannot easily be answered and is one reason why long-term solutions must be found to protect larger areas of natural habitats sustainably. Therefore it is also necessary to recognize areas with increased diversity levels, as for example many tropical rainforests.

This thesis is largely based on an intensive inventory of the Kakamega Forest ant fauna and the surrounding agricultural area in Western Kenya. For the updated species checklist ant material was used that was collected during the BIOTA East Africa project, and before, altogether between the years 1999 and 2010. All material is located in the two Hymenoptera collections of the Zoological Research Museum Alexander Koenig in Bonn, Germany, and the Natural History Museum in Los Angeles, USA. Additional species records for the Kakamega Forest in the scientific literature were included and available ecological niche data was used for an analysis of the relationships between the known biogeographical distributions and niche properties of the ant community. Although the forest, with an area of about 11,000 ha, is comparatively small, in parts highly disturbed and situated in a relatively high altitude of around 1650 m a.s.l., the checklist now comprises an astonishing 329 ant species in 55 genera and 11 subfamilies. This currently represents the highest ant diversity for the whole Afrotropical region, which is also by far the highest for a mid-altitudinal locality above 1500 m a.s.l. worldwide. Also it needs to be mentioned that the inventory was one of the most intensive yet published studies in terms of processed individuals, which were more than 150,000 ants in total.

Of the 329 species, 227 were identified to species level; the rest was not identifiable due to mostly unresolved taxonomies for several genera and probably a high amount of undescribed species. It turned out that half of the identified ants (113 species) were elements of the Congo-Guinean rainforest system and that most of them relied completely on forest habitats and could not be found outside of the forest borders. On the other hand about 30 % (99 species) of the ant community consists of purely open habitat species that are found in the farmland, but also in grasslands, alongside roads and in other clearings inside the forest. These habitats are clearly dominated by more widespread taxa, especially by species with Afrotropical distributions and by others that probably originated in East African / South African open or woodland habitats. About 15 % of all species (49) were habitat generalists and occurred in both habitat types. Chi-square tests revealed highly significant relationships between the three different ecological niche variables (habitat, microhabitat, and feeding type), and between them and species distributions, except feeding type, which was only marginally significantly associated with biogeographical distribution class. This combined analyses for ecological and biogeographical data showed that ant species distributions and ecological niches are forming a strong relationship with each other and that this characterizes a diverse ant community more detailed than either of them alone would.

Another ecological analysis for the ground ant communities in three different habitats along an anthropogenic disturbance gradient provided a detailed comparison of the species diversity, functional diversity and community compositions in response to land-use intensification. The total of 21 study sites was divided with eight sites in the forest, seven sites in low-intensity subsistence agriculture in the highly populated matrix surrounding the forest, and six study sites in intensified sugarcane agriculture, which were located in two large sugar company monocultures in the vicinity of the forest. For the functional diversity analyses morphometric measures of ecologically important body structures, such as mandibles, legs and eyes, and trophic position in the food web (measured via stable isotope analysis for 84 species). The results of a highly significant and positive relationship between species and functional diversity are corroborating similar results of most other studies. Both, species diversity and functional diversity indices decreased along the degradation gradient. While the first decreased between 20 and 40 % on average, the values for the latter in the intensive sugarcane agriculture were up to 53 % lower than in the forest. Especially the proportions of predatory species in the farmland ant communities was about half as high (48 %) than in the forest, which in theory should lead to decreased food chain lengths in the farmland. These were determined with the positions of the predator on the highest level in the food web, and function as an estimate of the influence of human disturbances on the hight and complexity of the respective food web. And indeed the trophic chain lengths were significantly and about half (48 %) a trophic level shorter in the subsistence sugarcane sites and also some of the intensive sites revealed very low values. But, on average, the trophic chain lengths were higher in intensive sugarcane than in the subsistence agriculture and not significantly different from those in the forest. One explanation for the high chain length variability in the intensive sugarcane production sites could be the use of chemical fertilizers. Higher plant net production rates might explain the longer food chains. But this hypothesis would need to be verified with experiments.

An additional baiting experiment with fly larvae to measure the ecosystem function scavenging, conducted in 5 study sites in each of the three habitats, found that the scavenging rates in the farmland were significantly higher (plus 57 %) than in the forest. They were however positively associated with higher ant activities at baits in the farmland, which decreased significantly with growing species richness. This seems to contradict the other results of the ants' functional diversity. But it can be explained by the dominance and high abundance of a few opportunistic species (especially *Myrmicaria* and *Camponotus*) in the farmland, which were relatively large (compared to the majority of forest species) and had high activity-levels during the day. A single worker could easily carry a mid-sized larva away, in contrast to many of the abundant forest species, which first had to recruit their nest mates.

The world of the ants is highly fascinating in its complexity, because of their eusocial biology and an enormous ecological diversity and importance for the stability of natural and anthropogenically modified ecosystems. One genus seems to be especially dominant and species-rich. With more than 1000 species distributed worldwide members of the genus *Pheidole* can be found in almost every habitat and microhabitat, occupying a large variety of ecological niches and functions. Many of them are seed harvesters and dispersers, highly competitive scavengers and opportunists, and some are also predators of other invertebrates. However, the taxonomy of this genus is in a relatively poor state, especially in the Afrotropical region, which is due to mostly old and inadequate descriptions and the complete lack of identification keys. But, also because of the chaos of still valid, yet sometimes synonymic described subspecies and varieties. That is why *Pheidole* ants in African inventories and ecological studies are mostly unidentifiable and thus cannot be used for any larger-scale analyses. My goal here is to start the process of a modern taxonomic treatment and revisions for the African fauna, with a description of the *Pheidole pulchella* species group, which is distributed in forest ecosystems along the Equatorial rainforest belt. With fresh material from Kenya, Uganda and Tanzania and museum specimens from the Hymenoptera collections of the

Natural History Museum in London, Uk, and the California Academy of Sciences, San Francisco, USA, I was able to describe seven new and to revise four previously described species, which all together seem to form a group of closely related sister taxa. This part of my work also includes a general overview of taxonomically important morphological characters for the Afrotropical *Pheidole* fauna, as well as the preliminary definition of five other species groups, based on a relatively large amount of examined type specimens from different museum collections and unidentified material that has been collected from several localities in Africa. I am providing an illustrated identification key to all species of the *pulchella* group for the two very distinct worker castes, as well as high focal depth images and morphometric measurements for all revised taxa. This combination will enable researchers and other myrmecologically interested persons to identify material of the species belonging to this group.

Zusammenfassung

Überall auf der Erde werden natürliche Ökosysteme in steigendem Ausmaße von menschlichen Störungen beeinflußt und verändert, zu den schlimmsten Faktoren gehören dabei Entwaldung, Klimaveränderungen und eingeschleppte Arten. Doch es gibt ein steigendes Bewußtsein in der Wissenschaft und Öffentlichkeit für den Zusammenhang von unserem eigenen Überleben und dem Erhalt einer intakten Umwelt, stabilen Ökosystemen und der biologischen Vielfalt im allgemeinen. Trotz dessen und mehreren Initiativen um den weiteren Verlust von empfindlichen und artenreichen Lebensräumen zu verhindern, wirkt der Druck einer weiter wachsenden Bevölkerung und Globalisierung dagegen. Ein Dilemma der Wissenschaft ist das fehlende Wissen über tatsächliche Größenordnung in der sich die Anzahl der existierenden Arten bewegt, geschweige denn darüber wie viele davon gefährdet oder bereits ausgestorben sind. Dennoch gibt es Hoffnung für den Erhalt eines Großteils der biologischen Diversität und die globalen Anstrengungen für entsprechende Schutzmaßnahmen sind hoch. Die Frage ist, ob diese auch hoch genug sein werden? Das kann nicht leicht beantwortet werden und ist ein Grund, warum Langzeitlösungen gefunden werden müssen, um größere Flächen natürlicher Lebensräume nachhaltig zu beschützen. Dafür ist es auch nötig die Gebiete mit erhöhter Artenvielfalt festzustellen, wie es beispielsweise bei tropischen Regenwäldern allgemein der Fall ist.

Diese Dissertation beruht zum großen Teil auf einer intensiven Inventarisierung der Ameisenfauna des Kakamega Forest und der umgebenden Agrarlandschaft im Westen Kenias. Für die aktualisierte Artencheckliste wurde Ameisenmaterial verwendet das während des BIOTA Ost Afrika Projekts und vorher gesammelt wurde, insgesamt in den Jahren 1999 bis 2010. Dieses befindet sich in den Hymenopterensammlungen des Zoologischen Forschungsmuseums Alexander König in Bonn und im Natural History Musuem in Los Angeles, USA. Zusätzliche, für

den Kakamega Forest gelistete, Arten wurden aus der Literatur hinzugefügt und die vorhandenen Ökologiedaten wurde für Analyse der Zusammenhänge zwischen biogeographischer Verbreitung und den ökologischen Nischen innerhalb der Ameisengemeinschaft genutzt.

Obwohl der Wald mit ca. 11.000 ha relativ klein und zudem teilweise stark gestört ist und in einer mittleren Höhe von 1650 Metern über dem Meeresspiegel liegt, beinhaltet die Gesamtartenliste nun eine erstaunliche Anzahl von 329 Arten in 55 Gattungen und 11 Unterfamilien. Das stellt gegenwärtig die höchste Ameisenartenvielfalt für die gesamte Afrotropische Region dar, zudem auch mit Abstand und weltweit die höchste für auf einer Höhe von über 1500 Meter gelegenen Umgebung. Außerdem noch erwähnt werden, daß diese Bestandsaufnahme mit mehr als 150.000 gesammelten und bestimmten Individuen sicherlich eine der intensivsten Studie darstellt, die bisher veröffentlich wurden.

Von den 329 Arten sind 227 bis auf Artniveau bestimmt worden; der Rest ist nicht identifizierbar teils wegen einigen taxonomisch noch unbearbeiteten Gattungen und fehlenden Bestimmungshilfen, teils wegen einer wahrscheinlich recht hohen Anzahl an noch unbeschriebenen Spezies. Es hat sich dabei herausgestellt, daß etwa die Hälfte der bestimmten Ameisen (113 Arten) aus den äquatorialen Regenwäldern West- und Zentralafrikas stammen und daß die meisten von ihnen Habitatspezialisten sind, die nicht außerhalb des Waldes vorkommen. Auf der anderen Seite waren ein Anteil von 30 % (99 Arten) der Ameisengemeinschaft zusammengesetzt aus Arten mit einer reinen Vorliebe für offene Habitate. Diese kamen nur in den landwirtschaftlichen Flächen vor und innerhalb des Waldes in den Grassländern, entlang der Straßen und in anderen Freiflächen. Diese Habitate sind eindeutig dominiert von Taxa mit allgemeiner afrikanischer Verbreitung und von Arten, die ihren Ursprung wahrscheinlich in ost- und südafrikanischen offeneren Gebieten und Wäldern besitzen. Etwa 15 % aller Arten (49) waren Habitatgeneralisten und kamen sowohl in den offenen Lebensräumen, als auch innerhalb des Waldes vor. Chi-quadrat Tests zeigten einen starken Zusammenhang zwischen den drei ökologischen Nischen Variablen (Habitat, Mikrohabitat und Ernährungsweise) und zwischen diesen und der geographischen Verbreitung der Arten, außer zwischen der Verbreitung und der Ernährungsweise, welche nur ein marginal signifikantes Ergebnis lieferte. Diese kombinierte Analyse zeigt, daß biogeographische Verbreitung und ökologischen Nische von Ameisen in starkem Zusammenhang miteinander stehen und daß damit die Ameisengemeinschaft detaillierter beschrieben werden kann, als es die beiden Analysen getrennt vermögen.

Eine andere ökologische Analyse über den Einfluß von anthropogener Störung auf die Ameisengemeinschaften in drei verschieden intensiv genutzten Habitaten entlang eines Gradienten, ermöglichte einen detaillierten Vergleich der jeweiligen Diversität der Arten, der funktionellen Diversität und der Artenzusammensetzung in Bezug zu asteigender Landnutzung. Die insgesamt 21 Untersuchungsflächen waren aufgeteilt in acht Flächen in naturnahem Regenwald, sieben im Agrarland mit Subsistenzanbau und niedriger Nutzungsintensität nahe des Waldes und sechs Flächen, die sich in intensiv bewirtschafteten Zuckerrohranbauplantagen zweier großer Zuckerfabriken in der Umgebung des Kakamega Forest befanden. Für die Analyse der funktionellen Diversität wurden morphometrische Daten von ökologisch wichtigen Körperstrukturen verwendet, z. B. der Mandibeln, Beine und Augen, und die trophische Ebene im Nahrungsnetzwerk (gemessen durch Analyse von stabilen Isotopen Zusammensetzungen für 84 Arten).

Die Ergebnisse mit hochsignifikanten und positiven Beziehungen zwischen den unterschiedlichen Indizes der Arten- und der funktionellen Diversität unterstützen ähnliche Ergebnisse anderer Studien in diesem Gebiet. Sowohl Artenvielfalt als auch funktionelle Diversität nahmen entlang des Störungsgradienten stark ab. Während die Artenzahl im Schnitt zwischen 20 und 40 % sank, lagen die Werte der funktionellen Diversität für in den intensiven genutzten Zuckerrohrplantagen sogar bis zu 53 % niedriger lagen als im Wald. Besonds der Anteil der räuberischern Arten in den Ameisengemeinschaften des Farmland lag etwa auf der Hälfte (48 %) des Anteils im Wald, was theoretisch dazu führen sollte, daß die Längen der Nahrungsketten im Farmland abnehmen. Diese entsprechen der Position des Prädators auf der obersten Ebene der Nahrungskette und dienen als Maß für Auswirkung von menschlicher Störungen auf die Höhe und Komplexität des jeweiligen Nahrungsnetzwerks. Und tatsächlich lagen die Längen der Nahrungsketten in Zuckerrohrsubsistenzanbau signifikant und etwa eine halbe trophische Ebene unter denen des Waldes (2.9 trophische Ebenen) und auch in manchen Untersuchungsgebieten im intensiven Zuckerrohranbau traten sehr geringe Werte auf. Dennoch war der Mittelwert in den intensiven Plantagen höher als im Subsistenzanbau und nicht mehr signifikant unterschiedlich von denen im Wald. Eine Erklärung für die hohe Variabilität der Nahrungskettenlängen im intensiven Zuckerrohranbau könnte eventuell das Ausbringen von chemischen Düngern sein. Gesteigerte Nettoproduktivitätsraten der Pflanzen wären dem zufolge für höhere Nahrungskettenlängen verantwortlich. Das ist allerdings eine Hypothese, die mit entsprechenden Experimenten nachgeprüft werden müsste.

In einem zusätzlichen Köderexperiment mit Fliegenlarven zur Messung der Ökosystemfunktion Aasbeseitigung, durchgeführt in jeweils 5 Untersuchungsflächen in allen drei Lebensräumen, zeigte es sich, daß die Abtragsraten der Larven durch Ameisen im Zuckerrohranbaugebiet signifikant höher (plus 57 %) lagen, als im Wald. Die Abtragsraten waren jedoch positiv mit erhöhter Ameisenaktivität an den Ködern im Farmland assoziiert und nahmen signifikant ab mit steigender Artenvielfalt. Das scheint den Resultaten der funktionellen Diversität zwar zu widersprechen. Doch können die Unterschiede der beiden Methoden dadurch erklärt werden, daß einige wenige opportunistische Arten (besonders *Myrmicaria* und *Camponotus*) in hohen Individuendichten im Farmland auftraten. Diese waren relativ groß im Vergleich zur Mehrheit der Waldarten und zeigten ein hohes Aktivitätslevel während des Tages. Eine einzelne

Arbeiterin war leicht dazu in Lage eine Larve mittlerer Größe davon zu tragen, ganz im Gegensatz zu vielen der häufigeren Waldarten, die zuerst ihre Nestgenossinin rekrutieren mussten.

Die Welt der Ameisen ist faszinierend in ihrer Komplexität, wegen ihrer eusozialen Biologie, und der hohen ökologischen Vielfalt und Wichtigkeit für die Stabilität von natürlichen und menschlich veränderten Lebensräumen. Eine Gattung sticht dabei besonders hervor durch ihre Dominanz und ihren Artenreichtum. Mit weltweit mehr als 1000 Arten können die Mitglieder der Gattung *Pheidole* in fast jedem Lebensraum und Mikrohabitat gefunden werden und kennzeichnen sich durch eine insgesamt sehr breite ökologische Nische mit vielen Ökosystemfunktionen aus. Viele von ihnen sind wichtige Sammler und Verbreiter von Pflanzensamen, konkurrenzfähige Aasbeseitiger und Opportunisten, und manche gelten auch als Räuber anderer Invertebraten. Jedoch ist die taxonomie dieser Gattung in einem vergleichsweise schlechten Zustand, besonders in der Afrotropischen Region, was hauptsächlich den alten und unzureichenden Beschreibungen und dem kompletten Fehlen von Bestimmungsliteratur zuzuschreiben ist. Aber auch dem Chaos von noch immer gültigen, jedoch oftmals synonymen, beschriebenen Unterarten und Varietäten. Darum sind die meisten in afrikanischen Bestandsaufnahmen und ökologischen Studien aufgeführten *Pheidole*-Arten nicht identifizierbar und für übergreifende Analysen verwendbar. Mein Ziel ist es hier mit der Beschreibung der *Pheidole pulchella* Gruppe, die in den Waldgebieten der Äquatorialen Congo-Guineischen Regenwäldern vorkommt, den Prozess einer umfassender taxonomischen Bearbeitung und Revision für die Afrikanische Fauna ingang zu setzen. Mit frischem Material aus Kenia, Uganda und Tanzania und Museumpräparaten aus den Hymenopterensammlungen des Natural History Museum in London, Uk und der California Academy of Sciences in San Francisco, USA, war ich in der Lage sieben neue Arten und vier weitere, schon bekannte, Arten - die alle zusammen eine Gruppe nah verwandter Arten zu bilden scheinen - mit modernen Methoden und Messungen entweder neu oder genauer zu definieren und zu beschreiben. Dieser Teil

meiner Arbeit beinhaltet auch einen allgemeinen Überblick über die taxonomisch wichtigen morphologischen Merkmale für die Afrotropische *Pheidole*-Fauna, sowie auch die Vorläufige Definition fünf weiterer Artengruppen. Diese beruhen auf der Untersuchung einer relativ großen Anzahl von Art-Typen aus verschiedenen Museumskollektionen und unbestimmtem Material von einer Reihe verschiedener afrikanischer Sammellokalitäten. Für die beiden verschiedenen Arbeiterinnenkasten wird ein illustrierter Bestimmungsschlüssel für alle Arten der *pulchella* Gruppe zur Verfügung gestellt, sowie Bilder mit erhöhter Tiefenschärfe und morphometrische Messungen für alle bearbeiteten Taxa. Diese Kombination wird es sowohl Experten als auch anderen myrmekologisch Interessierten ermöglichen Material der Gruppe zugehörige Arten zu identifizieren.

Chapter 1:

General Introduction

Biodiversity crisis

Ever since the appearance of the first organisms, planet earth has been transformed from an arrangement of inanimate waters and barren rocks into the wonders of nature with sophisticated reef architecture, beautiful underwater gardens, and tropical forests that are teeming with millions of different plant and animal species. Gradual modifications of landscapes and ecosystems, major global climate changes and species extinctions are natural processes, constantly interacting in shaping the planets' surface and the diversity of life. The term biodiversity in its broadest sense (Wilson, 1997) includes all levels of the living world from genes, individuals, populations, and species up to complete communities and ecosystems. In most studies, however, biodiversity is used analogous to species diversity. Normally, the rates of speciation and natural extinctions are expected to be relatively balanced in times of stability. But today the general concerns are high that the human species currently causes the sixth mass-extinction, referring to the five previous catastrophic extinction events where large proportions of the organismic diversity vanished in only short periods of time (Barnosky et al., 2011). Scientific evidence indicates that current extinction rates caused by (post-) industrial time human activities are hundreds or thousands of times higher than earlier background extinction rates (Pimm, 1995). The last major extinctions in prehistoric times (50.000 – 7.000 BC) most probably have been caused by a mix of anthropogenic influences, glacial, and post-glacial climate changes, which primarily affected many megafaunal and the most vulnerable of species. Today’s highly increased extinction rates, however, is the result of a more complex and far-reaching influence of human disturbance on life in general (Barnosky, 2008; Barnosky et al., 2011; Boyer, 2008; Burney & Flannery, 2005; Pimm, 1995). The present destruction of natural diversity is especially severe from a human perspective, as it is causing systematic damage to ecosystems with unknown consequences to the overall quality of life (Chapin et al., 2000; Díaz et al., 2006; 2011). Most of the damage concentrates on also on the regions with highest overall biodiversity, which are considered to be the tropical forests of the world. Rainforests near the equator are the terrestrial ecosystems with the highest levels of species diversity and ecological complexity (Myers, 1984) and today they are probably covering less than 7 % of the Earths’ surface (Wilson, 1988). Yet, the total area of natural forest is declining continuously (FAO 2011) and despite the CBD 2010 target to reduce the current rate of global biodiversity loss, a change seems not to be in sight (Butchart et al., 2010).

Habitat destruction and degradation

Knowing about potential dangers of an impoverished biosphere, a large body of ecological studies and experiments has documented and tried to explain the main causes of species and general diversity loss. It can be summarized that after the initial and severe impacts of habitat transformation and fragmentation, alien species invasions, pollution, overharvesting and human-caused climate change probably affect natural communities the most (Brook et al., 2008).

Habitat conversion of diverse tropical forest habitats into agricultural landscapes, generally shows highly damaging effects on several interacting levels of biodiversity, from the disruption and isolation of populations at the landscape level, to decreased genetic variability within these isolated and reduced populations and to the complete extinction of endemic taxa, which are found nowhere else (Brook et al., 2008). One important factor for conservation management is the decrease in total habitat area, which leads to a decrease in the total species richness that can be supported by an area, according to island biogeography theory (MacArthur & Wilson, 1967). In general forest specialists have reduced dispersal abilities along open and disturbed habitats and are thus hindered from (re)colonizing forest regrowth or other unsuitable habitats, resulting in increasingly constricted distributions and population sizes. This is especially true for ants, with their wingless worker castes and queens that rarely fly more than a few hundred meters for reproduction and to found their own nests (Hölldobler & Wilson, 1990). Even old-growth secondary forests are depleted of the most specialized and vulnerable species, that are often unique in the functions and ecosystem services they provide (Bihn et al., 2010). These are some of the reasons, why the majority of obligate forest species is unlikely to survive without undisturbed or at least near-natural refuge areas and migration corridors for genetic exchange. Unfortunately, the areas with the highest biodiversities are also often the ones with strongly increasing human population densities and thus rapidly growing pressures on the remaining natural habitats (Brooks et al., 2002; Cincotta et al., 2000). Biofuel production, increasing natural resource consumption in newly industrializing and developing countries, and global climate change are posing the most serious recent threats for natural habitats and will increase present extinction rates even further (Jenkins et al., 2011; Malhi & Wright, 2004; Malhi et al., 2008). Increasing biofuel production could become a major driver of further deforestation in the tropics, if intended substitution rates for fossil fuels are increased even further in the future (Fargione et al., 2010). This could highly impact regional biodiversity and drive already threatened species into extinction. That destructive potential is probably as high as that of global warming itself. Thus, strong arguments against crop derived biofuels are fundamental for conservation management. An array of scientific investigations and publications argues the downsides of large-scale biofuel production, which demands valuable arable land and resources that would be better used for the sustenance of a constantly growing human population (Groom et al., 2008; Hill et al., 2006; Koh & Ghazoul, 2008). Several authors pointed out that protection of natural forests, acting as carbon sinks, is an efficient strategy to reduce carbon dioxide greenhouse gas emissions and that reforestation has a much stronger capacity to mitigate future climate change in the short and in the middle term than the production of crops for biofuels on the same area of land (Danielsen et al., 2009; Luyssaert et al., 2008; Righelato & Spracklen, 2007).

Even the relatively few well-protected areas are not completely safe from human influence and exploitation, because often the local people are not aware of or even excluded from the benefits and advantages of conserving their native flora and fauna (Díaz et al., 2006). Many of these protected areas have been in extensive use and underwent at least partial and selective logging activities before, and the pressures around their borders are likely to increase in the future. Still there remains a small chance that concentrated conservation efforts could turn the page and prevent a mass extension which would be unprecedented in the modern age, and since the disappearance of the dominant elements of the Cretaceous period. Otherwise a large number of species that are just a few steps away from extinction will be extinguished until the end of the century (Sala et al., 2000).

Species and functional diversity

Ants are an abundant, diverse and ecologically important insect family, with more than 12.000 described and maybe as many undescribed extent species (Ward, 2009), divided into 21 subfamilies and 298 genera (Bolton, 2011). As for many other taxa, tropical forests clearly represent the core area of their distribution with the highest species diversities in tropical lowland forests of South- and Mesoamerica, sub-Saharan Africa, Asia and Australia (Brown, 2000; Ward, 2000). But also in temperate regions, the abundance of a few species and their importance for forest ecosystems can be very high, e.g. several *Formica* species in Northern Europe (Hölldobler & Wilson, 1990). Functional diversity is a measure for the range of organismal traits (genetic, morphological and ecological) present in a (Petchey & Gaston, 2006). These traits have to be defined, and ideally evaluated in experiments, in such a way that they actually reflect the functions and processes performed by this community that are relevant for the identity and integrity of their respective ecosystems.

Functional diversity measures are usually highly correlated to species diversity (Bihn et al., 2009; Petchey & Gaston, 2002a; 2002b), relative to the degree of redundancy present in the functional traits of the species within a certain community. In other words, the more functionally unique species are present within a community of species, the higher will be the functional diversity (Flynn et al., 2009). Both, species and functional diversity are strongly affected by increasing outside pressures on and disturbances within natural ecosystems. The effects of biodiversity loss, usually assessed on the species level, on functional diversity have been closely investigated in theory and in experiments in the last few decades (reviewed in Balvanera et al., 2006; Cardinale et al. 2006, 2011; Flynn et al., 2009; Hooper et al., 2005). The results for the studies concerning animals were mostly that species and functional diversity were closely related and functional redundancy is less pronounced than in plant communities for example.

With an ongoing habitat destruction rate that is still alarmingly high, priority areas and conservation strategies are being defined and redefined to protect as much of the overall diversity as possible. Biodiversity hotspots for concentrated conservation efforts in the 25 most species rich regions worldwide have been outlined (Myers et al., 1988; 2000; Sechrest et al., 2002), however not without critique about the selection of relevant criteria (Orme et al., 2005). Fact is that human populations in biodiversity hotspots are growing higher than average and that immediate measures are necessary to prevent further habitat reductions (Cincotta et al., 2000). More recently the debate about applicable conservation strategies included diverse agricultural areas such as agroforestry systems, which – under the right management – are able to support a range of forest species (Bos et al., 2007; Steffan-Dewenter et al., 2007, Tscharntke et al., 2008). Wright and Muller-Landau's (2006) published a paper with highly theoretical demographic projections and the provoking assumption that increasing forest regrowth will support most of the biodiversity that is endangered by destructions of natural forest biotas. Although it received a lot of criticism (e. g. Brook & Bradshaw, 2006; Gardner et al., 2006; Laurance et al., 2007) it provided ground for discussions of past and future research directions.

Ants have been intensively used as biological indicators of ecosystems, with several advantages. For one, ants are diverse, ubiquitous and highly abundant in almost every terrestrial habitat and microhabitat, except in the Antarctica, plus the workers are wingless and thus easy to sample, and they are also identifiable by non-experts. And most importantly, ants are sensitive to environmental change and habitat disturbance in their community compositions and species abundances (Andersen, 1997; 1998; Crist, 2008; King et al., 1998; Peck et al., 1998; Underwood & Fisher 2006).

Trophic chains and food web complexity

Knowledge about the length of trophic chains and natural food web complexity in terrestrial habitats is still relatively scarce, because the size of food webs is directly related to the number of species (and even individuals) involved and many species have ranges across habitats. Food chain length and food web complexity are theoretically dependent to several factors, such as ecosystem size, resource availability, predator-prey interactions, intraguild predation and habitat disturbance (Post, 2002a; Post & Takimoto, 2007. But research about food-webs seems to be difficult in complex systems, where interacting factors show inconsistent responses in natural communities, and is often limited to well-defined model systems, e. g. lakes and islands (Post & Takimoto, 2007; Takimoto et al., 2008).

Stable isotope analysis of the heavy nitrogen isotope ^{15}N, which is enriched with every trophic transition, is a widely used method to ascertain both trophic positions of organisms and their trophic interactions in local food webs. In brown food webs ants typically fill the complete range of possible trophic positions from strict herbivores to top-predators (Blüthgen et al., 2003; Davidson et al., 2003; Feldhaar et al., 2010). The highest position, occupied by the top predator, can provide a good estimate for the total length or height of trophic chains in local food webs (Post, 2002a). As specialized predators from the top of the food chain are vulnerable to disturbances within the food web they are often the first to disappear with increasing habitat alteration (Duffy, 2002), which in practice must be reflected in shorter food chain length, unless opportunistic predators filled out their vacated niches (Post & Takimoto, 2007). Recently it has been shown that in the removal of both strong and weaker interactors in complex marine food webs the functioning and the stability ecosystem processes were significantly damaged (O'Gorman & Emmerson, 2009). This again emphasizes the importance of biodiversity conservation in order to maintain the complexity and thus the stability of trophic food webs as an insurance for unperturbed ecosystem functioning.

Ant taxonomy

One important and basic requirement in the attempt to slow or even halt the ongoing loss of biodiversity is to acquire knowledge of all the species concerned. Only with a sound taxonomic foundation, ecologists and conservationists will be able to provide information about the biology, endemicity, threat status and importance of species in their respective communities (Wilson, 2011). About 1.4 - 1.8 million species have been described, which is just a fraction of the extant diversity believed to live on the planet, as the estimated number of different species lies between 3 and 100 million species (Stork, 1993; Wilson, 2003). Probably a better estimate of about 8.7 (±1.3) million species was published by Mora et al. (2011), which means that the diversity of life is still largely unknown and undescribed. This discrepancy represents a large information vacuum, the 'taxonomic impediment' which needs to be solved in order to manage and conserve biodiversity effectively (Global Taxonomy Initiative 2011). Without a sound taxonomic basis many studies about ecology, biogeography and evolutionary dynamics are limited in their general comparability, which considerably slows the general progress in biological science. Ants in general are a focal taxon in ecology, which is partly based on their ecological and evolutionary success as the most diverse and abundant eusocial animal family (Hölldobler & Wilson, 1990; Wilson & Hölldobler, 2005). The ancestors of modern ants most likely appeared during the early or mid-Cretaceous period around 120 million years ago (Brady et al., 2006). The fossil record and molecular phylogenetic analyses suggest that subfamilies evolved in the late Cretaceous and modern genera probably did not appear before the Paleogene, after the breakup of the Gondwana continent (Fisher, 2009). Which is why, today the ant faunas of the major biogeographic regions are distinct in their generic compositions. One of the genera with the highest dispersal and radiation rates is the genus *Pheidole* Westwood. In terms of species diversity and ecological dominance it is indeed one of the most successful genera in ants and together with *Camponotus* and *Crematogaster* they account for about one quarter of the validly described species and subspecies. Unfortunately, the overall taxonomy for these three globally abundant and hyperdiverse genera is in a poor state, compared to most of the other genera which are often considerably smaller and globally less abundantly distributed.

Beginning with the large-scale application of the binominal nomenclature system Carl Linnaeus described the first ant species in his Systema Naturae (1758), where they were still belonging to one single genus, the genus *Formica*. But after only a few decades new genera were described (Fabricius, 1793) in order to incorporate the increasingly recognized diversity within the family

Formicidae. For about one hundred fifty years after the publication of the Systema Naturae the general pattern in Myrmecology seems to be that a few entomologists and ant specialists, such as A. Forel and F. Santschi, described more or less randomly collected material. During this time a huge quantity of species, subspecies and further sub-divisions of previously defined taxa were described without much consideration for intraspecific and geographic variability. As a result modern taxonomists and ecologists are facing severe problems in species-level identification for these groups, especially in the Palaeotropical region. Identifying African *Pheidole* for example is a challenge due to an almost impervious jungle of described synonymic taxa, subspecies and varieties, insufficient and highly outdated descriptions, widely scattered type material and more than incomplete reference collections. The only long-term solution will be the combined efforts of large-scale taxonomic revisions, systematic molecular studies and intensive inventories in the largely under-sampled Afrotropical region. In Myrmecology the subspecies concept has been abandoned decades ago with the first modern taxonomic treatments by E. O. Wilson and W. L. Brown (Wilson & Brown, 1953). Brown also merits credit for his work on the reclassification of the entire family Formicidae and he later also criticized the lack of systematic treatments within the genus *Pheidole* (Brown, 1981). Wilson as the most renowned ant scientist strongly contributed to the research of ants in general and is the founding-father of sociobiology, the branch of biology concerned with all social forms of life, including many arthropod taxa and also primates (Wilson, 1975; 1976). From around 1970 on B. Bolton became the most productive and successful modern ant taxonomist, mostly with a variety of revisions for complete genera or higher taxa either on a global basis, or for entire biogeographic regions. He also published several synoptic surveys (Bolton, 1995; 2003) and the highly useful "Identification guide to the ant genera of the world" (Bolton, 1994). He also revised ants on the subfamily-level recognizing 21 extant subfamilies with morphological characters (Bolton, 2003), of which 19 are also supported as monophyletic groups based on molecular analyses (Brady & Ward, 2006). In the same year Wilson also published his *Pheidole* monograph with the description of 314 new species in the New World (Wilson, 2003), with that improving the overall taxonomy for this region and creating new interest for further revisions. Despite all past and ongoing systematic efforts, the number of undescribed and unrevised taxa is still very high. Furthermore, constantly growing ant collections and improving methods of species delimitation additionally challenge previous works and provide the current generation of taxonomists with new possibilities and insights (e.g. LaPolla et al., 2010).

Kakamega Forest and study area

Kakamega Forest is a mid-altitudinal tropical rainforest in Western Kenya and represents the eastern-most relic of the Congo-Guinean rainforest system. After the last glaciation period, during a wetter climate, it was probably connected to the forests of the Congo basin. The average annual rainfall is about 2000 mm and the mean temperature is 19°C (Mitchell, 2008). The forest is situated about 30 km north of the equator (0°17’N, 34°53’E) in the Western Province of Kenya and about 50 km north of Lake Victoria (see Fig. 1.1A). It lies on a high plateau at altitudes mostly between 1550 m and 1750 m a.s.l. (average 1650 m). Elevations in the surrounding area around the forest are generally rising from West to East, from about 1300 m a.s.l. at Mumias to over 2000 m at the Eastern and Southern Nandi escarpment, two montane forests of the Rift valley system, which are separated from the Kakamega Forest by stretches of farmland and villages.

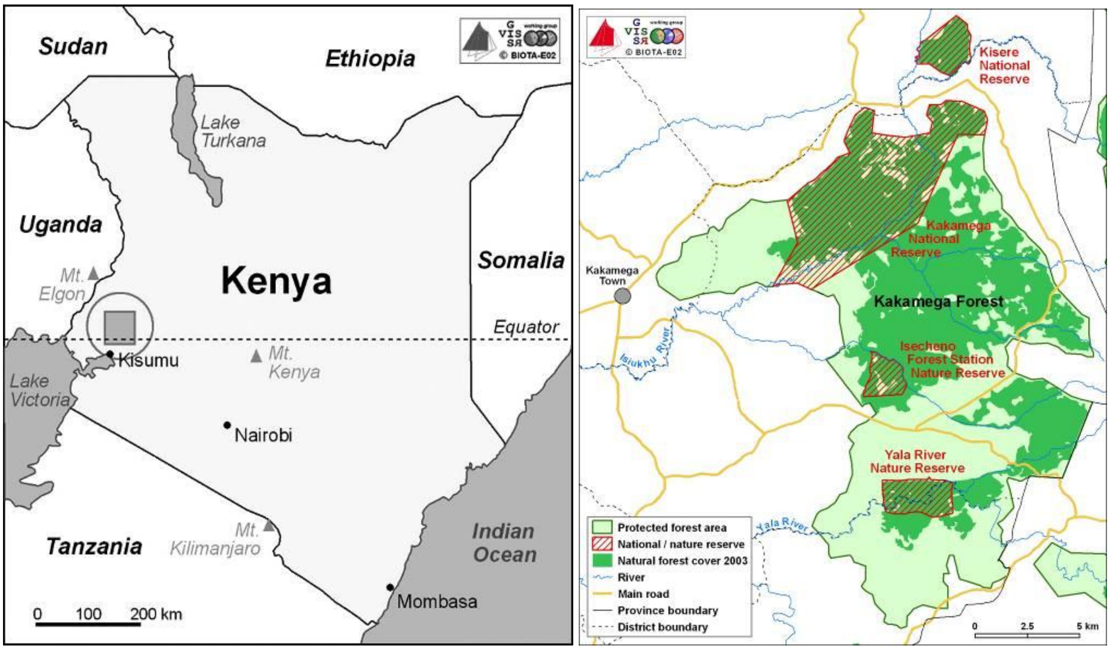

Figure 1.1 Map of Kenya indicating the location of the Kakamega Forest in Western Kenya (square in circle). **A.** Protected areas of Kakamega Forest **B.** (Maps kindly provided by BIOTA subproject E02).

From an original area of almost 24000 ha in 1933 (Kokwaro, 1988) around 11,000 ha natural forest cover have remained in 2001 (Mitchell et al., 2006) distributed over a central large forest fragment of 8245 ha and six smaller forest islands (65 to 1370 ha). Its flora and fauna represent a unique mixture of species. Most of these have their origins in the lowland forests of the Congo basin, with Kakamega as their eastern distribution limit, while the association with other Afrotropical or montane forest faunas is significantly less pronounced (Bennun & Njoroge, 1999; Althof, 2005). In a biogeographical analysis of the reptiles of the Kakamega Forest and 16 other Equatorial-Afrotropical forests by Wagner et al. (2008), Kakamega Forest formed a distinct clade with other East African rain forests in Uganda and in the Democratic Republic of the Congo. This clade was sister clade to forests in Western Africa, several thousand km away. The geographically much closer Arabuko Sokoke Forest at the coast of Kenya and two of the Eastern Arc Mountain forests in Tanzania were strongly separated from this Congo-Guinean forest clade.

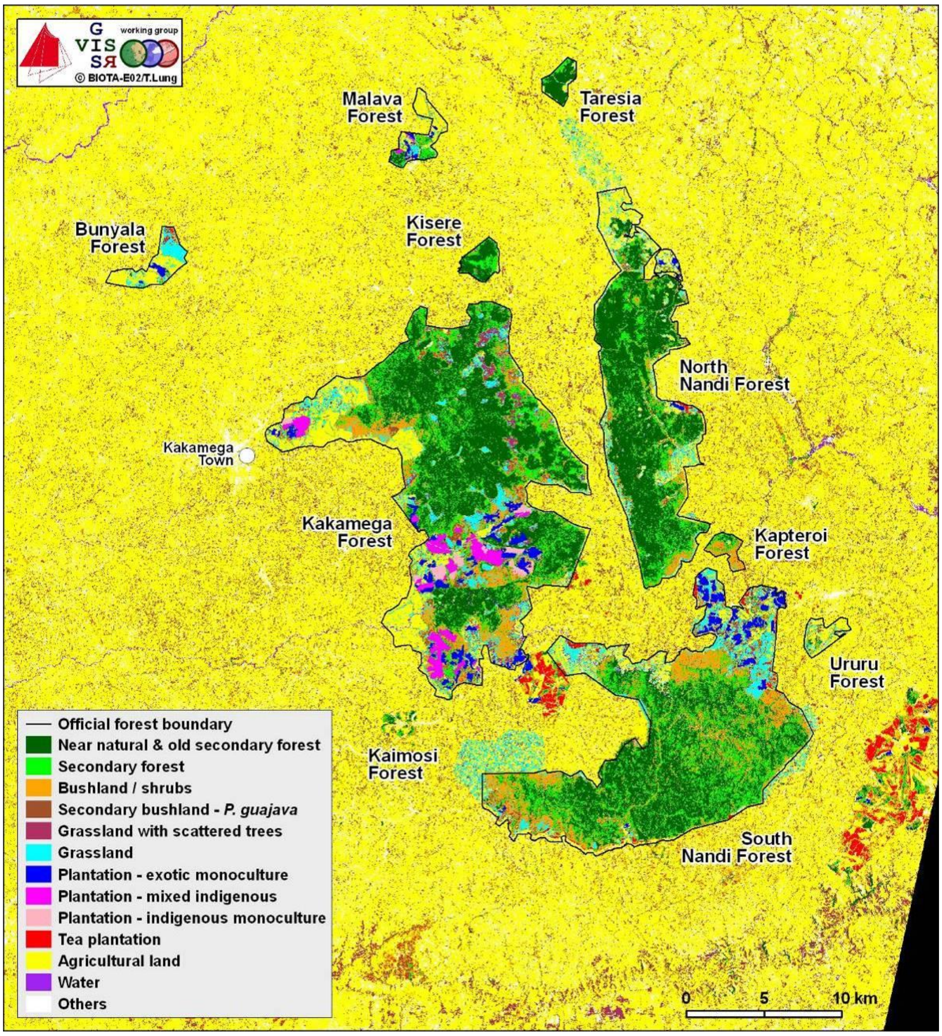

Figure 1.2 Map for habitat and land-use types in and around the Kakamega Forest (kindly provided by BIOTA subproject E02).

Today's forest borders are inhabited by a habitat-mix of near-natural forest with a relatively high canopy up to 30 m and several vegetation strata, secondary forest in different succession stages, gallery forest along the Isiukhu river, several grassland glades and a few rocky hill-tops. It is divided into two different management areas, the National Reserve in the north, managed by the Kenyan Wildlife Service (KWS) since 1986, and the southern part of the forest managed by the Forestry Department (FD) (Fig. 1.1B). The human population density in the surrounding area is one of the highest on the continent (Blackett, 1994), and the anthropogenic pressure on the forest ecosystem is accordingly pronounced, with logging, fire-wood collecting and poaching as serious threats to the survival of many vulnerable species and the forest as a functionally intact ecosystem (Bleher et al., 2006). The habitat matrix surrounding the forest is mainly characterized by subsistence agriculture (the shambas of the local Luhya tribe), a few exotic tree plantations, small to medium-sized tea plantations, and medium-sized sugarcane fields (Fig. 1.2). The shambas are usually only a few acres in size and characterized by a variety of cultivated food plants for private consumption, with the typical cash crops being sugarcane and, to a lesser extent, maize and tea.

Biogeographically the Kakamega Forest is assumed to be a small remnant of the Congo-Guinean Equatorial-African rainforest belt and might have been its' eastern-most extension during a once wetter climate (Wagner et al., 2008). A large proportion of its' unique diversity can be found nowhere else in the country (Zimmermann, 1972; Clausnitzer, 1999; 2005; Wagner & Böhme, 2007; Hita Garcia et al., 2009), including many species of the currently most diverse ant fauna in the Afrotropical region. Despite their small size and the wingless worker caste many ant genera and species seem to have relatively good dispersal abilities, so that many non-tramp species showed a wide geographic distribution even across continents. In the Afrotropis a relatively high number of such widespread open habitat and woodland species can be found nearly everywhere in the grasslands and semi-arid savannahs south of the Sahara. On the other hand, there is also a considerable range of taxa that occur only along the Congo-Guinean rainforest belt from West to East Africa. In the Kakamega Forest area, the two differently adapted ant faunas are forming a unique mixture of communities inside and outside of the forest borders (Hita Garcia et al., 2009). Confirming previous works for other groups (Wagner et al., 2008; Zimmermann, 1972) and based on the composition of its' ant community it can be inferred that the Kakamega Forest must have once been connected, at least by stable corridor (s), to the Congo-Guinean rainforests, which cover a large proportion of Central Africa and are poorly studied in until today.

Table 1.1 Abbreviations for all museum collections that appear in Chapters 2 - 4.

BMNH	The Natural History Museum (British Museum, Natural History), London, U.K.
CASC	California Academy of Sciences, San Francisco, California, U.S.A.
LACM	Natural History Museum in Los Angeles, USA
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHMW	Naturhistorisches Museum, Wien, Austria
NMK	National Museums of Kenya, Nairobi
USNM	National Museum of Natural History (United States National Museum), Washington, D.C., U.S.A
ZFMK	Zoological Research Museum König, Bonn, Germany

Outline

The topics treated in this dissertation are dealing with Afrotropical ant biodiversity research, which is relatively underrepresented in comparison to the more thoroughly investigated New World tropics. The purpose was to emphasize the importance and increase the understanding of ant diversity and ecosystem functions in complex tropical landscapes. In the wet tropics human modified habitats are often coexisting with and economically depending on biodiversity hotspots, where in many cases the diversity of several taxa can far exceed that within other much larger areas. This thesis was part of the interdisciplinary BIOTA East Africa project (subproject E16) in Western Kenya. One goal of it was to determine the responses of the highly diverse ant fauna in a near-natural rainforest and the surrounding agricultural landscape towards anthropogenic habitat disturbance. The main hypotheses were: 1) the diversity of ground and leaf-litter ant species is negatively influenced by human disturbance and habitat degradation. 2) the community composition changes dramatically with disturbance and habitat disturbance. 3) intensified agricultural production of sugarcane dramatically reduces species and functional diversity and has very little value for forest species that depend on an intact leaf-litter layer as suitable microhabitat for foraging and nesting.

The basis for all analyses in the following two chapters was an intensive inventory of the Kakamega Forest, and the surrounding agricultural matrix which was mostly conducted between 2007 and 2009, but also relied on other, earlier collected material. The most important collection methods employed were pitfall-traps and Winkler leaf-litter samples in order to comprehensively capture the diversity of ground-living ants present in each habitat. Altogether 298 different ant species were collected during the duration of the Biota project, with voucher specimens deposited in the entomological collection of the Zoological Research Museum Koenig, Bonn. Additional specimens collected by the late R. R. Snelling and species records in the literature were used for a complete species list for the whole Kakamega area in **Chapter 2**.

Because the material was collected in several different habitats and microhabitats, patterns of species ecological niches and distributions began to emerge in the initial phase of sample sorting and processing. **Chapter 2** summarized this data and comprises ecological and biogeographical analyses of the entire known Kakamega ant fauna, also including the improved and updated species checklist. In this chapter the whole ant community is characterized and analyzed ecologically, with three important niche variables (habitat, microhabitat and feeding strategy). Biogeographical distributions were determined for all taxa that could be identified to species-level. These analyses visualize how community composition of different ant assemblages seems to be largely dependent on different aspects of different species ecologies and geographic distributions. Furthermore, possible reasons for the high ant diversity in the Kakamega Forest, which is not only the highest in the Afrotropical region but also from all studies in altitudes above 1500 m a.s.l. in general, will be discussed.

In **Chapter 3** responses to differences in habitat and the level of disturbance were evaluated along a land-use gradient from near-natural rainforest to different intensities of sugarcane production in a densely populated and degraded matrix around the forest. The approach was to incorporate not only data on species diversity, which are mostly used in this type of ecological research, but also to use data on the ecosystem functions and services that are performed by ants in their respective habitats. Therefore, seven morphological and ecological traits for the species within the different ant communities were analyzed in order to determine the potential range of functions performed in the different habitats. Especially predators are an important indication of the functioning and stability of ecosystems and are usually highly affected by human disturbances. As many of them were very specialized elements within the food chain, many predatory ants disappeared in the farmland, especially in the intensively managed sugarcane monocultures. Many farmland ant species are, however, generalized opportunists taking almost any kind of food available, from sugary liquids and seeds, to vertebrate faeces, dead or live invertebrates and carrion. They seem to be both, highly competitive in human disturbed habitats and adapted to efficiently exploit food resources. Thus, additional experiments on the efficiency of the different ant communities to remove immobilized fly larvae were performed, to test if this ecosystem service was linked to species diversity or to community composition.

Chapter 4 finally is dedicated to improve the current taxonomic situation of the globally distributed and ecologically dominant ant genus *Pheidole* in the Afrotropical region, which was also the second most diverse genus in Kakamega and in other African ant inventories. The here treated *P. pulchella* species group seems to be restricted to the Congo-Guinean rainforests near the equator, with a distribution from Guinea in West Africa to Kakamega Forest and Gombe, both in East Africa. Currently eleven species are known for this group, seven of them being new to science. These species are also characterized by relatively long propodeal spines and a combination of other characters, indicating that they might form a group of closely related species. In fact most African species in this genus seem to have several closely related, undescribed sibling species, which all together can be defined as a set of different species groups. A preliminary definition of five other species groups is provided in order to give an introduction to the spectrum of revisionary studies that should be processed in the future to further the basic for research on this hyperdiverse genus in general and in particular for the Afrotropical region. Many subspecies and varieties need to be revised and either synonymized or raised to species level. When extrapolated from the proportion of new species found for the here described *Pheidole pulchella* group, the currently known fauna of 136 valid Afrotropical taxa is likely to more than double with future revisionary treatments for this highly diverse genus.

Chapter 2:

The ants (Hymeoptera, Formicidae) of Kakamega Forest: Ecology and biogeography of a highly diverse mid-altitudinal rainforest fauna, with an updated species checklist

with F. Hita Garcia, E. Wiesel, J. W. Wägele, M. K. Peters - unpublished

Abstract

An intensive ant inventory for the Kakamega Forest, Western Kenya, and the surrounding area revealed the presently most diverse ant community of the whole Afrotropical region. This community currently comprises 329 species, more than half of the entire known Kenyan ant fauna, and of which 227 species (69%) could be assigned with scientific names. This extraordinary high diversity is of particular faunistic relevance when considering the high altitudinal level of the Kakamega Forest area, which is on average 1650 m a.s.l. with only a small altitudinal amplitude. In all other ant inventories published so far the ant fauna above 1500 m a.s.l. had already decreased to a fraction of the diversity that can be found at lower altitudinal ranges. Furthermore, ecological niche and biogeographical distribution data were collected and analyzed for the Kakamega ant community, which are key to understanding biodiversity patterns, and essential for species and ecosystem conservation. With 113 species having a Congo-Guinean distribution and representing half of the identified taxa, the results are concordant with those of previous studies, where the Kakamega Forest fauna was much closer related to the equatorial rainforests in Central and Western Africa than to East African coastal and Afromontane Forests. However, the fauna as a whole represents a unique mixture of species from several different biogeographic regions in the Afrotropics, with several species widely distributed over other continents. Chi-square tests for the relationships between biogeographical distributions and two of the three niche variables revealed strong associations between geographic distributions and habitat ($p = 0.0005$), and microhabitat ($p = 0.006$). Strong associations were also found between the ecological niche variables themselves: habitat-microhabitat ($p = 0.0005$), habitat-feeding ($p = 0.003$) and microhabitat-feeding ($p = 0.0005$). The unique ant diversity and community composition emphasizes the importance and high protection value of the Kakamega Forest area for National and East African biodiversity conservation in general.

Keywords: Afrotropical region; Formicidae; biodiversity; conservation; species checklist; biogeography; species distribution; ecological niche

Introduction

Ants are important and diverse not only in species numbers but also in interactions with their environment. As ecosystem engineers they are essential components in nearly any terrestrial habitat. They provide important ecosystem services, both enhancing soil quality and local nutrient richness, shaping plant communities as indirect herbivores, seed predators and as dispersers. Opportunistic species and scavengers are analogue to cleaning crews, and effectively remove dead animals and faeces (Folgarait, 1998). Many species live in mutualistic relationships with trophobiotic sap sucking insects, myrmecophytes or fungi (leaf-cutter ants). As fierce predators and keystone species, ants are shaping the structure of invertebrate communities. Army ants of the genera *Eciton* and *Dorylus*, for example, are known to increase arthropod species diversity by decimating dominant species of other ants and thus creating space for rarer species (Franks & Bossert, 1983). Due to their ecological relevance, and ease of sampling, ants have become an often utilized indicator taxon for biodiversity monitoring and conservation programs (Crist, 2008; Underwood & Fisher 2006). Especially in tropical rainforests, which are considered to be the globally most threatened terrestrial ecosystem (Balmford et al., 2001; Brooks et al., 2002; Myers, 1988; 2000) ant monitoring can be cheaply used to assess ecosystem functioning (Bihn et al., 2009, Chapter 3).

Ant diversity typically is highest in lowland tropical forests, and species numbers usually decline in higher latitudes and altitudes (Brühl et al., 1999; Ward, 2000; Kaspari et al., 2004; LaPolla et al., 2007; Longino & Colwell, 2011; Malsch et al., 2008; Ryder Wilkie et al., 2010) and with decreasing temperatures and humidity. Several studies in the wet tropics documented highly diverse ant faunas, either only in lowland forests or along elevation gradients at mountain slopes. Two studies in South East Asia at Mount Kinabalu National Park, Borneo collected 524 morphospecies in altitudes between 550 and 800 m a.s.l. (Brühl et al., 1998), and 376 morphospecies between 580 and 1520 m a.s.l. (Malsch et al., 2008), respectively. One study in South America found an astonishing 489 species in 0.16 square kilometres at the Tiputini Biodiversity Station in a Western Amazonian rainforest in Ecuador, between 206 and 224 m a.s.l. (Ryder Wilkie et al., 2010). From a 1000-ha area in Panguana Reserve, Peru, at about 220 m a.s.l. 520 species were recorded (Verhaagh, 1990). And in Central America, at the La Selva Biological Station in Costa Rica (50-150 m a.s.l.), a diversity of 437 species was registered (Longino et al., 2002). For the Afrotropics Monts Doudou in Gabon harbours the formerly highest ant diversity of 310 ant species, collected in lowland forest at elevations between 110 and 640 m a.s.l. (Fisher, 2004). Only a few studies assessed tropical ant species richness on altitudes above 1200 m a.s.l., most of them with linearly or exponentially decreasing diversities

(Table 2.1). Exceptions are a few studies where the lowest altitudes showed decreased ant diversities compared to mid-altitudinal sites (Fisher, 1998; 1999; 2002; Sabu et al., 2008; Samson et. al., 1997). However, the general pattern in elevation gradient and other studies above 1500 m is that ant species richness has already strongly declined in comparison to lowland forest sites, often representing only a small fraction of the diversity at lower altitudes (Brühl et al., 1998; Fisher, 1998; Robertson, 2002). Finally, rainforests above 2300 m elevation, where ants seem to be completely absent are probably too cold, too moist or unproductive for them to reproduce and forage successfully (Brown, 1973).

In general, species checklists are an essential foundation for ecological studies, not only as lists of species names and numbers, but depending on the amount of identification effort, also for biogeographic studies and conservation. However, checklists of insects, including ants, from tropical localities usually suffer from an extensive listing of morphospecies instead of universally applicable scientific species names (Belshaw & Bolton, 1993; Deblauwe & Dekoninck, 2007; Fisher, 2004; Hita Garcia et al., 2009; Robertson, 2002). This is due to followig reasons: taxonomic revisions for several ecologically important and diverse genera are either missing or outdated, especially for the Afrotropical zoogeographic region, where several unrevised genera, such as *Camponotus*, *Crematogaster*, and *Pheidole* demonstrate an especially great need for intensive taxonomic studies within this decade and the following. Moreover, a large percentage of species found in tropical localities have not been taxonomically described yet, which makes faunal comparisons at species level nearly impossible. Currently, this can only be achieved with few recently revised model taxa, for example the ant tribe Dacetini (Bolton, 2000). Knowledge about the ecological niche and biogeographical distribution of species are important for the conservation of vulnerable habitats and the services provided to humans and life in general. Especially the highly diverse communities in tropical rainforests are endangered by growing human populations and increasing exploitation, often resulting in severe size reductions and high fragmentation of existing natural forest areas. Agriculture is one of the most important threats, offering liitle survival opportunities for forest plants and animals and land-use intensification often leads to severe damage in natural communities (Carvalheiro et al., 2010; Dunn, 2004; Floren & Liensenmair, 2005; Green et al., 2005; Wilcove & Koh, 2010; Waltert et al., 2005). Endemics and forest dependent species will doubtlessly face extinction with ongoing reductions of their native habitats. Long-term conservation of biodiversity can only be achieved by protecting natural habitats, and their biotic characteristics and community compositions as a whole. Antropogenically caused biodiversity loss and other changes in community compositions can severely endanger the stability and functioning of habitats (Chapin et al., 2000). In this study an intensive ant inventory of the Kakamega Forest, a rainforest fragment in Western Kenya, and the surrounding agricultural matrix resulted in the highest ant diversity found in the Afrotropical region so far. This inventory provides the foundation for an improved and updated species checklist, which also summarizes a large amount of ecological data collected. This data was used in addition with the known biogeographical distribution ranges of all identified species for a comprehensive community analysis of the Kakamega ant fauna.

Material and Methods

Ant sampling and examined material

The ants presented here were collected between 1999 and 2010 by the authors and other entomologists. Collection methods were primarily pitfall trapping and leaf-litter (Winkler-) extraction (following ALL protocol: Agosti, 2000) with additional baiting (epigaeic & hypogaeic), soil-core samples (20 cm depth), hand-collections and sweep netting. Males have been collected with Malaise traps and improvised light traps (R. R. Snelling) and canopy species were obtained via fogging (W. Freund & T. Wagner). Habitats studied inside the borders of Kakamega Forest were near-natural forest and secondary forest with additional collections also in glades and along roads. Outside of the forest different agricultural fields and plantations were sampled for comparative studies (unpublished). During the authors' work, more than 400 one m² leaf-litter samples and more than 1000 pitfall traps were analyzed. All ants collected by the authors are deposited in the ZFMK, with a reference collection in the CAS and NMK each. With only very few exceptions the listed species are based on specimens of the worker caste, represented in the two museum collections mentioned above. Exceptions are nine species from the genera *Aenictus*, *Aenictogiton*, *Dorylus and Proceratium*, represented only by males and 26 species that are listed only in the literature. Identification to subfamily and genus level followed Bolton (1994) (exceptions see list below). For the identification to species level several genus revisions were employed (Bolton, 1973; 1974a; 1974b; 1975a; 1975b; 1976; 1980; 1981a; 1981b; 1982; 1986; 1987; 2000; 2007; Brown, 1975; 1976; 1978; Belshaw & Bolton, 1993; Fernández, 2004; LaPolla, 2004; LaPolla & Fisher, 2005; Snelling, 2007; Bolton & Fisher, 2008a; 2008b; LaPolla et al., 2010; Weber, 1950). Also original descriptions and web resources (AntWeb: www.antweb.org) were used for the identification process. The different sources are indicated in the appendix in the complete species list. For genera, where keys and literature on species identification were scarce or entirely absent, e.g. for the genus *Pheidole* Westwood, references from the Afrotropical ant collection in LACM and types from several different museum collections (especially NHMB and NHMW) were used for species identification and in order to reveal potential new species. Only unidentifiable specimens were assigned with a morphospecies code, representing determinator and a species number.

Ecological and geographic distribution data

The habitat type and microhabitat data in our list are derived directly from sampling and observations in the field. Nevertheless, for a few rarely collected species this might not reflect the entire extent of the ecological niche space. The feeding habits of genera are divided into the three categories: ‘predatory’: third (and forth) level consumers that are high in the trophic food chains; ‘generalized’: second level consumers that are feeding opportunistically from several levels in the food web; and ‘trophobiotic’: first level consumers that are tending sap sucking insects and feed on plant derived sugar and amino acids. The information basis for this division is derived from literature (Agosti & Alonso, 2000; Delabie, 2001; Blüthgen et al., 2003; Davidson et al., 2003; Feldhaar et al., 2010) and our own foraging observations. On genus level and for the greatest part of the species analyzed, they are in high concordance with stable Nitrogen measurements (Chapter 3, unpublished).

Geographic distribution was determined for the 227 identified species with Bolton’s catalogue (2000), AntWeb (www.antweb.org) and original revisions (see previous paragraph) as primary sources. Bolton’s catalogue provided information about type localities and in some extent to species distributions. AntWeb and the revisions were used in order to complete the known distribution ranges. The ten resulting biogeographical classes are: Afrotropical, Afrotropical-Malagasy, East African, East African-Southern African, Congo-Guinean, Kakamega (Kenya), Oriental-Afrotropical, Palaearctic-Afrotropical, ‘three or more biogeographical regions’ and tramp species (see checklist in Appendix 1). The Afrotropical region comprises all sub-Saharan countries (excluding Madagascar). Afrotropical-Malagasy combines the Afrotropical region and Madagascar. The East Africa region comprises areas from Ethiopia, Somalia and southern Sudan to Kenya, Uganda, Rwanda and Tanzania. East Africa-South Africa includes species which occur from the East African region in the North to Mozambique, Zimbabwe, and South Africa in the South. The Congo-Guinean region is defined by species distributions along the Congo-Guinean rainforest belt from the Gambia, Senegal and Guinea in the West to Kenya and Tanzania in the East. The Kakamega region defines species endemic to Kakamega Forest. Oriental-Afrotropical species occur in Asia and the Afrotropis, Palaearctic-Afrotropical species are distributed from the Palaearctis to the Afrotropis. ‘Three or more biogeographical regions’ represents a container for non-tramp widespread species, which occur in the Afrotropis, the Malagasy region, and at least one of the following major biogeographic regions: Australasia, Palaearctis, and Orient. Tramp species are species that were introduced into new areas by human activities and often confined to anthropogenically disturbed habitats. Note that the biogeographical classes are nested and of varying geographical scale (e.g. East African versus Afrotropical).

Statistic analyses

All data considered in the statistic analyses of this study are of nominal type and therefore Pearson's χ^2-tests were used to test on associations between biogeographical distribution, habitat, microhabitat and feeding strategy. In order to test for phylogenetic biases analyses within the three largest subfamilies Formicinae (N = 25 species), Myrmicinae (N = 115 species) and Ponerinae (N = 35 species) were performed separately. P-values in χ^2-tests were computed via Monte Carlo simulations (2000 runs). In the analysis for associations between ecological niche variables a dataset of 308 species was used, under exclusion of all species with unknown data for at least one variable. The dataset for analyses of relationships between niche variables and biogeography class was smaller and contained 216 species, again under exclusion of species with unknown data. All analyses were computed with the freeware R, Version 2.12 (R Development Core Team 2006).

Results

Faunal composition

The Kakamega Forest in Western Kenya is a lower montane rainforest, for the most part between 1500 and 1700 m above sea level. Yet a remarkable ant diversity was found there, the highest recorded for the African continent, including Madagascar, and considering its altitude one of the highest globally. 329 species from 55 genera and 11 subfamilies were recorded for the Kakamega Forest region, with 227 (69 %) of them identified to species level. A number of 102 morphospecies (31 %) remained unidentified. Most of the species are identified on the basis of worker caste specimens, exceptions are nine species where only the males were collected. By far the most important subfamily in terms of diversity and abundance are the Myrmicinae with 177 species and 23 genera (table 2.1), representing about half (54 %) of all species recorded, followed by Formicinae (53 species, 8 genera) and Ponerinae (42 species, 10 genera), Dolichoderinae (17 species), Dorylinae (12 species), Cerapachyinae (11 species) Aenictinae (6 species), Proceratiinae (5 species) and Pseudomyrmicinae (4 species). The two cryptic subfamilies Aenictogitoninae and Leptanillinae are represented by a single species each and only a few collected individuals.

Table 2.1 List for the number of species and genera for each of the 11 subfamilies present in Kakamega Forest (proportions in percent of the total diversity are indicated in paratheses).

Subfamily	Species (%)	Genera (%)
Aenictinae	6 (1.8)	1 (1.9)
Aenictogitoninae	1 (0.3)	1 (1.9)
Cerapachyinae	11 (3.3)	3 (5.8)
Dolichoderinae	17 (5.2)	3 (5.8)
Dorylinae	12 (3.6)	1 (1.9)
Formicinae	53 (16.1)	8 (15.4)
Leptanillinae	1 (0.3)	1 (1.9)
Myrmicinae	177 (53.8)	23 (40.4)
Ponerinae	42 (12.8)	10 (19.2)
Proceratiinae	5 (1.5)	3 (3.8)
Pseudomyrmecinae	4 (1.2)	1 (1.9)
Sum	**329 (100)**	**55 (100)**

The most diverse genera were *Tetramorium* (40 species), *Camponotus* (22), *Crematogaster* (22), *Pheidole* (19), *Monomorium* (19), *Pyramica* (17), *Pachycondyla* (15), and *Lepisiota* (15) (table 2.2). Genera without revisionary treatment for the African continent, for example *Camponotus*, *Pheidole*, *Crematogaster* and *Lepisiota*, generally showed a high number of morphospecies, with more than 50 % unidentified taxa. But even in genera with relatively recent revisions, e.g. *Monomorium* and *Pyramica* (Bolton, 1987; Bolton, 2000), several unidentifiable taxa and potentially new species were collected. Especially in the large genus *Tetramorium*, with its main distribution in Africa and treated by Bolton (1980), 16 out of a total 40 species initially remained unidentifiable and potentially new species, in spite of extensive identification efforts. Hitherto, four of them have already been described as new species (Hita Garcia et al., 2010a; 2010b; 2010c).

Table 2.2 The 12 most diverse genera of the Kakamega Forest are ranked by their dominance according to species numbers.

Genus	**No. of species**
Tetramorium Mayr. 1855	40
Camponotus Mayr. 1861	22
Crematogaster Lund. 1831	22
Pheidole Westwood. 1839	19
Monomorium Mayr. 1855	19
Pyramica Roger. 1862	17
Pachycondyla Smith. F.. 1858	15
Lepisiota Santschi. 1926	15
Cataulacus Smith. F.. 1853	13
Dorylus Fabricius. J.C. 1793	12
Carebara Westwood. 1940	11
Hypoponera Santschi. 1938	11

Ecological patterns

Most of the 329 listed species were exclusively found within near-natural and secondary forest habitats (165 spp., 50 %; Fig. 2.1, table 2.4, Appendix 1). Species confined to open areas, i.e. agricultural fields outside of, or grassland and other open habitats within the forest borders constituted 30 % of the Kakamega ant fauna. About 14 % of all species were found in both, forested and open habitat. For 6 % (20 species) the habitat use remained unknown.

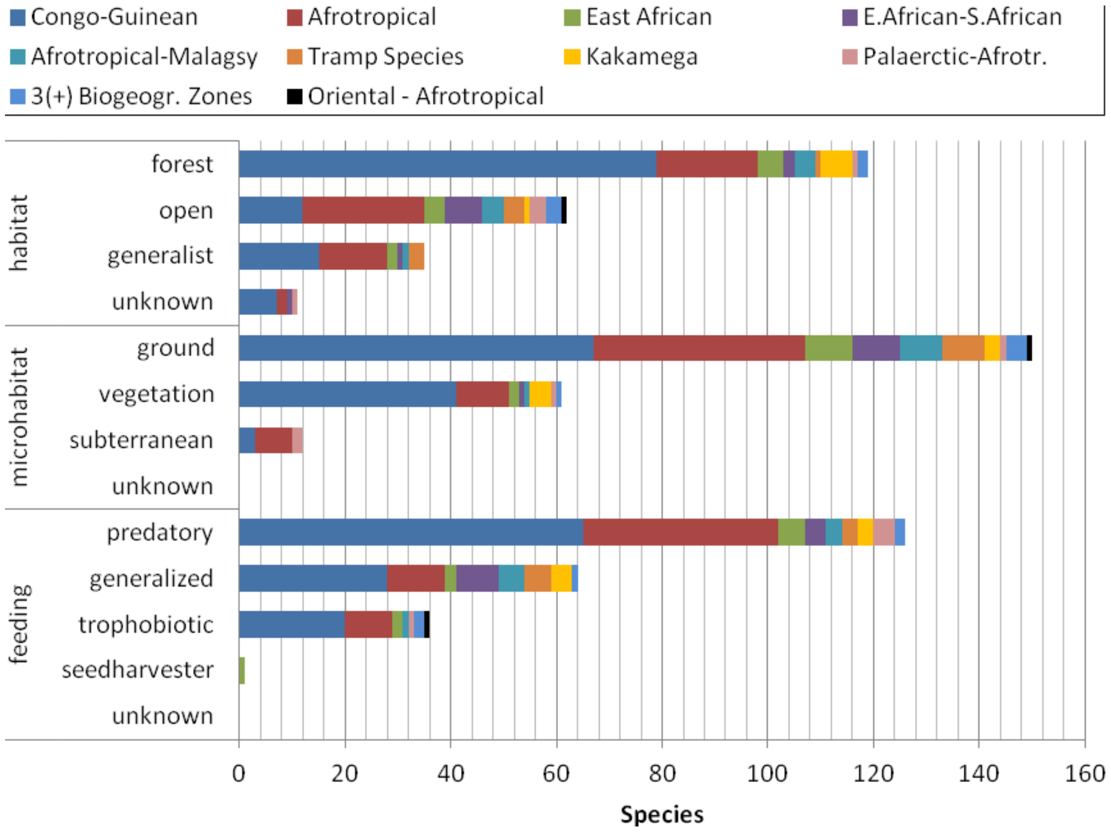

Figure 2.1 Relationships between biogeographic distributions (10 classes) and the three niche variables habitat, microhabitat and feeding.

The largest feeding group is formed by predators (166 spp., 50 %; see table 2.4), as for example doryline army ants, ponerines, and many myrmicine genera, followed by generalized foragers

(112 spp., 34 %), for example dolichoderines, many myrmicines and formicines, and trophobiotic species (48 spp., 14.6 %), like *Camponotus* and *Cataulacus*. *Messor angularis* is the single seed harvester, which was collected in the farmland outside of the forest (Espira, 2001). For *Aenictogiton* spec. (male) and *Dicroaspis* spec. feeding strategies are unknown. Since pitfall trapping and leaf-litter extraction were the main sampling techniques in this study, a majority of 204 species (62 %) of the collected ant fauna occurred in leaf-litter or on the ground. Still, species that are nesting and predominantly foraging in the vegetation constituted about 30 % (99 species) of the entire ant assembly and only about 4.3 % are soil inhabitants (14 subterranean species).

Table 2.3 Chi-square analyses results for two different data sets: **1.** Associations between ecological niche variables habitat, microhabitat and feeding for 308 species (excluding species with unknown data); **2.** Assiociations between biogeographical distributions and niche variables for 216 species (excluding morphospecies and unknown data).

1. Ecological Niche	**X-squared**	**P-value**
habitat. microhabitat. feeding	911.3247	0.0004998 (***)
habitat. microhabitat	47.7713	0.0004998 (***)
habitat. feeding	19.4214	0.002999 (**)
microhabitat. feeding	85.6058	0.0004998 (***)

2. Biogeography	**X-squared**	**P-value**
bgclass. habitat	54.8252	0.0004998 (***)
bgclass. microhabitat	41.6357	0.005997 (**)
bgclass. feeding	60.8006	0.06597 (.)

Analyses of three niche variables (with 308 species) revealed significant relationships between ecological niche characteristics of species (table 2.3). Associations between habitat and microhabitat ($\chi^2 = 47.77$, $p < 0.0005$), microhabitat and feeding type ($\chi^2 = 85.61$, $p < 0.0005$) and between habitat and feeding ($\chi^2 = 19.42$, $p < 0.005$) were all highly significant. The highest proportion of vegetation ants was found in the forest (84 spp., 51.3 %; see Fig. 2.1 and table 2.4), even though the farmland often showed a significant number of trees and and bushes. For open habitat and habitat generalist species, ground living ants made up the largest parts of the communities (77.3% and 79.6%, respectively). Subterranean ants were mostly found in open habitats (10 spp.), in contrast to only two forest and habitat generalist species, respectively. Forest ants comprised almost as many vegetation (78 spp., 47.3 %) as ground inhabiting species (85 spp., 51.5 %), whereas habitat generalists and open habitat species were mostly found on the ground of their habitats (37 spp., 82.2 % and 77 spp., 77.8 %, respectively). Forest specialists also had the highest number and proportion of trophobiotic species (29 spp., 17.6 %), although the open habitat showed a similar proportion (16 spp., 16.1 %). The highest proportions of predators occurred in forest (85 spp., 51.5 %) and habitat generalist species (28 spp., 62.2 %), whereas the highest proportion of generalized feeders belonged to open habitats species (44 spp., 44.4 %). The majority of the ground ants were clearly predatory (129 spp., 63.2 %), followed by generalized feeders (63 spp., 30.9 %), whereas most subterranean ants were specialized or unspecialized predators (11 spp., 78.6 %). Most of the vegetation species were generalized feeders (46 spp., 46.5 %) followed by trophobiotic ants (36 spp., 36.4%). Separate analyses of the three largest subfamilies Formicinae, Myrmicinae and Ponerinae showed significant associations only in the species-rich Myrmicinae and with habitat as dependent variable (115 species: $\chi^2 = 36.3718$, $p < 0.005$), whereas relationships between microhabitat and biogeography or feeding and biogeography were not significant. Also not significant were the results for the other two subfamilies Formicinae and Ponerinae (25 and 35 species, respectively).

Table 2.4 Species niche distributions between habitat and microhabitat (A), habitat and feeding (B), and microhabitat and feeding (C), corresponding to ecological niche analyses (in this table with 329 species in total, including unknowns). Values in parentheses are % of column total.

A)

Microhabitat **Habitat**	ground	subterranean	vegetation	unknown	**sum**
forest	85 (51.5)	2 (1.2)	78 (47.3)	0	163 (100.0)
generalist	37 (82.2)	1 (2.2)	7 (15.6)	0	49 (100.0)
open	77 (77.8)	11 (11.1)	11 (11.1)	0	97 (100.0)
unknown	6 (30.0)	0	2 (10.0)	12 (60.0)	20 (100.0)
sum	204	14	99	12	329

B)

Feeding **Habitat**	generalized	predatory	seedharvester	trophobiotic	unknown	**sum**
forest	50 (30.3)	85 (51.5)	0	29 (17.6)	1 (0.6)	165 (100.0)
generalist	15 (33.3)	28 (62.2)	0	2 (4.4)	0	44 (100.0)
open	44 (44.4)	38 (38.47)	1 (1.0)	16 (16.1)	0	99 (100.0)
unknown	3 (15.0)	15 (75.0)	0	1 (5.0)	1 (5.0)	20 (100.0)
sum	112	166	1	48	2	329

C)

Feeding **Microhabitat**	generalized	predatory	seedharvester	trophobiotic	unknown	**sum**
ground	63 (30.9)	129 (63.2)	1 (0.5)	10 (4.9)	1 (0.5)	204 (100.0)
subterranean	2 (14.3)	11 (78.6)	0	1 (7.1)	0	14 (100.0)
vegetation	46 (46.5)	17 (17.1)	0	36 (36.4)	0	99 (100.0)
unknown	1 (8.3)	9 (75.0)	0	1 (8.3)	1 (8.3)	12 (100.0)
sum	152	126	1	48	2	329

Biogeography

The Kakamega ant fauna is clearly dominated by species with a distribution restricted to the Congo-Guinean rainforest belt (113 of 227 species, ~50%). Another 25% are found in the whole Afrotropical region and only eleven species (~5%) have an East African distribution. The remaining 20% are divided between the other seven biogeographical classes: eleven species with a distribution from South Africa to East Africa (Kenya), nine species with a distribution from the Afrotropis and including Madagascar (e.g. *Cataulacus intrudens, Monomorium hanneli, Odontomachus troglodytes*), eight tramp species (e.g. *Hypoponera punctatissima*, *Monomorium pharaonis, Technomyrmex pallipes*), seven species endemic to the Kakamega region [four *Axinidris* species, *Hyponoera tecta*, *Tetramorium boehmei & T. kakamega*]. Altogether eleven species have distribution ranges beyond the Afrotropical region: five of them are also found in the Palaearctis (*Dorylus affinis, D. fulvus, D. helvolus, Melissotarsus emeryi, Pachycondyla sennaarensis*), one with a disjunct distribution in Africa, India, Sri Lanka and Vietnam (*Camponotus rufoglaucus*), and another five species that occur in Africa, on Madagascar and at least one other major biogeographic region (*Camponotus maculatus, C. sericeus, Lepisiota capensis, Tetramorium sericeiveintre, Hypoponera ragusai).* As chi-square test results indicate, there are significant relationships between biogeographical distribution class and two of the ecological niche variables (table xx). The association between habitat and biogeography class was highly significicant ($\chi^2 = 54.83$, $p < 0.0005$), followed by microhabitat and biogeography class ($\chi^2 = 41.64$, $p = 0.006$). The association with feeding strategy, however, was marginally significant ($\chi^2 = 60.8$ $p = 0.066$).

<u>*Habitats:*</u> In detail, two thirds (66 %) of 119 forest species have a Congo-Guinean distribution, compared to 43 % of the habitat generalists (35 spp.) and only 19 % of open habitat specialists (62 spp.). Instead, habitat generalists and open habitat species are composed of a relatively higher amount of Afrotropical (both 37 %) and tramp species (8.5 % and 6.5 %, respectively)

than the forest specialists (16 % Afrotropical and 0.8 % tramp species). East- & South African distributed species contribute significantly with 11.3 % (7 spp.) to the open habitat ant fauna, while all other distribution classes are generally less important for the overall species composition (0 % - 6.5 %).

Microhabitats: The vegetation (61 spp.) and ground microhabitat (150 spp.) are clearly dominated by Congo-Guinean ant species (67 % and 45 %, respectively), followed by species with Afrotropical distributions (16 % and 27 %). Subterranean ants (12 spp.), however, are mostly Afrotropical (58 %), with only few Congo-Guinean (25 %) and Palaerctic-Afrotropical (17 %) elements. Of the seven species endemic for the Kakamega Forest, six were found only inside the forest, while the other one was collected from open habitat. Tramp species occurred mainly in open habitats (4 spp.) and as habitat generalists (3 spp.), while *Tetramorium lucayanum* was restricted to forest habitat.

Feeding: The feeding strategies generalized foraging, predation, and trophobiosis are distributed in similar proportions among the three main biogeographical classes Congo-Guinean, Afrotropical and East African, while seed harvesting occurs only in one East African species (*Messor angularis*). About 87 % of the predatory and 86 % of the trophobiotic ants were elements of those three classes, but only about 69 % of generalized foragers displayed the same distributions. The other 31 % of generalized foragers divided between Kakamega endemics, East- & South African, Afrotropical-Malagasy, tramp, and non-tramp widespread species.

Discussion

Ant Diversity

The Kakamega Forest represents a diversity hotspot in Kenya and belongs to the regions with the highest ant diversities worldwide. With 329 different ant species and morphospecies, the number is higher than in any other Afrotropical locality. It harbors more than half of the known Kenyan ant fauna (around 600 species, Hita Garcia et al., unpublished) with 55 of 63 genera and 11 of the 12 subfamilies listed for the country. These numbers emphasize the high conservation value of the Kakamega Forest as a diversity repository for the whole country and for the East African region, where deforestation is a constant threat to most forested areas. Of the 329 species, 227 were identified to species level. One-hundred-and-two morphospecies were not identifiable with the current taxonomic literature, emphasizing the necessity of new broad-scale revisions for the Afrotropical fauna. These morphospecies mostly belong to the large and dominant taxa *Camponotus*, *Crematogaster*, *Pheidole* and *Tetramorium*, but also to less abundant and conspicuous genera, such as the surprisingly diverse, *Carebara* (6 of 11 sp. undetermined) and *Lepisiota* (15 of 17 sp. undetermined). Although *Tetramorium* was treated by Bolton in 1980, a large number of new species are accumulating in the different museum collections (Hita Garcia et al., 2010b). The taxonomic situation in the other three genera is far worse and highly confused. *Camponotus*, *Crematogaster*, and *Pheidole* are hyperdiverse and, unfortunately, never underwent a systematic taxonomic treatment in the Afrotropical region. But two smaller revisions for subgroups of the latter two genera (Blaimer, 2010; GF, FHG & MKP, unpublished) hopefully can be seen as first steps towards the large-scale taxonomic studies that are needed to process a large number of new species and the multitude of synonimies accumulated over more than one and a half century.

Ecological & biogeographical patterns

Most species presented here were found within the borders of the Kakamega Forest. Only a small minority seems to occur strictly outside of the forest borders, as for example Pachycondyla analis. Other species preferring open habitats, such as different grassland Camponotus species or the extremely opportunistic Myrmicaria opaciventris can be found along forest roads, in clearings and grasslands within the forest. High human activity levels caused diverse disturbances mostly during the last century, when parts of the forest underwent constant local changes of clear cutting, woodland conversion into grassland, and forest regrowth (Mitchell, 2004; 2008). Thus, Kakamega Forest contains a mix of different habitats, resulting in a rich and comprehensive ant fauna. The highly significant relationships between the three different niche variables showed, that several ecologically specialized communities are existing inside the forest and in the farmland. It is of high conservational value to find that most or the predatory species were found inside the forest, with several highly specialized taxa, as for example the genera Cerapachys, Discothyrea, Hypoponera and tiny dacetine ants of the genera Pyramica and Strumigenys, most of which only occurred in forest habitats. Also many of the trophobiotic or sap-sucking species from the genera Cataulacus, Melissotarsus, Polyrhachis and Camponotus depend on dense and intact forest vegetation to survive.

The open habitat community, however, seems to be much less specialized in terms of microhabitat and feeding, but rather consisted of many opportunistic and generalized species that occur practiacally in everywhere from savanna grassland, woodland, farmland, human settlements, and otherwise disturbed habitats. These species also occurred in larger clearings or grassland glades inside the forest and roads function as corridors along which they can successfully nest and forage. For some, foraging ranges might be extending a bit into the forest or others might be nesting in early secondary forest stages. Many of the rare specialists, that are found exclusively in old-growth forest, as for example endemic species of the genus

Axinidris and other vulnerable species, seem to depend on closed-canopy forest vegetation for their survival, which is why the protection of this forest is paramount for the conservation of a unique biological diversity, not only for ants. They are, however, very useful as indicator taxa. The three genera Pheidole, Pyramica, and Tetramorium, for example, were responding negatively to logging activity inside forested areas (Hita Garica et al., unpublished) and could be used effectively for (long-term) monitoring projects in order to assess the degree of human disturbance in protected and unprotected sites.

The ecological research in our project was clearly focused on ground ants, with additional samples taken from soil and vegetation strata. Thus, number and proportion of vegetation ants (99 species, 30.1 %) is slightly lower in Kakamega Forest. In Kinabalu National Park, Borneo, 202 of altogether 524 species (38.6 %) turned out to be restricted to the lower vegetation and canopy stratum (Brühl et al., 1998). In a canopy study at Budongo Forest, Uganda, 161 ant species in 30 genera were sampled after fogging of 61 individuals from four tree species (Schulz & Wagner, 2002). Because fogging in the Kakamega Forest was applied only on two small to medium sized species of trees, the canopy fauna is probably underrepresented in our study. The same is true for hypogaeic ant species, which are commonly undersampled in many inventories. Only since the last few years an inventory of the hypogaeic ant fauna found more consideration among researchers (Andersen & Brault, 2010; Berghoff et al., 2003; Fonseca et al., 2004; Silva & Silvestre, 2004; Schmidt & Solar, 2010; Ryder Wilkie et al., 2007). Especially after the recent discovery of the completely new subfamily Martialinae it should be a point of interest to study epigaeic ant communities more thoroughly (Rabeling et al., 2008). This means that for our own study the small number of strictly hypogaeic species could be an artifact resulting from insufficient sampling. Additional species from this stratum might be waiting for their discovery and it is not unlikely that worker caste specimens of species as yet represented only by male reproductives (e.g. *Aenictogiton*, some *Aenictus* and *Dorylus* species) turned up with intensified hypogaeic sampling. Also, species found in the literature that were absent from our samples (i.e. 23 species determined by Anton Espira (2001), *Axinidris kakamegensi*, *Dorylus cf. atriceps* and *D. staudingeri*) might be collected with additional hand-sampling or a sampling focus on strata different from the ground.

Biogeographically the Kakamega Forest ant fauna is a mix of species with different distributions zones. Almost half of the local ant fauna consists of species distributed along the Congo-Guinean rainforest belt, confirming our earlier results (Hita Garcia et al., 2009) and the status of Kakamega Forest as eastern-most remnant of a once continuous Equatorial-African rainforest system (Kokwaro, 1988; Wagner et al., 2008). This association becomes even stronger, when considering only forest specialists (119 spp.), of which about two thirds (66 %) are Congo-Guinean faunal elements, emphasizing the importance of the available niches for community compositions. The other third of the forest specialist species represents a mix of local endemics, pan-Afrotropical, Afrotropical-Malagasy, East African, and East- & South African species that also seem to depend on forest vegetation. Species with pan-Afrotropical distributions are the second important element representing about one quarter of the total ant fauna, with the highest affinity towards open habitats inside and outside of the forest borders. The last quarter is almost equally divided between species of other distribution ranges, from local endemics to very widespread species, such as *Camponotus sericeus*, *Hypoponera ragusai*, *Lepisiota capensis* and *Tetramorium sericeiventre*, which are found not only in Africa, but also on Madagascar and at least one of the other major zoogeographical regions, e.g. the Palaearctis or Orientalis. *Camponotus maculatus*, the non-tramp species with the widest distribution in this study, is known from the Afrotropics, Madagascar, the Palaearctis, South East Asia. Several tramp species from the Kakamega area occur in both, open and forest habitat, but so far none seems to be invasive or a threat to the local invertebrate and vertebrate fauna. Invasive ant species, as for example *Technomyrmex albipes*, which might be causing problems in coastal forests of Madagascar (Dejean et al., 2010) and Kenya (unpublished data), are not present in the Kakamega Forest area. With climate change at the doorstep, however, species communities are likely to change in the future (Jenkins et al., 2011) and probably will become more vulnerable to invasions of better adapted alien taxa. In order to learn about the potential risks for the local fauna and flora, to assess the possibility of associated large-scale species extinctions and in order to prevent such invasions more research and long-term ant monitoring projects will be needed.

Ants & Altitude

The high ant species diversity of the Kakamega Forest is extraordinary, seen on a global scale, because it is by far the highest recorded in a montane habitat above 1600 m elevation. Higher species densities were hitherto found only in lowland or mid-altitudinal rainforests in Asia and South America. So far, studies along elevational gradients were facing usually severe diversity drop-offs in ant species richness above 1500 m elevation (table 2.5), with species numbers ranging from 5 to 59 at sites between 1500 and 1700 m (Brühl et al., 1999; Fisher, 1996; 1998; 1999; 2002; Longino & Nadkarni, 1990; Longino & Colwell, 2011; Malsch et al., 2008).

A direct comparison of the results, however, is hampered by strong differences in the amount of sampling sites and effort in general, especially at the highest elevations. Strict inventories were usually confined to or biased toward the lowland sites and no elevational zone above 1500 m was collected with comparable intensity or amount of samples, as is the case in our study (Table 4). Maybe more importantly, climate suitability for ant reproduction and available area usually decrease with rising altitude for elevation gradients mountain study sites. These studies usually have to face a decrease in area and primary productivity with rising altitude, which has been discussed to cause reduced species richness (Laurance et al., 2011; Sanders et al., 2002).

Locality	Species	Genera	Elevation	Individuals analyzed	Highest species no. at altitude	No. of species above 1500 m	Latitude	Publication
Kinabalu NP, Borneo	524	73	550-800	?	---	---	6.08333	Brühl et al., 1998
Panguana, Peru	520	78	220	?	---	---	9.61667	Verhaagh, 1990
Tiputini Biodiv. Station, Equador	489	64	206-224	?	---	---	0.61667	Ryder Wilkie et al, 2010
Pasoh Forest Reserve, Malaysia	467	75	(81-643)	?	---	---	3.00000	Rosciszewski, 1995 (in Brühl et al., 1998)
La Selva Biol. Station, CR	437	?	50-150	?	---	---	10.41667	Longino et al., 2002
La Selva Biol. Station, CR	400	69	50-2000	121,133	500 m	ca. 55	2.28333	Longino & Colwell, 2011
Kinabalu NP, Borneo	376	65	580-1520	37,997	580 m	23	6.03333	Malsch et al., 2008
Kakamega Forest, Kenya	329	55	1550 (±100)	150,000+	**---**	**329**	0.28333	this study
Monts Doudou, Gabon	310	56	110-640	?	110 m	---	0.31667	Fisher, 2004
Kinabalu NP, Borneo	283	55	560-2300	7,622+	560 m	27	6.08333	Brühl et al., 1999
Lambir Hills NP, Malaysia	257	56	(47-443)	?	---	---	4.19833	Yamane & Nona, 1994 (in Brühl et al., 1998)
RNI d'Anjanaharibe-Sud, MDG	213	25	875-1985	27,484	875 m	55 (1565 m)	14.75000	Fisher, 1998
RS d'Monangarivo, MDG	211	33	400-1860	?	780 m	55 (1580 m)	14.00000	Fisher, 2002a
Masoala Peninsula, MDG	197	25	25-1080	52,300	825 m	---	15.62500	Fisher, 1998
Budongo Forest NP, Uganda	161	30	1200	?	---	---	1.75000	Schulz & Wagner, 2002
RNI d'Andringita, MDG	148	28	785-1680	29,562	785 m	31	22.21667	Fisher, 1996
RNI d'Andohahela, MDG	137	25	430-1250	13,717	800 m	---	24.56111	Fisher, 1999
Ankazomivady, MDG	59	19	1670-1700	?	---	59	20.77583	Fisher, 2002b
Monteverde Cl. For. Res., CR	53	25	1550	?	---	53	10.30000	Longino & Nadkari, 1990

Table 2.5 Species diversities of tropical ant faunas in SE-Asia, South America (CR = Costa Rica) and Africa (MDG = Madagascar). Elevations are indicated in meters, latitudes in decimal degrees. Minimum and maximum elevations are displayed for studies with sites located in different altitudes. Altitudes in studies without available references (in parentheses) are derived via GoogleEarth. An important measure is species density at sites above 1500 m altitude.

Because Kakamega Forest and the surrounding area are located on a high plateau with a stable tropical rainforest climate (classified as Köppen's climate Af; Peel et al., 2007), species richness is probably not influenced by these factors here. Another reason for the unusually high ant diversity could be a higher degree of habitat heterogeneity among the sampling sites. But compared to other studies, where different habitat types were sampled (Fisher & Robertson, 2002; Robertson, 2002), the Kakamega Forest ant diversity is several times higher. Generally, the negative relationship of elevation and mean temperature seems to be an important factor correlating with species density (Brühl et al., 1999; Malsch et al., 2008). Where vegetation and climate in the Kakamega Forest are comparable to tropical lowland rainforests, the same elevational zones in several of the gradient studies mentioned above are cooler and moister montane cloud forests. In a global meta-analysis of tropical ant species diversity by Jenkins et al. (2011) a model including different climate variables, biogeographic region, and their interactions constituted the best overall model and temperature was the best single predictor. At the moment it can only be speculated that, together with the differences in sampling intensity, the dissimilarity between the local climates maybe is the ultimate reason for the high discrepancy in species diversities among the studies cited here.

Conclusions

Ants are an often utilized indicator taxon in ecological studies and monitoring projects, and may be a useful surrogate for measuring the influence of human disturbance for biodiversity in general (Crist, 2009). Conversion of old-growth forest into plantations, pasture or agricultural land, leads to seriously modified and reduced ant communities. Even old-growth secondary forest can be depleted of the rarest and most vulnerable species in comparison to uncut natural forests (Bihn et al., 2008). Also species that forage or even nest in the vicinity of human settlements around the forest most likely will not be able to successfully reproduce and, hence, survive without an intact forest in the long-term. For Africa the Kakamega Forest presents not only refuge for the most diverse Afrotropical ant fauna, but also for many vertebrates, especially birds (Bennun & Njoroge, 1999; Zimmermann, 1972) and other invertebrates (Clausnitzer, 2005; Freund, 2005). The facts that a large portion of its fauna and flora are Congo-Guinean elements and that it is a comparatively young forest with a relatively low endemism rate could act as arguments against a priority conservation status. However, the unique transitional locality between the Congo-Guinean rainforest belt, the East African Montane forests and the vast East African savanna ecosystem and the tropical rainforest climate are likely to have caused the unique mixture of species and the highly elevated biodiversity level in this area. Considering the ongoing destruction of pristine habitats in (Afro-) tropical countries, the threats of climate change and a human-caused mass extinction event, biodiversity hotspots are especially valuable for conservation priorities (Myers, 2000). All this should be good reason to consider a full conservation status of the complete forest area, which is currently limited to the National Park zone in the northern parts of the forest.

Appendix: Species checklist for the ants of Kakamega Forest and Western Kenya

Updated species checklist with information about the caste that was used for determination, sources for species identification, ecological data (habitat, microhabitat, feeding), and geographic distribution data (for all species identified to species-level). The last column indicates changes in identification since the first checklist published for Kakamega (Hita Garcia et al., 2009). Morphospecies are indicated with a number and a code for the determinator (AE: A. Espira, CS: C. Schöning, GF: G. Fischer, FHG: F. Hita Garcia, RRS: R. R. Snelling). Abbreviations: ?: unknown; Caste: W: worker, M: male; Determination: for museum collections see chapter 1, table 1.1; Habitat: Gener.: generalist; Microhabitat: Subter.: subterranean, Veget.: vegetation; Feeding: Predat.: predatory, Gener.: generalized, Tropho.: trophobiotic; Biogeography: Afrotr.-Mal.: Afrotropical-Malagasy, EA-SA: East African-Southern African, Congo-Guin.: Congo-Guinean, Orien-Afrotr.: Oriental-Afrotropical, Palae-Afrotr.: Palaearctic-Afrotropical, 3+regions: occurring in three or more biogeographic regions. Previous ID refers the older species identifications in the preliminary checklist (Hita-Garcia et al., 2009).

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**Previous ID**
Subfamily Aenictinae								
Aenictus eugenii Emery, 1895	W	LACM	open	Subter.	Predat.	Afrotropical	East Africa	
Aenictus decolor (Mayr, 1879)	W	LACM	open	Subter.	Predat.	Afrotropical	South Africa	
Aenictus rotundatus Mayr, 1901	W	LACM	open	Subter.	Predat.	Afrotropical	South Africa	
Aenictus sp. FHG 3	M	unidentified	?	?	Predat.			
Aenictus sp. FHG 4	M	unidentified	?	?	Predat.			
Aenictus sp. FHG 5	M	unidentified	?	?	Predat.			

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**Previous ID**
<u>Subfamily Aenictogitoninae</u>								
Aenictogiton sp. FHG 1	M	unidentified	?	?	?			
<u>Subfamily Cerapachyinae</u>								
Cerapachys foreli (Santschi, 1914)	W	Brown, 1975	Forest	Ground	Predat.	Congo-Guin.	Ghana	
Cerapachys kenyensis Consani, 1951	W	Brown, 1975	Forest	Ground	Predat.	East African	Kenya	
Cerapachys nitidulus Brown, 1975	?	A. Espira, 2001	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Cerapachys nkomoensis (Forel, 1916)	W	Brown, 1975	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Cerapachys vespula (Weber, 1949)	W	Brown, 1975	Forest	Ground	Predat.	EA-SA	Kenya	
Cerapachys sp. GF 1	W	unidentified	Forest	Ground	Predat.			
Simopone conradti Emery, 1899	W	Brown, 1975	Forest	Veget.	Predat.	Congo-Guin.	Cameroon	
Simopone grandis Santschi, 1923	W	det. R. R. Snelling	Forest	Veget.	Predat.	Congo-Guin.	D.R. Congo	
Simopone schoutedeni Santschi, 1923	W	Brown, 1975	Forest	Veget.	Predat.	Congo-Guin.	D.R. Congo	
Sphinctomyrmex sp. FHG 1	W	unidentified	Forest	Ground	Predat.			
Sphinctomyrmex sp. FHG 2	W	unidentified	Forest	Ground	Predat.			
<u>Subfamily Dolichoderinae</u>								
Axinidris acholli Weber, 1941	W	Snelling 2007	Forest	Veget.	Gener.	Congo-Guin.	Sudan	
Axinidris bidens Shattuck, 1991	W	Snelling 2007	Forest	Veget.	Gener.	Congo-Guin.	Ghana	
Axinidris hypoclinoides (Santschi, 1919)	W	Snelling 2007	Forest	Veget.	Gener.	Congo-Guin.	D.R. Congo	
Axinidris icipe Snelling, 2007	W	paratype ZFMK	Forest	Veget.	Gener.	Kakamega	Kenya	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**Previous ID**
Axinidris kakamegensis Shattuck, 1991	W	type in BMHN	Forest	Veget.	Gener.	Kakamega	Kenya	
Axinidris luhya Snelling, 2007	W	paratype ZFMK	Forest	Veget.	Gener.	Kakamega	Kenya	
Axinidris murielae Shattuck, 1991	W	Snelling 2007	Forest	Veget.	Gener.	Congo-Guin.	Cameroon	
Axinidris okekai Snelling, 2007	W	paratype ZFMK	Forest	Veget.	Gener.	Kakamega	Kenya	
Tapinoma sp. FHG 1	W	unidentified	Forest	Veget.	Gener.			
Technomyrmex andrei Emery, 1899	W	Bolton, 2007	Forest	Ground	Gener.	Congo-Guin.	Gabon	
Technomyrmex camerunensis Emery, 1899	W	Bolton, 2007	Forest	Ground	Gener.	Congo-Guin.	Cameroon	
Technomyrmex ilgi (Forel, 1910)	W	Bolton, 2007	open	Ground	Gener.	EA-SA	Ethiopia	
Technomyrmex moerens Santschi, 1913	W	Bolton, 2007	Forest	Ground	Gener.	Congo-Guin.	D.R. Congo	
Technomyrmex nigriventris Santschi, 1910	W	Bolton, 2007	Forest	Veget.	Gener.	Congo-Guin.	D.R. Congo	
Technomyrmex pallipes (Smith, F., 1876)	W	Bolton, 2007	Gener.	Ground	Gener.	Tramp Sp.	Mauritius	
Technomyrmex voeltzkowi (Forel, 1907)	W	Bolton, 2007	open	Ground	Gener.	Afrotr.-Mal.	Kenya	
Technomyrmex sp. FHG 5	W	unidentified	Forest	Veget.	Gener.			
<u>Subfamily Dorylinae</u>								
Dorylus affinis Shuckard, 1840	W	det. C. Schöning	open	Subter.	Predat.	Palae.-Afrotr.	Gambia	
Dorylus cf. atriceps Shuckard, 1840	M	det. C. Schöning	?	?	Predat.	Congo-Guin.	Gambia	
Dorylus braunsi Emery, 1895	W	det. C. Schöning	open	Subter.	Predat.	Congo-Guin.	Liberia	
Dorylus conradti Emery, 1895	W	ZFMK	open	Subter.	Predat.	Congo-Guin.	Togo	
Dorylus fimbriatus (Shuckard, 1840)	W	ZFMK	open	Subter.	Predat.	Afrotropical	Gambia	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**Previous ID**
Dorylus fulvus (Westwood, 1839)	W	ZFMK	open	Subter.	Predat.	Palae.-Afrotr.	North Africa	
Dorylus helvolus Linnaeus 1764	M	LACM	?	?	Predat.	Palae.-Afrotr.	South Africa	
Dorylus kohli Wasmann, 1904	W	det. C. Schöning	Gener.	Subter.	Predat.	Congo-Guin.	D.R. Congo	
Dorylus nigricans molestus (Gerstäcker, 1859)	W	ZFMK	Gener.	Ground	Predat.	EA-SA	Mozambique	
Dorylus staudingeri Emery, 1895	M	det. C. Schöning	?	?	Predat.	Congo-Guin.	D.R. Congo	
Dorylus wilverthi Emery, 1899	W	det. C. Schöning	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Dorylus (Typhlopone) sp. CS 01	M	det. C. Schöning	?	?	Predat.			
<u>Subfamily Formicinae</u>								
Acropyga silvestrii Emery, 1915	W	LaPolla & Fisher, 2005	Forest	Subter.	Tropho.	Afrotropical	Eritrea	
Camponotus bayeri Forel, 1913	W	LACM	open	Ground	Tropho.	Congo-Guin.	D.R. Congo	
Camponotus brutus Forel, 1886	W	LACM	Forest	Veget.	Tropho.	Congo-Guin.	Angola	
Camponotus chrysurus Gerstäcker, 1871	W	Santschi, 1926	Forest	Veget.	Tropho.	Congo-Guin.	Kenya	
Camponotus erinaceus Gerstaecker, 1871	W	Forel, 1899	open	Ground	Tropho.	East African	Tanzania	
Camponotus flavomarginatus Mayr, 1862	W	LACM	open	Ground	Tropho.	Afrotropical	Ghana	
Camponotus foraminosus Forel, 1879	W	LACM	Gener.	Ground	Tropho.	Afrotropical	Senegambia	
Camponotus maculatus (Fabricius, 1782)	W	Mayr, 1862; LACM	open	Ground	Tropho.	3+ regions	West Africa	
Camponotus perrisii Forel, 1886	W	LACM	open	Ground	Tropho.	Congo-Guin.	Angola	
Camponotus pompeius Forel, 1886	W	LACM	Forest	Veget.	Tropho.	Congo-Guin.	Gabon	

Species Identification	Caste	Determination	Habitat	Microhabitat	Feeding	Biogeography	Type Locality	previous ID
Camponotus rufoglaucus Jerdon, 1851	W	LACM	open	Ground	Tropho.	Orien.-Afrotr.	India	
Camponotus rubripes (Latreille, 1802)	?	A. Espira, 2001	Forest	Ground	Tropho.	Congo-Guin.	Sierra Leone	
Camponotus sericeus (Fabricius, 1798)	W	Mayr, 1862	open	Veget.	Tropho.	3+ regions	Senegal	
Camponotus solon Forel, 1886	W	LACM	Forest	Veget.	Tropho.	Congo-Guin.	Angola	
Camponotus vividus Smith, F., 1858	W	Santschi, 1926	Forest	Veget.	Tropho.	Congo-Guin.	Sierra Leone	
Camponotus sp. FHG 2	W	unidentified	open	Veget.	Tropho.			
Camponotus sp. FHG 4	W	unidentified	open	Veget.	Tropho.			
Camponotus sp. FHG 10	W	unidentified	open	Veget.	Tropho.			
Camponotus sp. FHG 11	W	unidentified	open	Veget.	Tropho.			
Camponotus sp. FHG 20	W	unidentified	open	Veget.	Tropho.			
Camponotus sp. FHG 21	W	unidentified	Forest	Veget.	Tropho.			
Camponotus sp. FHG 23	W	unidentified	open	Veget.	Tropho.			
Camponotus sp. GF 24	W	unidentified	open	Ground	Tropho.			
Camponotus sp. GF 25	W	unidentified	open	Veget.	Tropho.			
Lepisiota capensis (Mayr, 1862)	?	A. Espira, 2001	Forest	Ground	Gener.	3+ regions	South Africa	
Lepisiota crinita (Mayr, 1895)	?	A. Espira, 2001	?	?	Gener.	EA-SA	South Africa	
Lepisiota sp. FHG 1	W	unidentified	open	Veget.	Gener.			
Lepisiota sp. FHG 2	W	unidentified	open	Ground	Gener.			
Lepisiota sp. FHG 3	W	unidentified	Gener.	Veget.	Gener.			

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Lepisiota sp. FHG 4	W	unidentified	open	Ground	Gener.			
Lepisiota sp. FHG 5	W	unidentified	open	Ground	Gener.			*L. guineensis*
Lepisiota sp. FHG 6	W	unidentified	Forest	Veget.	Gener.			
Lepisiota sp. FHG 7	W	unidentified	Gener.	Ground	Gener.			
Lepisiota sp. FHG 8	W	unidentified	Forest	Ground	Gener.			
Lepisiota sp. FHG 10	W	unidentified	open	Ground	Gener.			
Lepisiota sp. FHG 11	W	unidentified	Forest	Veget.	Gener.			
Lepisiota sp. FHG 12	W	unidentified	open	Ground	Gener.			
Lepisiota sp. FHG 13	W	unidentified	open	Ground	Gener.			
Lepisiota sp. FHG 14	W	unidentified	open	Ground	Gener.			
Nylanderia sp. FHG 1	W	unidentified	Gener.	Ground	Gener.			
Nylanderia sp. FHG 2	W	unidentified	Forest	Ground	Gener.			
Paraparatrechina umbranatis LaPolla & Cheng, 2010	W	LaPolla, 2004	Gener.	Ground	Gener.	Congo-Guin.	Gabon	
Paraparatrechina brunella LaPolla & Cheng, 2010	W	LaPolla, 2004	open	Ground	Gener.	Congo-Guin.	Cameroon	
Paraparatrechina weissi (Santschi, 1910)	W	LaPolla, 2004	Forest	Ground	Gener.	Congo-Guin.	Congo	
Phasmomyrmex sp. FHG 1	W	tentative new species	Forest	Veget.	Gener.			*P. wolfi*
Plagiolepis decora Santschi, 1914	W	LACM	Forest	Veget.	Gener.	EA-SA	South Africa	
Plagiolepis brunni Mayr, 1895	W	Mayr, 1895	open	Veget.	Gener.	Afrotropical	Mozambique	
Plagiolepis sp. FHG 1	W	unidentified	Forest	Veget.	Gener.			

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Polyrhachis latispina Emery, 1925	W	Bolton, 1973	Gener.	Veget.	Tropho.	Congo-Guin.	D.R. Congo	
Polyrhachis lestoni Bolton, 1973	W	Bolton, 1973	Forest	Veget.	Tropho.	Congo-Guin.	Ghana	
Polyrhachis militaris (Fabricius, 1782)	W	Bolton, 1973	Forest	Veget.	Tropho.	Afrotropical	Tropical Africa	
Polyrhachis schistacea (Gerstäcker, 1859)	W	Bolton, 1973	open	Ground	Tropho.	Afrotropical	Mozambique	*P.* sp. FHG 4
Polyrhachis sp. GF 1	W	tentative new species	?	?	Tropho.			
<u>Subfamily Leptanillinae</u>								
Leptanilla sp. FHG 1	W	unidentified	Forest	Subter.	Predat.			
<u>Subfamily Myrmicinae</u>								
Atopomyrmex mocquerysi Andre, 1889	W	Bolton, 1981	Forest	Veget.	Gener.	Afrotropical	Senegal	
Calyptomyrmex brunneus Arnold, 1948	W	Bolton, 1981	Gener.	Ground	Predat.	EA-SA	South Africa	
Calyptomyrmex clavatus Weber, 1952	W	Bolton, 1981	Gener.	Ground	Predat.	Afrotropical	Kenya	
Calyptomyrmex duhun Bolton, 1981	W	Bolton, 1981	Forest	Ground	Predat.	Congo-Guin.	Uganda	
Calyptomyrmex foreli Emery, 1915	W	Bolton, 1981	open	Ground	Predat.	Afrotropical	Ethiopia	
Calyptomyrmex piripilis Santschi, 1923	W	Bolton, 1981	Gener.	Ground	Predat.	Afrotropical	D.R. Congo	
Calyptomyrmex tensus Bolton, 1981	?	A. Espira, 2001	?	Ground	Predat.	Congo-Guin.	Uganda	
Cardiocondyla emeryi Forel, 1881	W	Bolton, 1982; Rigato 2002	open	Ground	Gener.	Tramp Sp.	Virgin Islands	
Cardiocondyla sp. FHG 1	W	unidentified	open	Ground	Gener.			*C. shuckardi*
Cardiocondyla sp. FHG 3	W	unidentified	open	Ground	Gener.			
Carebara distincta (Bolton & Belshaw, 1993)	W	Bolton & Belshaw, 1993	Forest	Ground	Predat.	Congo-Guin.	Ghana	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Carebara elmenteitae (Patrizi, 1948)	W	Patrizi, 1948	Forest	Ground	Predat.	East African	Kenya	
Carebara polita (Santschi, 1914)	W	Arnold, 1948	Gener.	Ground	Predat.	Afrotropical	Kenya	
Carebara rara (Bolton & Belshaw, 1993)	W	Bolton & Belshaw, 1993	Gener.	Ground	Predat.	Congo-Guin.	Kenya	
Carebara thoracica (Weber, 1950)	W	Weber, 1950	Gener.	Ground	Predat.	Congo-Guin.	Uganda	
Carebara sp. GF 4	W	tentative new species	Gener.	Ground	Predat.			
Carebara sp. GF 5	W	tentative new species	Gener.	Ground	Predat.			
Carebara sp. GF 6	W	tentative new species	Gener.	Ground	Predat.			
Carebara sp. GF 7	W	tentative new species	Forest	Ground	Predat.			
Carebara sp. GF 8	W	tentative new species	open	Ground	Predat.			
Carebara sp. GF 9	W	tentative new species	Forest	Ground	Predat.			
Cataulacus brevisetosus Forel, 1901	W	Bolton, 1982	Forest	Veget.	Tropho.	Afrotropical	Angola	
Cataulacus egenus Santschi, 1911	W	Bolton, 1982	Forest	Veget.	Tropho.	Congo-Guin.	Congo	
Cataulacus guineensis Smith, 1853	W	Bolton, 1982	Forest	Veget.	Tropho.	Congo-Guin.	Tr. West Africa	
Cataulacus intrudens (Smith, F., 1876)	W	Bolton, 1982	Forest	Veget.	Tropho.	Afrotr.-Mal.	South Africa	
Cataulacus jeanneli Santschi 1914	W	Bolton, 1982	Forest	Veget.	Tropho.	Afrotropical	Kenya	
Cataulacus lujae Forel, 1911	W	Bolton, 1982	Forest	Veget.	Tropho.	Congo-Guin.	D.R. Congo	
Cataulacus kenyensis Santschi, 1935	W	Bolton, 1982	Forest	Veget.	Tropho.	East African	Kenya	
Cataulacus moloch Bolton, 1982	W	Bolton, 1982	Forest	Veget.	Tropho.	Congo-Guin.	Ghana	
Cataulacus pullus Santschi, 1910	W	Bolton, 1982	Forest	Veget.	Tropho.	Congo-Guin.	Congo	

Species Identification	Caste	Determination	Habitat	Microhabitat	Feeding	Biogeography	Type Locality	previous ID
Cataulacus striativentris Santschi, 1924	W	Bolton, 1982	Forest	Veget.	Tropho.	Congo-Guin.	D.R. Congo	
Cataulacus tardus Santschi, 1914	W	Bolton, 1982	Forest	Veget.	Tropho.	Congo-Guin.	Guinea	
Cataulacus traegaordhi Santschi, 1914	W	Bolton, 1982	Forest	Veget.	Tropho.	Afrotropical	South Africa	
Cataulacus vorticus Bolton, 1974	W	Bolton, 1982	Forest	Veget.	Tropho.	Congo-Guin.	Nigeria	
Crematogaster africana Mayr, 1895	?	A. Espira, 2001	Forest	Veget.	Gener.	Congo-Guin.	Cameroon	
Crematogaster clariventris Mayr, 1895	W	LACM	Forest	Veget.	Gener.	Congo-Guin.	Congo	
Crematogaster concava Emery, 1899	W	LACM	Forest	Veget.	Gener.	Congo-Guin.	Cameroon	
Crematogaster gabonensis Emery, 1899	?	A. Espira, 2001	?	Veget.	Gener.	Congo-Guin.	Gabon	
Crematogaster gambiensis André, 1889	?	A. Espira, 2001	Forest	Veget.	Gener.	Afrotropical	Gambia	
Crematogaster litoralis Arnold, 1955	W	Arnold, 1955	Gener.	Veget.	Gener.	East African	Kenya	
Crematogaster rugosa André, 1895	?	A. Espira, 2001	Forest	Veget.	Gener.	Congo-Guin.	Congo	
Crematogaster stadelmanni Mayr, 1895	?	A. Espira, 2001	?	Veget.	Gener.	Congo-Guin.	Liberia	
Crematogaster striatula Emery, 1892	?	A. Espira, 2001	Gener.	Veget.	Gener.	Congo-Guin.	Ivory Coast	
Crematogaster wellmani Forel, 1909	W	Forel, 1909	Forest	Veget.	Gener.	Afrotropical	Angola	
Crematogaster sp. FHG 1	W	unidentified	open	Veget.	Gener.			
Crematogaster sp. FHG 4	W	unidentified	Forest	Veget.	Gener.			
Crematogaster sp. FHG 7	W	unidentified	Forest	Veget.	Gener.			
Crematogaster sp. FHG 8	W	unidentified	Gener.	Veget.	Gener.			
Crematogaster sp. FHG 9	W	unidentified	Gener.	Veget.	Gener.			

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Crematogaster sp. FHG 10	W	unidentified	open	Veget.	Gener.			
Crematogaster sp. FHG 11	W	unidentified	Forest	Veget.	Gener.			
Crematogaster sp. FHG 15	W	unidentified	Forest	Veget.	Gener.			
Crematogaster sp. FHG 16	W	unidentified	Gener.	Veget.	Gener.			
Crematogaster sp. FHG 17	W	unidentified	Forest	Veget.	Gener.			
Crematogaster sp. GF 18	W	unidentified	Forest	Veget.	Gener.			
Crematogaster sp. GF 19	W	unidentified	Forest	Veget.	Gener.			
Cyphoidris spinosa Weber, 1952	W	Bolton, 1981	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Decamorium decem (Forel, 1913)	W	Bolton, 1976	Forest	Ground	Predat.	Afrotropical	Zimbabwe	
Dicroaspis sp. AE 1	?	A. Espira, 2001	Forest	Ground	?			
Meranoplus inermis Emery 1895	W	Bolton, 1981	Gener.	Ground	Predat.	Afrotropical	South Africa	
Melissotarsus emeryi Forel, 1907	?	A. Espira, 2001	Forest	Veget.	Tropho.	Palae.-Afrotr.	Ethiopia	
Melissotarsus weissi Santschi, 1910	W	Bolton, 1982	Forest	Veget.	Tropho.	Congo-Guin.	Congo	
Messor angularis Santschi, 1928	?	A. Espira, 2001	open	Ground	Seed H.	East African	Kenya	
Microdaceton tibialis Weber, 1952	W	Bolton, 2000	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Monomorium afrum André, 1884	W	Bolton, 1987	open	Ground	Gener.	Afrotropical	Sudan	
Monomorium arboreum Weber, 1943	?	A. Espira, 2001	Forest	Ground	Gener.	Congo-Guin.	Sudan	
Monomorium bicolor Emery, 1877	W	Bolton, 1987	open	Ground	Gener.	Tramp Sp.	Ethiopia	
Monomorium cryptobium (Santschi, 1921)	W	Bolton, 1987	Forest	Ground	Gener.	Afrotr.-Mal.	D.R. Congo	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Monomorium draxocum Bolton,1987	W	Bolton, 1987	Forest	Ground	Gener.	Congo-Guin.	Cameroon	
Monomorium hanneli Forel, 1907	W	Bolton, 1987	Gener.	Ground	Gener.	Afrotr.-Mal.	Kenya	
Monomorium iyenasu Bolton, 1987	W	Bolton, 1987	open	Ground	Gener.	East African	Tanzania	
Monomorium madecassum Forel, 1892	W	Bolton, 1987	open	Ground	Gener.	Afrotr.-Mal.	Madagascar	
Monomorium malatu Bolton, 1987	W	Bolton, 1987	open	Ground	Gener.	Congo-Guin.	D.R. Congo	
Monomorium mictile Forel, 1910	W	Bolton, 1987	open	Ground	Gener.	Afrotropical	Ethiopia	
Monomorium paternum Bolton, 1987	W	Bolton, 1987	open	Ground	Gener.	EA-SA	South Africa	
Monomorium pharaonis (Linnaeus, 1758)	W	Bolton, 1987	open	Ground	Gener.	Tramp Sp.	Egypt	
Monomorium robustior Forel, 1892	W	Bolton, 1987	open	Ground	Gener.	Afrotr.-Mal.	Somalia	
Monomorium rosae Santschi, 1920	W	Bolton, 1987	open	Ground	Gener.	Afrotropical	D.R. Congo	
Monomorium rotundatum Santschi, 1920	W	Bolton, 1987	open	Ground	Gener.	EA-SA	South Africa	
Monomorium spectrum Bolton, 1987	?	A. Espira, 2001	Forest	Ground	Gener.	Congo-Guin.	Gabon	
Monomorium sp. GF 17	W	tentative new species	Forest	Veget.	Gener.			
Monomorium sp. GF 21	W	tentative new species	Gener.	Ground	Gener.			
Myrmicaria natelensis eumenoides (Gerstäcker, 1859)	?	A. Espira, 2001	open	Ground	Gener.	EA-SA	Mozambique	
Myrmicaria opaciventris Emery, 1893	W	LACM	open	Ground	Gener.	Afrotropical	Angola	
Nesomyrmex cataulacoides Snelling, 1992	W	LACM	Forest	Veget.	Gener.	Congo-Guin.	Cameroon	
Nesomyrmex evelynae (Forel, 1916)	W	LACM	Forest	Veget.	Gener.	Congo-Guin.	D.R. Congo	
Pheidole aurivillii Mayr, 1896	W	type NHMW	Forest	Veget.	Gener.	Congo-Guin.	Cameroon	*P.* sp. FHG 15

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Pheidole crassinoda Emery, 1895	W	cotype MHNG	open	Ground	Gener.	EA-SA	South Africa	*P.* sp. FHG 17
Pheidole dea Santschi 1921	W	Santschi, 1921	Forest	Ground	Gener.	Congo-Guin.	D.R. Congo	*P. pulchella*
Pheidole megacephala (Fabricius, 1793)	W	LACM	open	Ground	Gener.	Tramp Sp.	unknown	
Pheidole nigeriensis Santschi, 1914	W	type NMB	Gener.	Ground	Gener.	Congo-Guin.	Nigeria	*P.* sp. FHG 5
Pheidole prelli Forel, 1911	W	type MHNG	open	Ground	Gener.	Afrotropical	Kenya	*P.* sp. FHG 2
Pheidole speculifera Emery, 1877	W	cotype NMB	Forest	Ground	Gener.	Afrotropical	Ethiopia	
Pheidole sp. FHG 3	W	unidentified	Forest	Ground	Gener.			
Pheidole sp. FHG 7	W	unidentified	Forest	Ground	Gener.			
Pheidole sp. FHG 8	W	unidentified	open	Ground	Gener.			*P. aurivillii*
Pheidole sp. FHG 9	W	unidentified	Gener.	Ground	Gener.			
Pheidole sp. FHG 10	W	unidentified	open	Ground	Gener.			
Pheidole sp. FHG 12	W	unidentified	Forest	Ground	Gener.			
Pheidole sp. FHG 18	W	unidentified	open	Ground	Gener.			
Pheidole sp. FHG 19	W	unidentified	open	Ground	Gener.			
Pheidole sp. FHG 20	W	unidentified	Gener.	Ground	Gener.			
Pheidole sp. FHG 21	W	unidentified	open	Ground	Gener.			
Pheidole sp. FHG 22	W	unidentified	open	Ground	Gener.			
Pheidole sp. GF 23	W	unidentified	open	Ground	Gener.			
Pristomyrmex africanus Karavaiev, 1931	W	Bolton, 1981	Forest	Ground	Predat.	Afrotropical	Kenya	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Pyramica bellatrix Bolton, 2000	W	Bolton, 2000	Forest	Ground	Predat.	Congo-Guin.	Burundi	
Pyramica cavinasis (Brown, 1950)	W	Bolton, 2000	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Pyramica concolor (Santschi, 1914)	W	Bolton, 2000	Gener.	Ground	Predat.	Congo-Guin.	Ghana	
Pyramica geoterra (Bolton, 1983)	W	Bolton, 2000	Forest	Ground	Predat.	Congo-Guin.	Cameroon	
Pyramica hensekta (Bolton, 1983)	W	Bolton, 2000	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Pyramica ludovici (Forel, 1904)	W	Bolton, 2000	Forest	Ground	Predat.	Afrotr.-Mal.	Madagascar	
Pyramica lujae (Forel, 1902)	W	Bolton, 2000	Gener.	Ground	Predat.	Afrotropical	Mozambique	
Pyramica marginata (Santschi, 1914)	W	Bolton, 2000	Forest	Ground	Predat.	Afrotropical	Kenya	
Pyramica minkara (Bolton, 1983)	W	Bolton, 2000	Forest	Ground	Predat.	Congo-Guin.	Ivory Coast	
Pyramica serrula (Santschi, 1910)	W	Bolton, 2000	Gener.	Ground	Predat.	Afrotropical	Congo	
Pyramica simoni (Emery, 1895)	W	Bolton, 2000	Forest	Veget.	Predat.			
Pyramica sulumana (Bolton, 1983)	W	Bolton, 2000	Gener.	Ground	Predat.	Congo-Guin.	Cameroon	
Pyramica tetragnatha Taylor, 1966	W	Bolton, 2000	Forest	Ground	Predat.	Congo-Guin.	Angola	
Pyramica thuvida (Bolton, 1983)	W	Bolton, 2000	Forest	Ground	Predat.	East African	Kenya	
Pyramica sp. GF 9	W	tentative new species	Forest	Ground	Predat.			
Pyramica sp. GF 16	W	tentative new species	Forest	Ground	Predat.			
Pyramica sp. GF 17	W	tentative new species	Gener.	Ground	Predat.			
Rhoptromyrmex opacus Forel, 1909	W	Bolton, 1986	open	Ground	Gener.	Congo-Guin.	Cameroon	
Rhoptromyrmex transversinodis Mayr, 1901	W	Bolton, 1986	open	Ground	Gener.	EA-SA	South Africa	

Species Identification	Caste	Determination	Habitat	Microhabitat	Feeding	Biogeography	Type Locality	previous ID
Solenopsis punctaticeps Mayr, 1865	W	LACM	open	Subter.	Gener.	Afrotropical	South Africa	
Solenopsis sp. FHG 2	W	unidentified	open	Subter.	Gener.			
Strumigenys arnoldi Forel, 1913	W	Bolton, 2000	open	Ground	Predat.	EA-SA	Zimbabwe	
Strumigenys cacaoensis Bolton, 1983	W	Bolton, 2000	Forest	Ground	Predat.	Congo-Guin.	Nigeria	
Strumigenys dextra Brown, 1954	?	A. Espira, 2001	?	Ground	Predat.			
Strumigenys katapelta Bolton,1983	?	A. Espira, 2001	?	Ground	Predat.	Congo-Guin.	Burundi	
Strumigenys korahyla Bolton, 1983	W	Bolton, 2000	Gener.	Ground	Predat.	Congo-Guin.	Cameroon	
Strumigenys petiolata Bernard, 1953	?	A. Espira, 2001	Forest	Ground	Predat.	Congo-Guin.	Guinea	
Strumigenys rukha Bolton, 1983	W	Bolton, 2000	Gener.	Ground	Predat.	Congo-Guin.	Kenya	
Strumigenys tetraphanes Brown, 1954	W	Bolton, 2000	Forest	Ground	Predat.	Congo-Guin.	Uganda	
Strumigenys sp. GF 3	W	unidentified	Forest	Ground	Predat.			
Strumigenys sp. GF 7	W	unidentified	open	Ground	Predat.			
Tetramorium aculeatum (Mayr, 1866)	W	Bolton, 1980	Forest	Veget.	Predat.	Congo-Guin.	Ghana	
Tetramorium boehmei Hita Garcia & Fischer, 2010	W	Hita Garcia et al., 2010c	Forest	Ground	Predat.	Kakamega	Kenya	
Tetramorium boltoni Hita Garcia et al., 2010	W	Hita Garcia et al, 2010b	Forest	Ground	Predat.	Congo-Guin.	Kenya	*T. guineense*
Tetramorium brevispinosum (Stitz, 1910)	W	Bolton, 1976	Gener.	Ground	Predat.	Congo-Guin.	Togo	
Tetramorium caldarium (Roger, 1857)	W	Bolton, 1980	open	Ground	Predat.	Tramp Sp.	Germany	
Tetramorium cristatum Stitz, 1910	W	Bolton, 1980	open	Ground	Predat.	Congo-Guin.	Togo	
Tetramorium dedefra Bolton, 1976	W	Bolton, 1976	Forest	Ground	Predat.	Congo-Guin.	Angola	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Tetramorium dumezi Menozzi, 1942	W	Bolton, 1980	open	Ground	Predat.	Congo-Guin.	Ghana	*T.* sp. FHG 36
Tetramorium edouardi Forel 1894	W	Bolton, 1980	open	Ground	Predat.	East African	Ethiopia	
Tetramorium eminii (Forel, 1894)	W	Bolton, 1976	open	Ground	Predat.	Afrotropical	Ethiopia	
Tetramorium gazense Arnold, 1958	W	Bolton, 1980	open	Ground	Predat.	Afrotropical	Zimbabwe	
Tetramorium kakamega Hita Garcia et al., 2010	W	Hita Garcia et al, 2010b	Forest	Ground	Predat.	Kakamega	Kenya	*T.* sp. FHG 14
Tetramorium kestrum Bolton, 1980	W	Bolton, 1980	Forest	Ground	Predat.	Congo-Guin.	Uganda	
Tetramorium laevithorax Emery, 1895	W	Bolton, 1980	open	Ground	Predat.	Afrotropical	South Africa	
Tetramorium lucayanum Wheeler, W.M., 1905	W	Bolton, 1980	Forest	Ground	Predat.	Tramp Sp.	Bahamas	
Tetramorium metactum Bolton, 1980	W	Bolton, 1980	Forest	Veget.	Predat.	Congo-Guin.	Kenya	
Tetramorium nodiferum (Emery, 1901)	W	Bolton, 1980	open	Ground	Predat.	Congo-Guin.	Cameroon	
Tetramorium pialtum Bolton, 1980	W	Bolton, 1980	Forest	Veget.	Predat.			
Tetramorium pinnipilum Bolton, 1980	W	Bolton, 1980	Forest	Ground	Predat.	Congo-Guin.	Angola	
Tetramorium pullulum Santschi, 1924	W	Bolton, 1980	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Tetramorium quadridentatum Stitz, 1910	W	Bolton, 1980	Forest	Veget.	Predat.	Congo-Guin.	Cameroon	
Tetramorium sericeiventre Emery, 1877	W	Bolton, 1980	open	Ground	Predat.	3+ regions	Ethiopia	
Tetramorium setigerum Mayr, 1901	W	Bolton, 1981	open	Ground	Predat.	Afrotropical	South Africa	
Tetramorium snellingi Hita Garcia et al., 2009	W	Hita Garcia et al., 2010a	Forest	Ground	Predat.	Congo-Guin.	Kenya	*T.* sp. FHG *2*
Tetramorium viticola Weber, 1943	W	Bolton, 1980	Forest	Veget.	Predat.	Congo-Guin.	Sudan	
Tetramorium weitzeckeri Emery, 1895	W	Bolton, 1980	open	Ground	Predat.	Afrotropical	South Africa	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Tetramorium zambezium Santschi, 1939	W	Bolton, 1980	Gener.	Ground	Predat.	Afrotropical	Zimbabwe	*T. delagoense*
Tetramorium zonacaciae (Weber, 1943)	W	Bolton, 1980	open	Ground	Predat.	Congo-Guin.	Sudan	
Tetramorium sp. FHG 1	W	unidentified	Forest	Ground	Predat.			
Tetramorium sp. FHG 11	W	unidentified	Forest	Veget.	Predat.			*T. candidum*
Tetramorium sp. FHG 12	W	unidentified	Forest	Veget.	Predat.			*T. camerunense*
Tetramorium sp. FHG 19	W	unidentified	Forest	Veget.	Predat.			
Tetramorium sp. FHG 21	W	unidentified	Forest	Veget.	Predat.			
Tetramorium sp. FHG 27	W	tentative new species	open	Ground	Predat.			*T. zapyrum*
Tetramorium sp. FHG 39	W	unidentified	Forest	Ground	Predat.			
Tetramorium sp. FHG 40	W	unidentified	Forest	Ground	Predat.			
Tetramorium sp. FHG 42	W	unidentified	open	Ground	Predat.			
Tetramorium sp. FHG 44	W	unidentified	open	Ground	Predat.			
Tetramorium sp. FHG 46	W	unidentified	Forest	Veget.	Predat.			
Tetramorium sp. FHG 47	W	unidentified	open	Ground	Predat.			
Subfamily Ponerinae								
Anochetus africanus (Mayr, 1865)	W	Brown, 1978	Gener.	Ground	Predat.	Congo-Guin.	Ghana	
Anochetus bequaerti Forel, 1913	W	Brown, 1978	Gener.	Ground	Predat.	Afrotropical	D.R. Congo	
Anochetus katonae Forel, 1907	W	Brown, 1978	Forest	Ground	Predat.	Afrotropical	Tanzania	
Anochetus maynei Forel, 1913	W	Brown, 1978	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Anochetus pellucidus Emery, 1902	W	Brown, 1978	Forest	Veget.	Predat.	Congo-Guin.	Cameroon	
Anochetus sp. GF 6	W	unidentified	Gener.	Ground	Predat.			
Centromyrmex sellaris Mayr, 1896	W	Bolton & Fisher, 2008	open	Subter.	Predat.	Afrotropical	Cameroon	
Hypoponera angustata (Santschi, 1914)	W	Bolton & Fisher, 2011	Forest	Ground	Predat.	Congo-Guin.	Guinea	*H.* sp. FHG 5
Hypoponera coeca (Santschi, 1914)	W	Bolton & Fisher, 2011	Gener.	Ground	Predat.	Afrotropical	Cameroon	
Hypoponera dulcis (Forel 1907)	W	Bolton & Fisher, 2011	Forest	Ground	Predat.	Afrotropical	Tanzania	*H.* sp. FHG 1
Hypoponera inaudax (Santschi, 1919)	W	Bolton & Fisher, 2011	open	Ground	Predat.	Congo-Guin.	D.R. Congo	
Hypoponera jeanneli (Santschi, 1935)	W	Bolton & Fisher, 2011	Forest	Ground	Predat.	Afrotropical	Kenya	*H.* sp. FHG 7
Hypoponera occidentalis (Bernard, 1953)	W	Bolton & Fisher, 2011	Forest	Ground	Predat.	Afrotropical	Guinea	
Hypoponera punctatissima (Roger, 1859)	W	Bolton & Fisher, 2011	Gener.	Ground	Predat.	Tramp Sp.	Germany	*H.* sp. FHG 2
Hypoponera ragusai (Santschi, 1914)	W	Bolton & Fisher, 2011	Forest	Ground	Predat.	3+ regions	Italy	
Hypoponera importuna Bolton & Fisher 2011	W	Bolton & Fisher, 2011	Forest	Ground	Predat.	Congo-Guin.	Gabon	
Hypoponera fatiga Bolton & Fisher 2011	W	Bolton & Fisher, 2011	Forest	Ground	Predat.	Congo-Guin.	Ghana	
Hypoponera tecta Bolton & Fisher 2011	W	Bolton & Fisher, 2011	open	Ground	Predat.	Kakamega	Kenya	
Leptogenys elegans Bolton, 1975	W	Bolton, 1975	Forest	Veget.	Predat.	Congo-Guin.	Nigeria	
Leptogenys sp. FHG 1	W	unidentified	open	Ground	Predat.			
Odontomachus assiniensis Emery, 1892	W	Brown, 1976	Forest	Ground	Predat.	Afrotropical	Ivory Coast	
Odontomachus troglodytes Santschi, 1914	W	Brown, 1976	open	Ground	Predat.	Afrotr.-Mal.	Kenya	
Pachycondyla ambigua André, 1890	W	LACM	Forest	Ground	Predat.	Afrotr.-Mal.	Sierra Leone	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Pachycondyla analis (Latreille, 1802)	W	LACM	open	Ground	Predat.	Afrotropical	Guinea	
Pachycondyla brunoi Forel, 1913	W	LACM	open	Ground	Predat.	Afrotropical	Zimbabwe	
Pachycondyla caffraria (Smith, F., 1858)	?	A. Espira, 2001	?	Ground	Predat.	Afrotropical	South Africa	
Pachycondyla crassa (Emery, 1877)	W	LACM	Gener.	Ground	Predat.	Afrotropical	Ethiopia	
Pachycondyla pachyderma Emery, 1901	?	A. Espira, 2001	?	Ground	Predat.	Congo-Guin.	Cameroon	
Pachycondyla sennaarensis (Mayr, 1862)	W	LACM	open	Ground	Predat.	Palae.-Afrotr.	Sudan	
Pachycondyla sjostedti (Mayr, 1896)	W	LACM	Gener.	Ground	Predat.	Congo-Guin.	Cameroon	
Pachycondyla soror (Emery, 1899)	?	A. Espira, 2001	?	Ground	Predat.	Afrotropical	Cameroon	
Pachycondyla subiridescens (Wheeler, W.M., 1922)	W	LACM	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Pachycondyla suspecta (Santschi, 1914)	W	LACM	Forest	Ground	Predat.	East African	Tanzania	
Pachycondyla talpa (André, 1890)	W	LACM	Forest	Ground	Predat.	Congo-Guin.	Sierra Leone	
Pachycondyla tarsata (Fabricius, 1798)	W	LACM	open	Ground	Predat.	Afrotropical	Senegal	
Pachycondyla sp. nov (GF 10)	W	tentative new species	Forest	Ground	Predat.			
Phrynoponera gabonensis (André, 1892)	W	Bolton, 2008	Forest	Ground	Predat.	Congo-Guin.	Gabon	
Psalidomyrmex procerus Emery, 1901	W	Bolton, 1975	Forest	Ground	Predat.	Congo-Guin.	Cameroon	
Platythyrea gracillima Wheeler, W.M., 1922	W	Brown, 1975	Forest	Ground	Predat.	Congo-Guin.	D.R. Congo	
Platythyrea modesta Emery, 1899	W	Brown, 1975	open	Ground	Predat.	Afrotropical	Cameroon	
Platythyrea schultzei Forel, 1910	W	Brown, 1975	Forest	Veget.	Predat.	Afrotropical	Namibia	
Plectroctena subterranea Arnold, 1915	W	Bolton, 1974	Forest	Ground	Predat.	Afrotropical	Zimbabwe	

Species Identification	**Caste**	**Determination**	**Habitat**	**Microhabitat**	**Feeding**	**Biogeography**	**Type Locality**	**previous ID**
Subfamily Proceratiinae								
Discothyrea mixta Brown, 1958	W	LACM	Forest	Ground	Predat.	Congo-Guin.	Liberia	
Discothyrea sp. nov (GF 2)	W	tentative new species	Forest	Ground	Predat.			
Probolomyrmex guineensis Taylor, 1965	W	Taylor, 1965	Forest	Ground	Predat.	Congo-Guin.	Guinea	
Proceratium sp. RRS 1	M	LACM	?	?	Predat.			
Proceratium sp. RRS 2	M	LACM	?	?	Predat.			
Subfamily Pseudomyrmecinae								
Tetraponera mocquerysi (André, 1890)	W	LACM	Forest	Veget.	Tropho.	Afrotropical	Sierra Leone	
Tetraponera ophthalmica (Emery, 1912)	W	Ward, 2006	Forest	Veget.	Tropho.	Congo-Guin.	Cameroon	
Tetraponera sp. FHG 1	W	tentative new species	Forest	Veget.	Tropho.			
Tetraponera sp. FHG 2	W	tentative new species	Forest	Veget.	Tropho.			

Chapter 3:

Diversity, ecosystem functions and trophic ecology in a rainforest ant community (Hymenoptera, Formicidae) along a disturbance gradient in Western Kenya

with F. Hita Garcia, E. Wiesel, F. Herchen, G. Gebauer and M. K. Peters - unpublished

Abstract

Rapid loss of natural habitats and climate change are causes for increasing species extinctions with the highest impact in the biodiversity-rich tropical rain forests. Despite high efforts in the scientific community to investigate the link(s) between species diversity and ecosystem stability, fundamental knowledge about the actual consequences of biodiversity loss for ecosystem functions and services in complex ecosystems accumulates comparatively slowly. The functions and services performed by rare species seem to be especially important in natural habitats, while heavily disturbed areas are impoverished in both species numbers and functional diversity. In this study a highly diverse ant fauna was investigated along a land-use gradient in a Congo-Guinean rain forest remnant in Western Kenya and in the surrounding farmland, where sugarcane is one of the main cash crops. Altogether 162 ant species were collected in three different habitats: near-natural forest, subsistence sugarcane and intensive sugarcane production farmland. Additional to species diversity, also the functional diversity, relative predator proportions, trophic chain lengths and the ecosystem function scavenging were determined for the different ant communities. Functional diversity indices were computed on basis of a trait matrix containing continuous measurements for five morphological and two ecological characters (including stable isotope values) for 84 species in total. The results reveal a highly positive relationship between species and functional diversity (ANOVA: $p = 0.0000023$), which strongly decreased with growing habitat disturbance and land-use intensity ($p = 0.00023$). Habitat disturbance was also responsible for decreased predator diversity in farmland sites ($p = 0.00019$), especially in intensively managed sugarcane monocultures, where pesticides and herbicides are used regularly to increase crop production. Interestingly trophic chain length decreased only from forest to subsistence sugarcane farmland (ANOVA: $p = 0.047$; Tukey HSD test: $p = 0.0389$), but (on average) increased again in intensive sugarcane production areas (Tukey HSD test: $p = 0.299$). However, variability of trophic chain lengths in the intensive sugarcane fields was high, indicating that fertilizer and pesticide use were probably influencing plant net productivity and consumer trophic positions. Additional baiting experiments showed that the scavenging rates ($p = 0.0467$) were significantly higher in the farmland than in the forest and positively related ($p = 0.0005$) to higher ant activities. This contracting result to the functional diversity analyses can be explained by a methodological bias towards opportunistic generalized feeders, which are usually responding much better to baiting than specialized taxa. Specialized ants, such as many predators and rare species, which are often considered as good indicators of overall biodiversity levels, were mostly absent in sugarcane monocultures, highlighting the biologically and ecologically deprived state of the intensively managed habitat and the importance of undisturbed forests for diversity conservation.

Keywords: Kakamega Forest; Afrotopical; species diversity; functional diversity; trophic chain length; food web complexity; ecosystem functions; land-use intensification; scavenging

Introduction

The present biodiversity crisis is driven primarily by anthropogenic land use change, habitat destruction and pollution (Sala et al., 2000). And climate change is most likely to become the latest and maybe most severe threat to life on the planet as we know it (Barnosky et al., 2011; Leakey & Lewin, 1995; Pimm, 1995; Wilson, 2003). If current rates of carbon dioxide green house gas emission are not significantly reduced within this decade, world temperatures are predicted to strongly increase during this century (Williams, 2000). Thus, the extensive use of fossil fuels urgently needs to be replaced with alternative energy sources (CBD, 2008). One solution proclaimed by many policy makers is the substitution of fossil with plant-derived energy, part of which is being grown from agricultural crops for the production of biofuels. The mandatory use of biofuels in the transportation system has already been legally adopted in several countries, in order to gain independence of increasingly expensive oil imports (Ren21, 2011). To date numerous biological studies were published, however, on the detrimental effects of natural forest conversion into agricultural landscapes and land-use intensification in complex agroecosystems on species diversity (Bisseleua et al, 2009; Dunn, 2004; Steffan-Dewenter et al., 2007). Oil palm production in South East Asia, for example, contributed significantly to the destruction and conversion of natural tropical forests with devastating effects on local species richness, with little or no conservation value for forest species, even compared to other plantations (Danielsen et al., 2009; Fitzherbert et al., 2008; Koh & Ghazoul, 2008 Wilcove & Koh, 2010; Pfeiffer et al, 2008; Wilcove & Koh, 2010). Sugarcane is one of the most important crops for biofuel production in the tropics and its agriculture is supposed to increase and to be intensified in the future (Fargione et al., 2010; Martinelly & Filoso, 2008). Still, the negative environmental impacts of industrialized sugarcane monocultures even outweigh the energy efficient production of sugarcane-derived ethanol, which is a major intensive-production crop fuelling the Brazilian economy. Yet, the consequences of the conversion of natural habitats to sugarcane agriculture and its intensification are still little understood (Scharlemann & Laurance, 2008).

Apart from the already mentioned loss of species, land-use intensification may also affect the functionality of ecosystems with implications for human well-being (MEA 2005). For example, natural and semi-natural habitats act as sources of beneficial organisms that ensure pest control and pollination services in agroecosytems (Klein et al., 2007; Ricketts et al., 2008). The pressures of changing biotic and abiotic environmental conditions on flora and fauna are manifold and the loss of keystone species, especially top-predators, can affect food-chains via cascading effects in vulnerable habitats (Terborgh et al., 2001; Terborgh et al., 2006). The connection between species diversity, and ecosystem functions and services has been extensively investigated, however, often in structurally relatively simple temperate grassland communities and not in complex forest ecosystems (Balvanera, 2006; Hooper et al., 2005). There is a significant amount of uncertainty about the consistency of the effects measured in spatially restricted studies, when they are scaled up to the level of complete ecosystems (Cardinale et al., 2011; Loreau et al., 2001). Moreover, the studied ecosystem functions and processes were mostly those that are provided by or related to plants, while just few studies concentrated on ecosystem processes maintained by animals (Cardinale et al., 2011). Processes found to be affected were for example primary productivity, plant biomass, leaf-litter decomposition and nutrient cycling. The vast diversity of invertebrates occupies fundamental roles in the functioning of natural ecosystems (Hölldobler & Wilson, 2009). Especially ants are considered essential organisms in ecosystems. They are ecologically important in providing several ecosystem services and functions, from increasing soil aeration and water drainage with their tunnels, seed dispersal, nutrient aggregation at their nesting sites, to scavenging and predation of dead and live animals, respectively (Folgarait, 1998; Hölldobler & Wilson, 1990). Ants are also an abundant and diverse taxon, and they are easy to sample and sensitive to the different levels of human disturbance (Agosti, 2000). For these reasons, they are an often utilized biological indicator and focal taxon in ecological research, species monitoring, and conservation planning (Andersen, 1997; 1998; King et al., 1998; Peck et al., 1998; Underwood & Fisher, 2006). Although some complex agricultural landscapes in the vicinity of natural forests may support the survival of forest species to some extent (Armbrecht et al., 2005; Belshaw & Bolton, 1993; Bos et al., 2007), the overall consensus is that both the permanent transformation of forest into agricultural land, and agricultural intensification cause a dramatic reduction in overall species richness (Brühl & Eltz, 2010; Floren & Linsenmair, 2005; Philpott et al., 2010). Yet, it remains relatively little understood how the transformation of natural habitats and complex agricultural landscapes to industrial agricultural production systems affects ecosystem processes and functions in complex tropical ant assemblages.

The aim of this publication is to analyze and discuss the consequences of the conversion of natural rainforest into agricultural landscapes and of the intensification of sugarcane production on the species diversity and functional ecology of ant communities. The research body concerning the relationship between biodiversity and functional diversity increased constantly during the last decades. Probably the most important issue in this research is the (long-term) conservation of ecosystem processes (Balvanera et al., 2006; O’Gorman, et al. 2011; Schmitz, 2007). Because direct measurements of ecosystem functions and processes of an entire natural community or even parts of it are practically impossible in complex habitats, the currently best alternative is to indirectly deduce ecosystem functions performed by a range of taxa or species via morphological characters for example. For ants there is already a wide basis of knowledge on the theoretical and concrete relationships between morphology and the functions performed in their respective environments (Weiser & Kaspari, 2006).

Functional diversity (FD) has been defined as the value and range of organismal traits that are important for the functioning of ecosystems (Tilman et al., 1997). In contrast to species richness indices, where every species contributes equally to a community, and implicitly to ecosystem properties and processes, FD measures take into account species’ or even individuals’ traits and facilitate identification of functionally unique or redundant organisms (O’Gorman et al., 2001). In the beginning analyses were conducted for functional groups, arbitrary units of supposedly functionally related species. In several Australian ant assemblages, for example, functional group diversity and species diversity were significantly related (Andersen & Majer, 2004; Andersen et al., 2004). One disadvantage of many functional group analyses has been the use of arbitrarily chosen classes, where differences within these groups are not considered (Petchey & Gaston, 2002b; Walker et al., 2008). Within recent years a growing number of studies accordingly used continuous measurements instead of groups, for ants this was done for some Neotropical communities (Bihn et al., 2010; Weiser & Kaspari, 2006, Silva & Brandao, 2010).

For this study, the changes in structure, species and functional diversity within ant assemblages along a habitat degradation gradient were investigated, as well as the differences in trophic chain lengths and in the ecosystem service scavenging. One way to provide adequate information about species niches is to investigate the trophic relationships of the species concerned. For complex food webs in diverse habitats direct observations for species assemblages are, however, not feasible. Therefore, stable nitrogen isotope measurements were employed as a measure for trophic positions of ant species within local food-webs (Hood-Nowotny & Knols, 2007; Post, 2002a) and in order to calculate the total length of local food-chains represented in ant communities (Post, 2002b). In local brown food webs ants often constitute the organisms at the top of food chains. Highly predacious ants like army ants prey on a variety of other predators like spiders, wasps, and other ants (Mirenda et al, 1980). Therefore, the lengths of food chains derived from ant communities (in comparison to local producer communities) often represent the total food chain lengths of local brown food webs.

The main hypotheses that are addressed here are:

1) Ant species and functional diversity are positively correlated and both decline with increasing anthropogenic habitat disturbance along the land-use gradient.
2) Complex subsistence farmland supports a variety of forest species that cannot be found in high-intensity sugarcane production sites.
3) Increasing habitat disturbance leads to modified community compositions and reduced predator diversities in the farmland. Results are a decline in local food-web complexity and shorter trophic chain lengths in the farmland, as compared to the forest.
4) Changes in community compositions along the land-use gradient majorly affect the ecosystem functions performed by ants, in this case scavenging of injured or dead animals, change.

Material and Methods

Research area & Study sites

The study was conducted between June 2007 and July 2009, in and near the Kakamega Forest. The land-use gradient included three different habitats: near-natural rainforest, subsistence sugarcane farmland in different distances from the forest and large-scale sugarcane agriculture in industrialized monocultures. The two intensive sugarcane monocultures studied were of much larger scale than the subsistence fields and plantations near the forest. The one was situated near Mumias (0°22' N, 34°31' E), 28 km west and the other near Bungoma, (0°33' N, 34°40' E), 25 km northwest from the forest borders, with a distance of about 18 km separating the two. Their estimated sizes were about 5300 ha and 4300 ha, respectively. The intensive monocultures differed from subsistence farms not only in size, but also in the use of mineral fertilizer, pesticides and herbicides, which was missing in small farms. Also they did not or barely contain hedges or other alternative kinds of vegetation, in contrast to the subsistence plots where farm borders are generally formed with hedges offering home to a variety of shrubs, bushes and trees, some usually also growing inside the fields.

Twenty-one study sites were established in total. Eight of them were located within near-natural forest of the main forest fragment. The other thirteen study sites are divided into seven plots in subsistence sugarcane fields and six plots in intensive monocultures (Fig. 3.1).

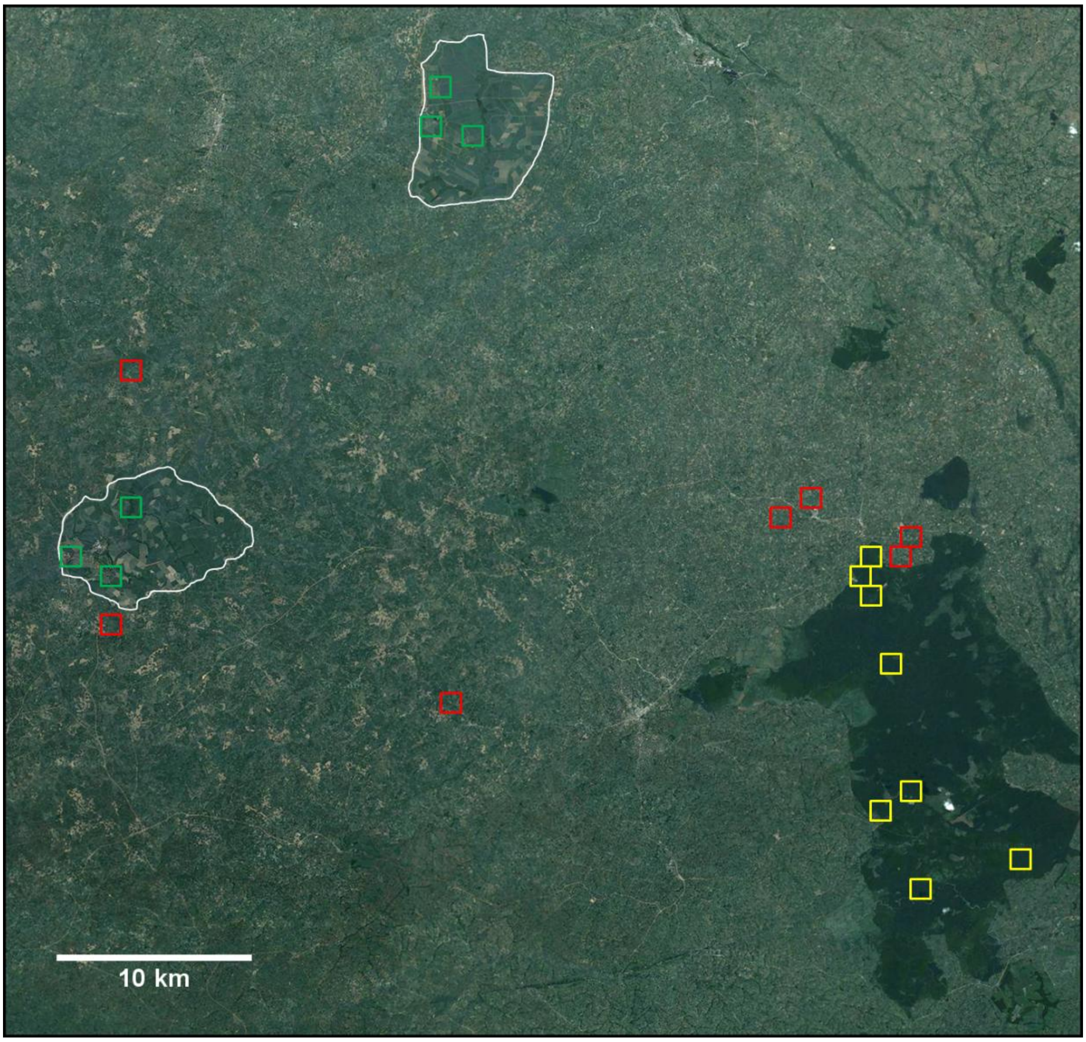

Figure 3.1 Satellite map of the Kakamega Forest (in dark green, with yellow squares indicating the eight study sites inside the forest) and the densely populated surrounding region in Western Kenya, which is mostly characterized by subsistence agriculture (seven sugarcane study sites, indicated in red). The dimensions of the two very large and intensively managed sugarcane monocultures are marked with white borders (six study sites, indicated by green squares). Source: http://www.maps-for-free.com.

Of the seven study sites in subsistence fields four were located in relatively short distances to the forest borders (0.065 km to 4.1 km), while the other three were located further away in direction towards the sugarcane monocultures (between 16 km and 37 km distance to the forest). In each of the two large sugarcane monocultures we established three transects. Due to the large extent of the sugarcane monocultures transects could be placed in large distances to each other, maximizing their spatial independence. The minimum distance between every two transects was 300 m inside the forest and 600 m outside of the forest, in order to reduce community overlaps between study sites. Therefore, every sampling transect can be considered as an independent replicate.

Ant sampling and statistics

Pitfall trapping and leaf-litter sampling with Winkler extraction, following the methodology described in Bestelmeyer (2000), were used to collect ground-foraging and leaf-litter inhabiting ants. One linear, 200 m long transect was established in each study site. In forest and intensive-production sugarcane monocultures transects were placed in the interior of each habitat, at least 50 m away from any other habitats to avoid edge effects. The small size and consequently the proximity of gardens, hedgerows and other crops is an integral part of the subsistence agriculture system. Therefore, even though the complete transect line was within sugarcane, the distance of the transect line to any other habitat was considerably less than 50 m. Twenty pitfall traps were placed at 10 m intervals along each transect, and collected after seven days. The traps were constructed of a standard plastic cup, dug in with the rim at ground level and filled with 3-5 cm (depending on climate at the different sites) of absolute ethanol (99.6 %), and protected by a wooden roof (20 cm x 20 cm, 10 cm above the ground) against dilution from rain fall. After trap collection ants were sorted out and stored in 2 ml tubes (or bigger vials if many ants were present) filled with absolute ethanol. Ten 1m^2 leaf-litter samples per transect were collected in 14 study sites and sieved in litter sifters with 10 mm mesh size to remove coarse organic matter. The leaf-litter invertebrates were extracted for seven days in Winkler sacks and stored in separate vials (100 ml) filled with absolute ethanol. Ants were sorted out later in the lab. Specimens of each morphospecies in every study site were mounted and, where possible, identified to species level. Where a scientific name could not be assigned, the specimens were given morphospecies codes consisting of a number and an abbreviation for the identifier. Absolute abundances (individual numbers) per sample were counted for rarefaction of the estimated species richness per site and the ‘individuals-per-trap’ index (see under functional diversity further below). With the pitfall trap data, the estimated species richness per study site was calculated as the average of five widely used estimators (Chao 1, Chao 2, Jack 1, Jack 2, Bootstrap) with the freeware EstimateS, Version 7 (Colwell, 2008). Species occurrences per transect, defined as relative abundances or species’ presence-absence data per sample, were used, because in the case of ants conspecific individuals in the same sample are most likely from the same colony, thus representing one reproductive unit. All statistical analyses including that for functional diversity were computed with the pitfall trap data set, because Winkler sample data were not obtained for 7 of the 21 study sites. They were conducted with the R, Version 2.12 (R Development Core Team 2006), using the additional packages APE and VEGAN for the functional dendrogram (see further below) and for functional diversity analyses. Standard ANOVA was used to investigate differences in mean species richness and diversity, functional diversity indices, predator proportions, trophic chain lengths, and scavenging rates among habitats. In case of a significant ANOVA, Tukey HSD posthoc tests were used to test on differences between habitat pairs. To analyse the relationship between functional diversity measures, species diversity, and habitat ordinary linear models were used. Species presence-absence data for all 21 transects was the basis for a non-metri multi-dimensional scaling (NMDS) ordination which was computed in order to infer differences in community compositions among the different habitats (Lee et al., 2005). Using the default setting of the metaMDS function (R-package: VEGAN), rank information of distances along environmental gradients was calculated with the Bray-Curtis index. The two predictor variables **S** (species richness) and 'ant activity' were correlated to the ordination using the envfit (environmental fit) function.

Stable isotopes and trophic chain length

Stable isotope ($\delta^{15}N$) data were used to measure the trophic positions of ant species. Ant communities typically span several trophic levels from primary consumers (herbivores) and secondary consumers (opportunists) to higher levels of specialized predators (Blüthgen et al., 2003; Bihn et al., 2010). Due to metabolic pathways the heavier $\delta^{15}N$ isotopes accumulate in trophic food webs from one level to the next and increase about 2-3‰ with each trophic level (Feldhaar et al., 2010; McCutchan et al., 2003). The number of species measured per study site varied with size and abundance of ants collected per transect. For accurate measurements with an average error rate of about 0.2 ‰ 0.1 mg to 1 mg of dry biomass per sample were needed, which was the case for most of our measurements. For slightly lower sample weights the average error rate increased to between 0.2 and 0.4 ‰, which is significantly lower than any intraspecific variation measured in this study (SD: 0.02 - 2.46 ‰). Very small ants with few individuals, as for example several *Monomorium* species, could not be considered for stable isotope analyses. We removed the gaster of each analyzed ant in order to avoid an influence of undigested food, which is often stored in the crop for distribution among nest mates. Prior to analysis, samples were oven-dried at 60°C for 48 hours. Stable isotope rates were measured with an elemental analyzer - isotope ratio mass spectrometer (EA-IRMS) coupling (EA type 1108, Carlo Erba, Milano, Italy; ConFlo III interface and gas-IRMS delta S, both Finnigan MAT, Bremen, Germany). The formula for the stable isotope ratio $\delta^{15}N$ is:

$$\delta^{15}N = ((R_{sample} / R_{standard}) -1) \times 10^3$$

where R_{sample} is the ratio of heavier to lighter isotopes ($^{15}N/^{14}N$) in one sample and $R_{standard}$ is the relation of heavier to lighter isotopes in the international standard (N_2 in air). We also collected, dried, grounded, and analyzed a mix of leaves from the most abundant plants along transects. This site-specific nitrogen baseline for the primary producers was measured in order to correct for site-specific variations in $\delta^{15}N$ values among consumers, so that measurements could be compared across sites and habitats. The formula used is:

$\delta^{15}N$ (corrected) = $\delta^{15}N$ (measured) - $\delta^{15}N$ (plant baseline).

From here on the corrected stable nitrogen values are simply referred to as $\delta^{15}N$. Food chain length was defined as a measure for the height of a food web (Post & Takimoto, 2007) and has been hypothesized to be ultimately determined factors as different as ecosystem stability (or external disturbance strength), resource availability, and ecosystem size (Takimoto et al., 2008).

Trophic chain length was determined for each study site as deviation between the plant baseline and the species with the highest mean $\delta^{15}N$ value. Several predatory ant species are keystone species (Hölldobler & Wilson, 1990; Mirenda et al., 1980) which perform important ecosystem functions and, in the case of army ants, seem to increase or maintain overall invertebrate diversity (Franks & Bossert, 1983). They have been shown to reduce crop pests (Way & Khoo, 1992) and affect lower trophic levels via cascading (or top-down) effects (Terborgh et al., 2006). Because of their high range of occupied trophic levels from mutualistic herbivores to higher-level predators (Blüthgen, 2003; Davidson, 2003; Tillberg et al., 2006) ants are ideal organisms for the determination of food-web complexity and trophic chain length. The proportion of predatory species, opposed to opportunistic and trophobiotic species, was determined for each study site, following Bolton (1980) and Brown (2000).

Ecosystem services scavenging

Because of their ubiquitous distribution and enormous abundances in most terrestrial habitats (Hölldobler & Wilson, 1990) ants are highly efficient in detecting and removing even larger carrion within a relatively short amount of time. We used baiting experiments with immobilized fly larvae to assess the ecosystem function scavenging in all three habitats (five transects each). At ten positions every 20 m along the transect one freshly injured fly larva was placed on a plant leaf on the ground. Then, ant activity at the bait and time until bait removal was monitored for up to 90 min, until either the larva was taken by ants, or until the time had passed. The two resulting response variables were:

1.) 'ant activity', defined as the proportion of baits in each study site that were visited by ants.

2.) 'scavenging rate', defined as the proportion of traps where the baits were removed by ants.

Functional Diversity

In addition to the qualitative methods described above, we also applied quantitative functional diversity analyses in order to assess structural differences among the investigated ant communities. Morphological and ecological traits have been frequently applied to classify species into functional groups of often closely related species (Andersen, 2000). When continuous measurements of functionally relevant traits are used instead, the resolution in the trait matrix increases to a species- or even individual-based level. Functional diversity results can be used to understand and predict community responses to different kinds of disturbances (Andersen, 1997; Bihn, 2010), and in order to simplify the utilization of ants as biological indicators. As many closely related ant species tend to have similar ecological niches (Weiser & Kaspari, 2006), functional group information does not provide the resolution necessary to fully determine the range of ecological functions provided in diverse communities. The same is usually true for single morphological or ecological traits, such as foraging or nesting strategies, which is why sets of different traits perform best in functional diversity analyses (Petchey & Gaston, 2006). Here we used a mix of five different morphological and two ecological measurements and indices, representing important aspects of species ecological niches and ecosystem functions performed by ants in general and derived from Bihn et al. (2010) and Weiser & Kaspari (2006). The morphological indices are calculated as measures relative to head length and width to correct for differences in overall body size. The presented functional traits are:

Head length (HL): Size of the head as a measure for body size and biomass of species, which are indications of several ecological traits. Head size for example is associated with prey size (Kaspari, 1996) and biomass with the amount of resource requirements.

Relative eye size (RES): eye size is most probably related to feeding strategy (e.g. predatory versus trophobiotic) and microhabitat, where a species lives and forages (e.g. bigger eyes in arboreal versus small or absent eyes in hypogaeic species) (Weiser & Kaspari, 2006).

Formula: $$\left(\frac{EL+EW}{HL} * 0.5 + \frac{EL+EW}{HW} * 0.5\right) * 0.5$$

Relative leg length (RLL): leg length is related to foraging speed (Franks et al., 1999; Feener et al., 1988), maximum prey size (Kaspari, 1996), and an indication of habitat preferences (e.g. long legs in epigaeic swarm raiding army ants versus short legs in hypogaeic foragers) (Kaspari & Weiser, 1999).

Formula: $$\left(\frac{FL+TL}{HL} + \frac{FL+TL}{HW}\right) * 0.5$$

Relative mandible length (RML): mandible length is associated with feeding preferences and can act as a measure for trophic specialization (e.g. the long mandibles of *Strumigenys* as trap jaws for Collembola) (Kaspari et al., 2000).

$$\text{Formula: } (\frac{MDL}{HL} + \frac{MDL}{HW}) * 0.5$$

Relative scape length (RSL): scape length is viewed as the range in which an ant can collect chemosensory and tactile information (Weiser & Kaspari, 2006).

$$\text{Formula: } (\frac{SL}{HW} + \frac{SL}{HL}) * 0.5$$

Stable nitrogen ratio (dN): Stable nitrogen values are a direct measurement of an organisms trophic level in the local food chain (reviewed in Hood-Nowotny & Knols, 2007).

$$\text{Formula: } \delta^{15}N = ((R_{sample} / R_{standard}) -1) \times 10^3$$

Individuals per trap (IPT): Average number of specimens of a species in a pitfall trap (only traps with > 0 individuals of the respective species were considered): this index incorporates information about colony size, foraging behaviour (e.g. mass recruiting army ants versus solitary ponerines) and preferred microhabitat (i.e. abundances of ground ants in pitfall traps much higher than those of hypogaeic or vegetation species).

All morphological traits were measured with an Olympus SZX 12 dissecting microscope and a dual-axis micrometer under magnifications up to 90x. Morphological traits represent the mean values of up to three measured individuals per species. Only for a few very rare species, the number of individuals measured was smaller. To cover for intraspecific variability in dimorphic and polymorphic species workers of different sub-castes were measured.

Functional richness and diversity

Functional diversity was analyzed on the basis of a functional trait matrix for all species collected in this study. Both weighted and unweighted indices were then calculated for the ant community in each separate study site. The two widely used unweighted indices were functional diversity (FD) (Petchey & Gaston, 2002b) and functional attribute diversity (FAD) (Walker et al., 1999). In contrast to FD the FAD index is sensitive to the addition or removal of redundant species in a community (Petchey & Gaston, 2006; Walker et al., 2008). Both indices are not weighted by abundances or species occurrences and are directly correlated to species richness (Walker et al., 2008). The FD is defined as the total length of all branches in the functional dendrogram. Calculating FD, the functional trait matrix was converted into a distance matrix for the pairwise distances between functional spaces of all species. Subsequently a cluster algorithm transformed the distance matrix into a functional dendrogram or similarity-tree (Fig. 1), displaying similarities in species' niches (Bihn et al., 2010). Prior to that, all functional trait values were standardized by z-transformation to ensure equal importance of all functional traits. As the calculated FD values are strongly affected by the choice of distance measure and cluster algorithm, we tested four common distance methods (Euclidean, Manhattan, Canberra, and Minkowski) in combination with seven different clustering methods (Ward, Single, Complete, Average, McQuitty, Median and Centroid) in order to find the best suited method for our dataset. The strongest cophenetic correlation of 0.82 was found for the combination of Euclidean distance and Average clustering methods, which were hence used for our analyses. The second unweighted index, the FAD, is calculated as the sum of all pairwise distances between species in the functional distance matrix (Walker et al., 2008). Again Euclidean distances were used as the dissimilarity measure. Because unweighted functional diversity indices do not take into account the differences in species abundances, they are more properly viewed as measures of functional richness in a given locality (Bihn et al., 2010).

Therefore, the FD index was used for investigating the link between functional and species richness between disturbed and undisturbed habitats. For the relationship between species diversity and functional diversity we used weighted indices, as proposed by Walker et al. (2008). These are derived from the unweighted indices by application of the rarefaction method (Hulbert, 1971; Sanders, 1968) to both, the FD and FAD indices, and to species richness values. The weights of species contributions to a local community are determined by the number of species occurrences per site, and the expected number of species (or species diversity) in a rarefied sample is calculated by randomly drawing *n* individuals from the total assemblage of N individuals (Hulbert, 1971). This way the rarefaction method corrects for sample-size related bias in the unweighted indices. Ants are highly abundant social insects with the colony as reproductive unit. Thus, the abundance-based rarefaction is used on the level of species occurrences per site, ignoring the number of individuals encountered per sample, because conspecific individuals most likely belong to the same colony. The rarefaction of FD_n and FAD_n was computed with the smallest number of species occurrences found on any of the transects, which varied between 27 and 141, so that all study site assemblages were randomly reduced to the smallest sample size of 27 occurrences. Altogether, for every study site and ant assemblage five diversity measures were calculated in addition to the encountered species richness (S):

1) rarefied species diversity (S_n),
2) functional richness (FD),
3) functional attribute diversity FAD,
4) rarefied functional diversity FD_n,
5) rarefied functional attribute diversity FAD_n.

Results

Altogether we collected 109 ant species in 420 pitfall traps (1674 species occurrences) and 123 species in 140 leaf-litter samples (1516 species occurrences). Winkler sampling yielded 53 species additional to those which were collected in pitfall traps, thus increasing the total number of ant species to 162. Altogether, the most diverse subfamilies were Mymicinae with 94 species (~58 %), Ponerinae with 27 species (~17 %) and Formicinae with 22 species (~14 %). The most abundant species in this study was *Myrmicaria opaciventris* with 216 species occurrences (pitfall trap and leaf-litter data combined), followed by *Pyramica serrula* and *Monomorium cryptobium* each with 79 occurrences. While the first was found only in sugarcane sites and once inside the forest, 80 % of the occurrences for *Pyramica serrula* and 92 % for *Monomorium cryptobium* were from forest sites. The three different habitat types revealed very different species compositions of their respective ant assemblages (Fig. 3.2). The proportion of species in the forest was highest with 61.1 % of the total 162 taxa and more than half of those (58 spp.) were restricted to this habitat. Intensive sugarcane supported only 34 % of the whole ant assemblage, and a mere 10 species were unique to this habitat. In comparison, the diversity of subsistence sugarcane farmland accounted for 56.8 % of all collected ant species with 34 species being unique to this habitat. The shared species richness between intensive and subsistence sugarcane farmland and between intensive sugarcane and forest was relatively low with 43 (26.5 %) and 21 species (13 %), respectively. Twenty-one species out of the total 162 (11.7 %) were collected in all three habitat types, although some of them like *Myrmicaria opaciventris* for example, were usually not found inside closed-canopy forest, but on clearings and roads. At the trophic level and according to current literature, the ants in this study are divided into 93 predatory, 56 generalist and 14 trophobiont species. A relatively high proportion of the total ant assemblage was collected only once (singletons: 36 spp.) or twice (doubletons: 25 spp.). Of these 61 rare species, 26 have been collected exclusively inside the forest and one species occurred in both, forest and sugarcane habitats. From the 34 open habitat singletons and doubletons 11 were collected from intensive monocultures.

Qualitatively, we recorded a broad range of morphological and ecological traits within the pitfall trap ant community. The smallest species had a mean head width and length of 0.29 mm and 0.34 mm, respectively (*Carebara* sp. 5), the largest one was an order of magnitude bigger, with a mean head width and length of 3.28 mm and 3.80 mm, respectively (*Camponotus pompeius*). Stable nitrogen values were obtained for 84 species from all three habitats, with a mean of 4.33 measurements per species (range: 1 - 16). The range in $\delta^{15}N$ values spanned three trophic levels (one level corresponding to approximately 3 ‰) between the lowest and the highest values (range: 1.95 ‰ in *Crematogaster wellmani*, 9.02 ‰ in *Carebara* sp. 5). Note, however, that 20 $\delta^{15}N$ measurements are single values, and that intraspecific variability in this study covered up to one trophic level, the SD ranging from 0.02 (*Pheidole* sp. 21) to 2.46 (*Tetramorium edouardi*). The 25 species, from the total of 109 pitfall trap species, where $\delta^{15}N$ measurements could not be obtained had to be excluded from further analyses. This reduction, however, did not influence the overall species richness patterns. In both datasets species richness decreased significantly from forest to intensive sugarcane monocultures (109 species: $R^2 = 0.294$, $F_{2, 18} = 3.753$, $p = 0.043$; 84 species: $R^2 = 0.384$, $F_{2, 18} = 5.611$, $p = 0.013$).

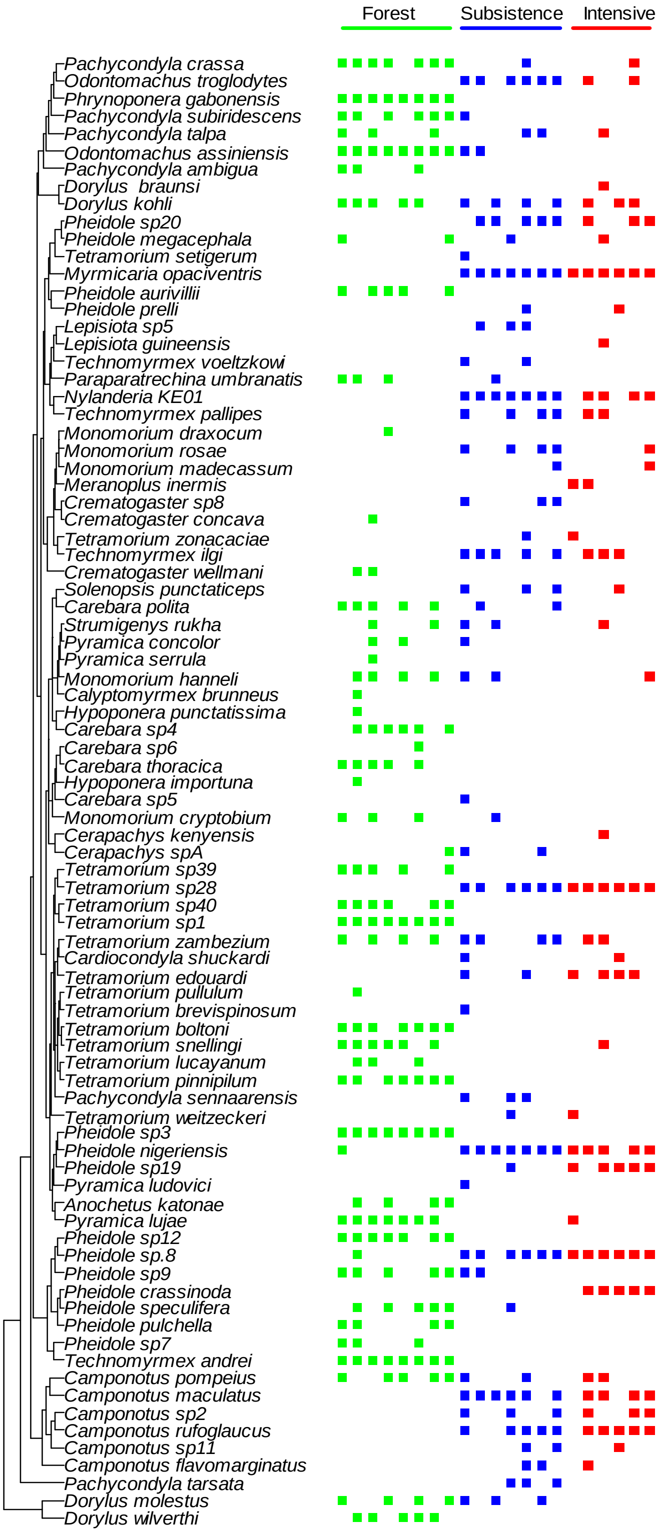

Figure 3.2 Functional dendrogram, derived from the functional distance matrix for 84 species, with branch lengths as a measure for morphological and ecological similarity among these. Thus, species and groups clustered together are resulting directly from similar morphological and / or ecological traits. One distinct group, for example, consists only of large and solitary foraging ponerines. Their main distributions

are mostly within the forest (only *O. troglodytes* being an open habitat specialist). Similarly, other clades of mostly predatory myrmicinies, like several *Carebara*, *Pyramica*, *Tetramorium* and some of the opportunistic *Pheidole* species prefer forest habitat. Hypogaeic and epigaeic *Dorylus* army ants are divided into two separate clusters, situated at very different positions in the dendrogram. The combined branch lengths in between are a reflection of the strong adaptations to their respective microhabitats and ecologies. Open habitat clades are characterized by a much higher prevalence of generalized foragers or opportunistic species. One clade consists of several *Pheidole* species, *Tetramorium setigerum* and *Myrmicaria opaciventris*, most of them being opportunists and scavengers in open habitats (except *Pheidole aurivillii*, which is a forest specialist). These relatively unspecialized ground foragers are of medium size, possess moderately large eyes, and moderately long legs, mandibles and scapes. Their stable nitrogen values were within the second trophic level (3.04 - 5.12 ‰ = secondary consumers), with their Nitrogen probably derived from a mix of plants sources, e.g. seeds, fruit, and nectar, as well as from scavenging and low-level predation. All *Camponotus* species form a single cluster with mostly open habitat species (except *C. pompeius*, a habitat generalist) and similar ecological niches, with stable nitrogen values on the first and second trophic level (2.55 - 4.65 ‰).

Species richness and diversity

In the pitfall trap samples the highest species diversity per habitat was found in subsistence farmland (67 spp.), followed by forest (51 spp.) and intensive sugarcane (47 spp.). In the Winkler leaf-litter samples, however, the sugarcane agriculture habitat (five subsistence and one intensive production site) harbored 40.9 % (55 species) less leaf-litter species than the forest (93 spp.). The analyses of species diversity estimated from the pitfall trap abundance data revealed two important results. Firstly, 75 % of the overall species richness estimated from accumulation curves for 420 pitfall traps in 21 study sites was collected with this method. Secondly, 140 leaf-litter and 320 pitfall samples combined yielded 136 % of the species richness estimated from pitfall sample data from 16 study sites. For these 16 sites, winkler samples alone collected 107 % of the ant assemblage estimated on the basis from the pitfall trap samples.

Species richness (**S**) and the rarefied species diversity index (**S_{27}**) both decreased significantly with increasing habitat disturbance (Fig. 3.3) from forest to intensive sugarcane (**S**: R^2 = 0.384,

$F_{2,\ 18}$ = 5.611, p = 0.013; **S_{27}**: R^2 = 0.5439, $F_{2,\ 18}$ = 10.73, p < 0.001). Species diversity revealed strong differences between forest and intensive sugarcane monocultures, where habitat degradation led to a significant drop in species diversity (Tukey HSD test: -4.349, P < 0.001). It also decreased distinctly from forest to subsistence sugarcane (Tukey HSD test: -3.066, p = 0.012), while increased disturbance from subsistence to intensive sugarcane showed no significant effect (Tukey HSD test: -1.284, P = 0.433). Species richness and diversity values of different farmland study sites were not significantly influenced by their respective distances from the main forest (S: p = 0.342; S_{27}: p = 0.819), which ranged from 0.065 to 36.7 km ($\text{mean}_{\text{(Subsistence)}}$ = 13 km, $\text{mean}_{\text{(Intensive)}}$ = 33 km). The same is true when controlling for habitat type (S: p = 0.4417; S27: 0.5371). Species richness data from winkler samples explained a high proportion of the variation (R^2 = 0.873, $F_{1,\ 12}$ = 82.67, p = 9.915e-07) observed between forest habitat (8 study sites) and sugarcane farmland in general (6 study sites). In this dataset species richness and estimated species richness derived from pitfall traps did not detect significant species reductions. Yet, the combination of both collection methods still explained about 70 % of the variation observed among the two habitats (R^2 = 0.698, $F_{1,\ 12}$ = 27.78, P = 0.0002).

Trophic chain length and predators

The effects of land-use intensity on trophic composition and ecology of ant communities was investigated in two different analyses. Firstly, the proportion of predators per study site (Fig. 3.4A) was significantly related to habitat type (R^2 = 0.7008, $F_{2,18}$ = 21.06, p = 1.931e-05), with strongly reduced values in the two sugarcane habitats compared to forest (Tukey HSD test forest-extensive: diff = 29.788, p = 0.00015, forest-intensive: diff = 34.049, p = 0.00005). There was also a relatively weak, but significant, association between predator proportion and species richness (**S**) and species diversity (**S_{27}**) among study sites (**S**: R^2 = 0.2419, $F_{1,\ 19}$ = 6.25, p = 0.0217; **S_{27}**: R^2 = 0.2471, $F_{1,\ 19}$ = 6.234, p = 0.0219). Secondly, trophic chain length (Fig. 3.3B) differed significantly among habitat types ($R^2 = 0.2889$, $F_{2,18} = 3.657$, $p = 0.0465$), however, showed no stepwise reduction along the land-use gradient (Tukey HSD test (subsistence-forest): diff = -1.729, p = 0.0389, but (intensive-forest): diff = -1.033, p = 0.2992).

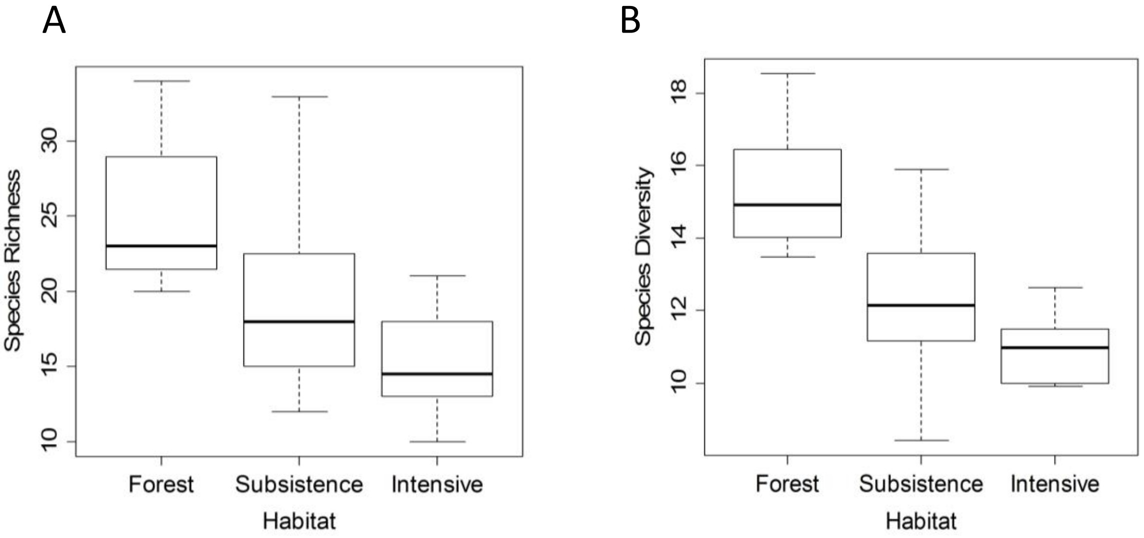

Figure 3.3 Species richness (A) and diversity (B) values in the different habitats decline with increasing habitat disturbance from forest to intensive sugarcane monocultures.

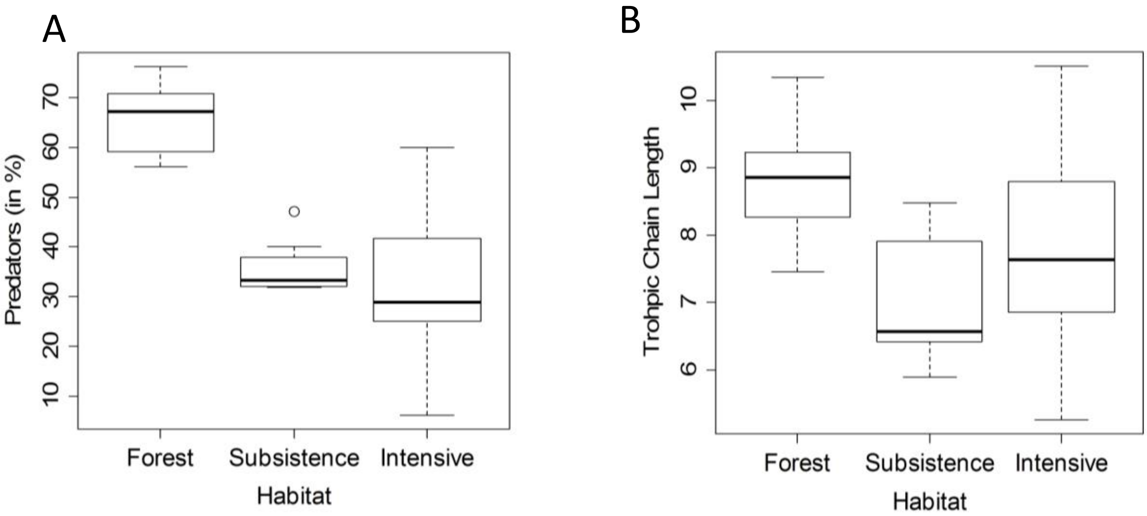

Figure 3.4 **A)** Proportion of predatory ant species per study site among habitats. **B)** Trophic chain lengths ($\delta^{15}N$ in ‰) of local food webs in three habitats.

The highest variation of trophic chain lengths occurred in intensive sugarcane farmland (SD = 1.827), while it was smallest in forest (SD = 0.866). Trophic chain length was independent of species richness and diversity, but positively associated to predator proportion per study site ($R^2 = 0.2568$, $F_{1, 19} = 6.566$, $p = 0.0191$). Please note, that the number of species analyzed per study site did not influence the length of trophic chains ($p = 0.4119$).

Ecosystem Function Scavenging

The scavenging rates (bait removal) across habitats were influenced by a number of different predictors. Firstly, they were clearly affected by habitat type and significantly higher in the two sugarcane habitats than inside the forest ($R^2 = 0.4$, $F_{2, 12} = 4$, $p = 0.0467$; Fig. 3.5A). Secondly, there was a negative relationship between scavenging rates and species richness **S** ($R^2 = 0.3834$, $F_{1, 13} = 0.383$, $p = 0.0138$), which was also significant when controlling for habitat ($R^2 = 0.5281$, $F_{3, 11} = 4.103$, $p = 0.0351$). And finally, scavenging rates were positively correlated to ant activity ($R^2 = 0.6229$, $F_{1, 13} = 21.47$, $p = 0.0005$, Fig. 3.5B), which also increased from forest to farmland on average, although it was not significantly associated with habitat type ($p = 0.25$). However, observed ant activity was significantly negatively associated to species richness ($R^2 = 0. 2747$, $F_{1, 13} = 4.923$, $p = 0.0449$; Fig. 3.5C). Concerning the composition of the ant communities, the NMDS ordination showed a strong distinction between the species compositions of the forest and the two different farmland types, with species richness decreasing along the first NMDS axis and ant activity increasing along both, NMDS axis 1 and 2 (Fig. 3.6).

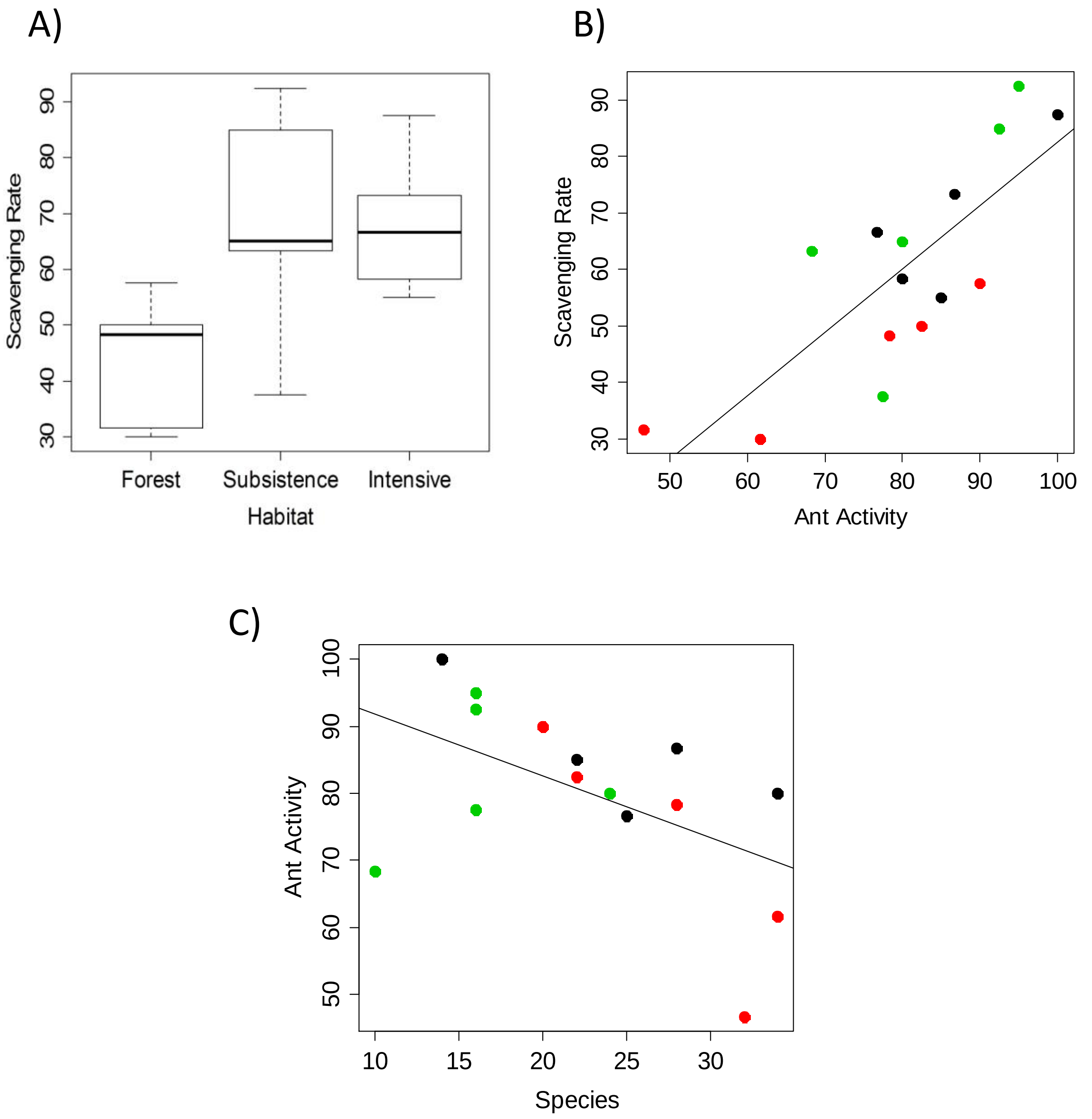

Figure 3.5 A) Scavenging rate as proportion of bait removals per study site, **B)** relationship between scavenging rates and ant activity, and **C)** between ant activity and species richness, each measured in 15 sites: forest (black points), subsistence sugarcane (red points), and intensive sugarcane sites (green points).

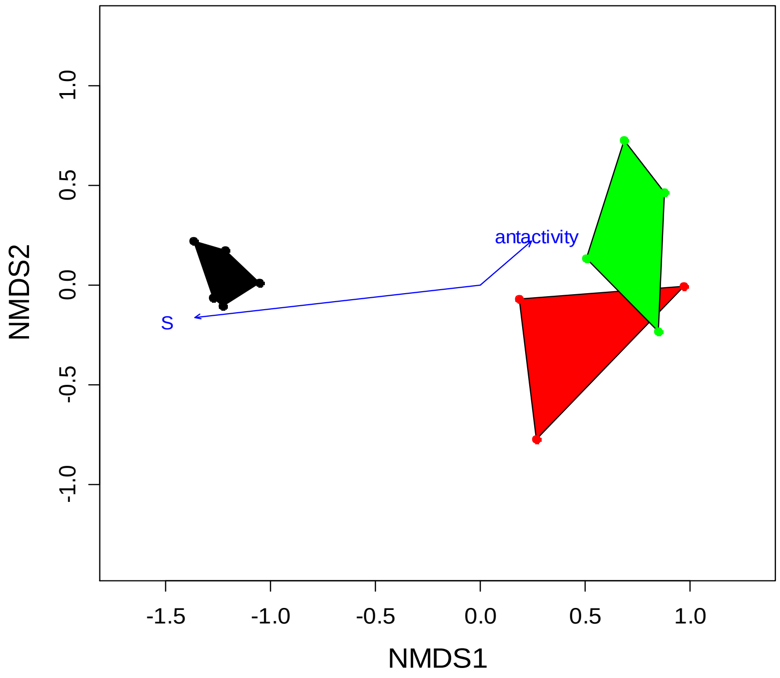

Figure 3.6 NMDS ordination for community composition of ant assemblages in forest (black), subsistence sugarcane (red) and intensive sugarcane farmland sites (green); environmental fits for **S** and ant activity are shown with blue arrows.

Functional richness and diversity

The two unweighted functional richness indices (**FD**) and (**FAD**) declined with increasing levels of habitat disturbance (**FD**: $R^2 = 0.5023$, $F_{2, 18} = 9.083$, $p = 0.00019$; **FAD**: $R^2 = 0.292$, $F_{2, 18} = 3.711$, $p = 0.04473$; Fig. 3.7A, B). With the former a strong decline in functional richness values from both, forest to intensive sugarcane monocultures (Tukey HSD test: -10.828, p = 0.0014) and from subsistence to intensive sugarcane was detected (Tukey HSD test: -7.324, p = 0.0317). With the latter index, significant differences could only be detected between forest and intensive sugarcane habitats (Tukey HSD test: -373.01, p = 0.0354).

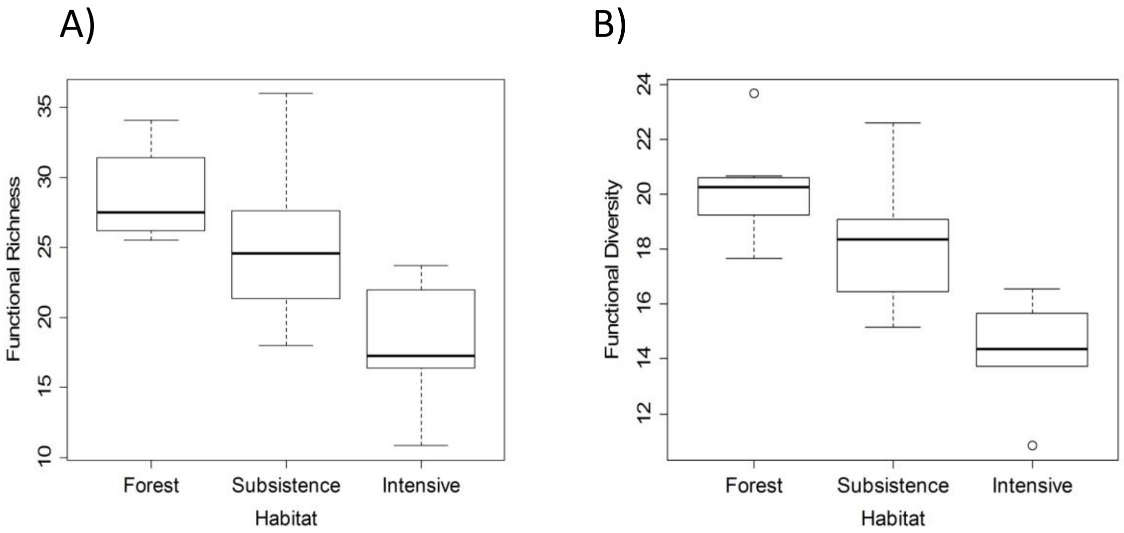

Figure 3.7 Functional richness (A) and diversity (B) values in the different habitats, declining from forest to intensive sugarcane monocultures.

The two rarefied indices **FD$_{27}$** and **FAD$_{27}$** are, in comparison to the unweighted **FD** and **FAD** indices, less biased toward abundant species, and habitat explained more variation in case of the weighted functional diversity indices (**FD$_{27}$** and **FAD$_{27}$**) than in case of the unweighted indices as response variables (**FD$_{27}$**: $R^2 = 0.6064$, $F_{2, 18} = 13.86$, p = 0.00023; **FAD$_{27}$**: $R^2 = 0.563$, $F_{2, 18} = 11.62$, p = 0.00058). **FD$_{27}$** values were significantly different between forest and intensive sugarcane (Tukey HSD test: -5.952, p = 0.00016) and between subsistence and intensive sugarcane (Tukey HSD test: -3.925, p = 0.0094). **FAD$_{27}$** values on the other hand differed significantly between forest and intensive sugarcane (Tukey HSD test: -195.74, p = 0.00054) and between forest and subsistence sugarcane (Tukey HSD test: -128.19, p = 0.0135). The association of **FD** and **S** was highly significant ($R^2 = 0.8927$, $F_{1, 19} = 158$, p = 1.18e-10), also after controlling for habitat type ($R^2 = 0.9409$, $F_{3, 17} = 90.28$, p = 1.20e-10). A model including a quadratic term for species richness ($R^2 = 0.9576$, $F_{4, 16} = 90.39$, p = 0.023, AIC = 81.975; Fig. 3.8A) was better supported than the simple models without the quadratic term (AIC = 95.490 and 86.946, respectively). The graph with the quadratic term shows a slightly decelerating curve, with increasing saturation for higher species richness values. However, an asymptote, where all additional species would be functionally redundant is not reached for observed richness values. Note the habitat specific functional richness increases, with the highest level in subsistence sugarcane, followed by forest and intensive sugarcane sites.

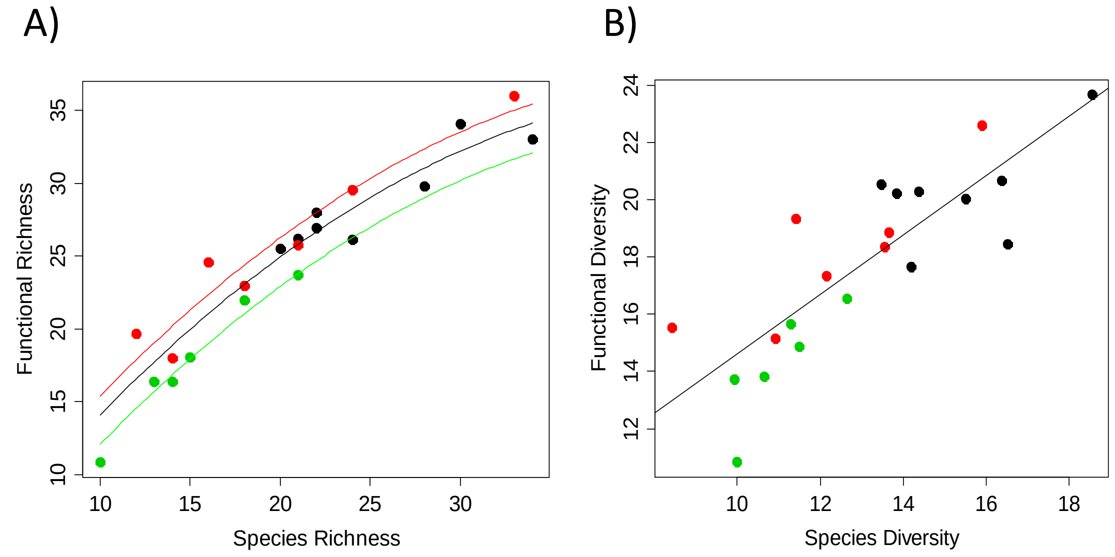

Figure 3.8 A) Exponential relationship between functional richness (**FD**) and species richness (**S**). **B)** Linear relationship between functional (**FD_{27}**) and species diversity (**S_{27}**), with values for 21 study sites: forest (black points), subsistence (red points), intensive sugarcane farmland (green points).

The association of **FD_{27}** and **S_{27}** forms a highly significant linear relationship ($R^2 = 0.6994$, $F_{1, 19} = 44.22$, $p = 2.32e-06$; Fig. 3.8B) without any saturation effect (the quadratic term was not significant: $p = 0.8318$). The constant increase in functional diversity along the land-use gradient indicates that all species added to the system are functionally unique. The functional attribute diversity indices **FAD** and **FAD_{27}** are both sensitive to functionally redundant species and highly associated with the corresponding species richness measures (**FAD**, **S**: $R^2 = 0.9616$, $F_{1, 19} = 475.4$, $p = 6.86e-15$, AIC = 233.662; **FAD_{27}**, **S_{27}**: $R^2 = 0.9686$, $F_{1, 19} = 586.6$, $p = 9.55e-16$, AIC = 189.926; Fig. 3.9A, B). Both, the relationship between **FAD** and **S** and the relationship between **FAD_{27}** and **S_{27}** revealed significant exponential relationships (**FAD**: $p = 0.0036$, AIC = 229.359; **FAD_{27}** = 0.0088, AIC = 184.636). The separation of forest and farmland site values, especially those in intensive sugarcane, along the regression curves was stronger consolidated with the rarefied **FAD$_{27}$** than with the unweighted **FAD** index. The latter, for example, found that several functional attribute richness values in farmland sites outperformed forest sites with the same level of species richness, most probably because species abundances in the farmland were higher. In the former, rare species were probably adding more weight to the functional composition of forest ant assemblages.

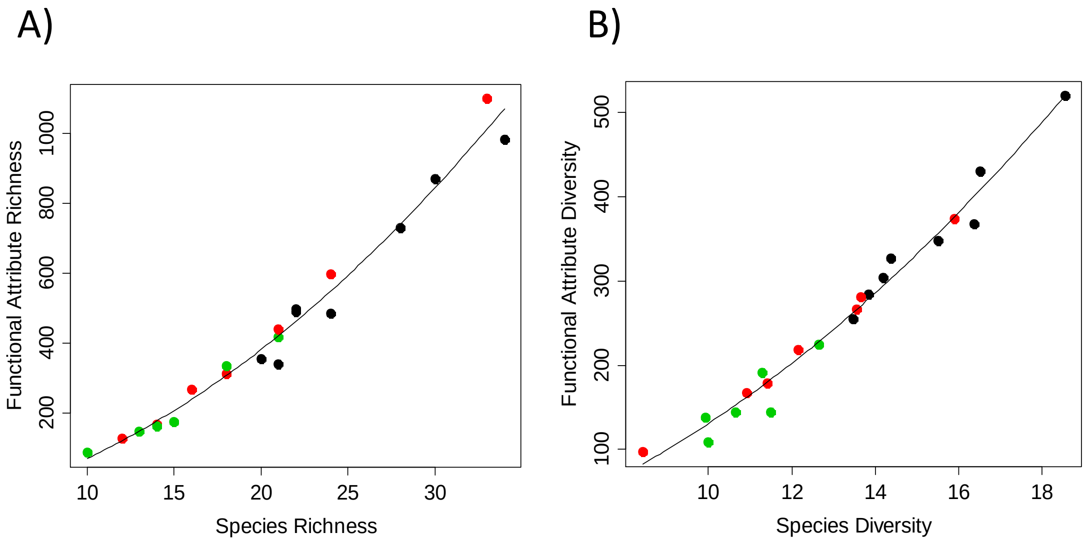

Figure 3.9 A) Exponential relationships between functional attribute richness FAD and species richness (S), and **B)** between FAD$_{27}$ and S$_{27}$ for 21 sites with regression curves: forest (black dots), subsistence (red dots), intensive sugarcane sites (green dots).

Discussion

Species richness

The results of this study showed that habitat degradation and increasing land-use intensity reduced species (as well as functional) diversity of the ant community along the land-use gradient from near-natural tropical rainforest to intensive sugarcane production farmland (overview of effect relationships: Fig. 3.10). These results are in concordance with the majority of ecological studies concerning tropical forest conversion into agricultural systems and plantations, intensification of crop production and simplification of agricultural landscapes. Most of these were unambiguous in their results about the loss of biodiversity in degraded systems (Chapin et al., 2000; Danielsen et al., 2009; Dunn eta al., 2004; Gardner et al., 2007; Irwin et al., 2010; Koh & Wilcove, 2008; Majer et al., 1997; Petit & Petit, 2002). Nevertheless, some authors pointed out the increasingly important role of complex modified landscapes, comprising both agricultural and natural components, as a compromise between the conflicting interests (Chadzon et al., 2009; Fahrig et al., 2011; Ricketts, 2004; Tscharntke et al., 2005). Interestingly the subsistence sugarcane farmland around the Kakamega Forest revealed a high amount of ant species diversity and functional diversity measured across the several sites. As a habitat with a limited amount of human disturbance and a relatively high diversity of microhabitats and plant species, subsistence farmland could be important in the overall conservation of biodiversity in general. A matrix consisting of subsistence farmland can act as a buffer between natural or near-natural habitats and more intensively exploited areas with high human disturbance levels. Yet the conservation value of the farmland for forest species, especially closed-canopy adapted ant species remains very limited, because many ants and other invertebrate species depend on an intact leaf-litter layer with a suitable microclimate for nesting and foraging. This means that ants, found in both habitats farmland and forest, are either ubiquitous species and distributed throughout a range of different habitats, or that they live in small pockets of semi-natural vegetation preserved along the hedges around the subsistence fields for example. Furthermore, it is not surprising that pitfall trap and Winkler leaf-litter collection methods showed high differences in species diversity between forest and farmland sites. Pitfall traps generally collected mostly medium-sized to large ant species moving on the ground and the top of the leaf-litter layer. The leaf-litter sampling technique captures mostly ants from within and below the leaf-litter layer, which are usually small and less conspicuous, and often possess small colonies.

Functional diversity

In comparison to functional groups, the analysis of continous measurements of functionally important characters provides results that are unaffected by arbitrary group formations (Petchey & Gaston, 2002a) and that can be easily compared with results of other studies. As expected species diversity and functional diversity decreased strongly for all indices employed, which is not surprising for a diverse community, where many species have unique niches and adaptations to their respective habitats and microhabitats, strongly differentiated trophic positions and life-styles in general. The same general observations were made in the ant functional diversity study by Bihn et al. (2010), on which most of the indices and functional traits used here were based on. That study compared the functional diversity patterns along a disturbance gradient from natural uncut forest and different reforestation stages from old-growth to young secondary forests in the Brazilian Mata Atlântica. Their results clearly showed a negative relationship between the diversity indices and habitat, with measurements of species and functional diversity decreasing linearly along the disturbance gradient (Bihn et al., 2010).

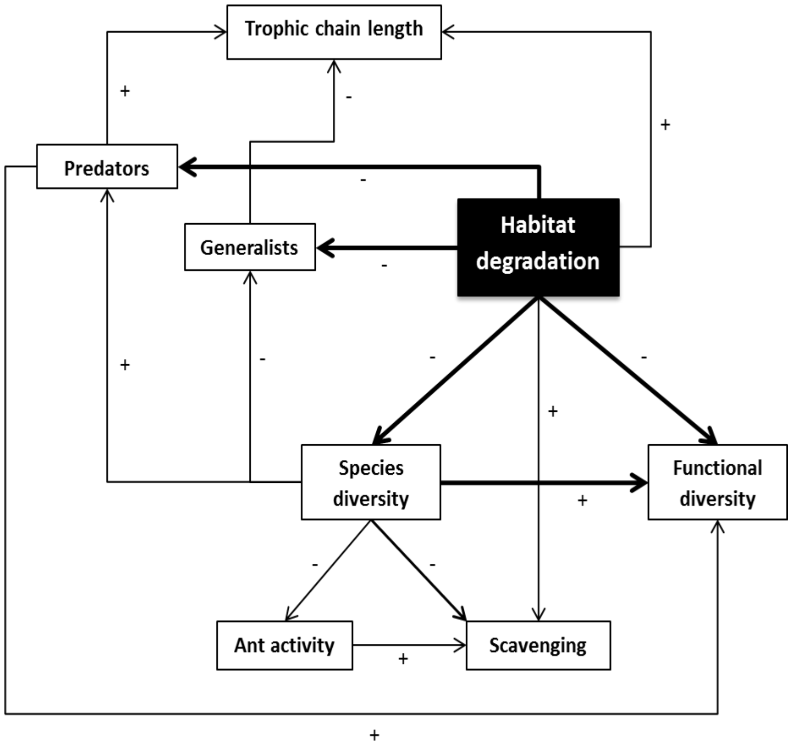

Figure 3.10 Significant effects and relationships from all analyses as results of increasing habitat degradation along a habitat disturbance gradient. (**+**) represent positive, (**-**) negative relationships; line width indicates the statistical strength of effects. Note that the relationships are not necessarily causal and that some are probably correlated.

Also the associations between the species and corresponding functional diversity indices were of linear nature and positively correlated. The results for the Kakamega ant fauna were slightly different in one aspect. Whereas the relationships between **S**, **S_{27}**, **FD**, and **FD_{27}** and habitat disturbance were also linear along the gradient from forest to intensively managed sugarcane agriculture and **FD_{27}** also decreased linearly with decreasing **S_{27}**, the relationships between **FD** and **S**, **FAD** and **S**, and **FAD_{27}** and **S_{27}** were of non-linear nature in this study. The easiest explanation is probably the high difference between the two different communities, which indeed have to be adapted to entirely different ecosystems that have little in common in terms of climate and usuable resources. Farmland ants in the structurally and biologically simple sugarcane sites clearly have fewer niches and strata that can be occupied, and experience a smaller diversity of predator-prey interactions together with higher amounts of ecosystem perturbations. This may well be the ultimate reason, why mostly generalized and opportunistic species were found in the intensively managed sugarcane monocultures. Similar patterns of strongly declining functional diversities related to habitat degradation and agricultural intensification were observed in communities of birds and mammals with sometimes much stronger functional diversity declines than expected from species losses (Flynn et al., 2009). If functionally unique species, which are also strong interactors, disappear this means that a rather high amount of ecosystem functions will be lost together with only a small number of species (Cardinale et al., 2006; O'Gormann, 2001; Petchey & Gasteon, 2002a). In these cases the analyses of functional diversity measures have more meaning for the stability of an ecosystem than species diversiy, because ecosystem services and processes will deteriorate at much faster rates. In a different meta-analysis, Cardinale et al. (2011) found that a high amount of experimental studies supported a positive, but decelerating, relationship between species diversity and functional diversity-related ecosystem processes. Which still means, that after the initial loss of more or less redundant species, whose functions can still be fulfilled by others, and with continued extinctions of then functionally unique species, the deterioration of ecosystem functions and processes sets in and can quickly lead to irreversible damage to the system. It still remains to be validated to which degree the experimental results scale-up to the level of natural communities and ecosystems.

Trophic chain length

One of the findings in this study is that trophic chain length among the different habitats was not directly linked to habitat disturbance, as has been hypothesized to be one of the important factors (see Post & Takimoto, 2007). Although subsistence and intensive sugarcane farmland had shorter chain lengths on average than forest habitat, the difference between forest and intensive sugarcane was not significant. But intensive sugarcane sites clearly showed a higher variation (SD = 1.827) in trophic chain lengths than forest sites (SD = 0.866). Maybe this can be partly explained by the frequent use of chemical fertilizers, herbicides and pesticides in intensive sugarcane agriculture. Fertilizers are used to increase plant primary production, which could theoretically lead to generally longer trophic chain lengths. Pesticides, however, affect trophic chain lengths by decimating both, primary consumer and predator populations. So, one explanation for decreased chain lengths could be the loss of apical predator(s) on the top of the food chain, e.g. specialized predators and top-predators that occupy the upper trophic level (Gibb & Cunningham, 2010; Takimoto et al., 2008). High trophic chain lengths in the sugarcane farmland are more difficult to explain, but could be a result of shifts in species' diets and increased intraguild predation (Post & Takimoto, 2007). This should probably also apply to subsistence farmland, where increased chain lengths however did not occur. A better explanation could be the use of fertilizers, which are used for nitrogen enrichment of the soil. The increased plant net production rates, or changed heavy nitrogen ratios in the soil, could be affecting the isotope compostion of the ant community, resulting in an absolute increase in measured food chain lengths. The habitat-dependant differences of trophic chain lengths and the possible effects of intensified agriculture should be addressed in detail in future investigations and experiments, as this is important for the understanding and conservation of ecosystem functions in natural and in anthropogenically modified habitats, especially in farmland. An area that is reduced of its predators can be highly vulnerable to pests and invasive species (Crist, 2009; Crozier et al., 2010; Irwin et al., 2010; Souza et al., 2010) with the result that more and more pesticides are needed to maintain high productivity levels.

Scavenging

Scavenging and ant activity rates at the baits were highest in the sugarcane farmland and comparatively low inside the forest, and they were negatively related to species diversity. In another scavenging bait-removal study on ants in a dipterocarp forest in Danum Valley, Sabah, bait-removal rates removal rates showed a postitive relationship to species diversity, although species diversity and bait removal rates did not significantly change along the disturbance gradient (Fayle et al., 2010). However, the two different kinds of results are not well comparable, because their disturbance gradient transects covered an anthropogenically used forest border area, the forest edge and interior up to 100 m inside. They also explain that the 100 m forest interior positions were quite disturbed, and non-native ant species were still present. Results in the present study were not directly related to predator or generalist species proportionis in the communities, but it has been argued before that baiting usually attracts more generalistic foraging species (Bestelmeyer et al., 2000). Higher scavenging rates in sugarcane farmland could be a result of the presence of large opportunistic species like *Myrmicaria opaciventris* and several *Camponotus* species, which were highly abundant in most of the farmland study sites and mostly the ones observed to carry the fly larvae away. They usually tended to forage alone and were able to carry mid-sized food items like the larvae on their own. In the forest, however, most ground-foraging ant species were smaller and the removal of baits took longer than the duration of the experiment, because the scouting ants first had to recruit other workers from their nests. This clearly shows that experiments are usually biased and their results have to be evaluated with care.

Still, the results of other ant functional diversity studies (Bihn et al., 2010; Silva & Brandao, 2010) and of the present one, suggest that species and functional diversity measures are highly associated, showing that the diversity of ant species in a local community seems to be a good indication for the diversity of functions and services which are performed. And that the amount and quality of functions fulfilled in forest ecosystems depends much more on the diversity of its inhabitants than baiting experiments will be able to resolve. The higher the overall diversity becomes, the more increases the amount of interactions, for example between predators and prey. Specialized predators and other species with unique ecological niches were almost absent from high-intensity sugarcane production sites and occurred mostly in those subsistence farmland sites which were located near to the forest borders.

What ant functional diversity studies accordingly seem to have in common is that functional diversity measures can be used in order to describe the morphological and ecological diversity within a complex rainforest ant community, even when prior knowledge about species diversity and taxon identification is low. This can be a valuable result for ecological and ecosystem monitoring studies that do not always have the resources and necessary expert-knowledge for time-intensive species identifications.

Implications for conservation management

The implications of the continued deforestation and destruction of vulnerable natural habitats for biodiversity have been discussed and investigated for several decades already. Although global deforestation now seems to decelerate slightly (FAO, 2001), large areas of pristine forests and biodiversity (Pimm, 1995) are still disappearing at high annual rates. Biofuel production has become an important factor in politics and economy, and might soon be a major driver of habitat conversion into diversity-poor crop production monocultures. This alarming development completely counteracts the ideals of the green revolution, i.e. to reduce human impacts on the environment and the climate. The question we need to ask ourselves is: Do we really want to protect life on earth and our own survival? The answer is crucial for the implications for the future development in society, economy and science. Other strategies exist to slow the speed of global extinctions. Feasible, as an investment into our future, alternative solutions for counteracting mass extinctions and climate change are large-scale reforestation and improved cultivation methods for the reduction of green-house gas emissions, as well as alternative regenerating energy sources.

Chapter 4:

Taxonomy of the ant genus *Pheidole* Westwood (Hymenoptera, Formicidae) in the Afrotropical zoogeographic region: definition of species groups and systematic revision of the *Pheidole pulchella* group

with F. Hita Garcia and M. K. Peters - Zootaxa, in review

Abstract

This paper is a starting point towards a much needed comprehensive taxonomic treatment of the genus *Pheidole* in the Afrotropical region. Despite its hyperdiversity, the taxonomy of this globally distributed ant genus is limited to important revisions for the New World and several Asian faunas. However, *Pheidole* of the Afrotropical zoogeographic region has never been revised. The most recent Afrotropical *Pheidole* species descriptions are already fifty years old and many are considerably older. Identification keys are not available and many species descriptions are of limited diagnostic value. This calls for a series of taxonomic revisions in order to resolve the complicated taxonomic situation for the complete Afrotropical *Pheidole* fauna. In this paper the following preliminary morphological species groups for the African continent are defined: *P. aurivillii* group, *P. excellens* group, *P. megacephala* group, *P. nigeriensis* group, and *P.*

speculifera group. We also establish and revise the *P. pulchella* group, which currently contains eleven species, of which seven are new. The four species described prior to this study are: *P. pulchella* Santschi, *P. dea* Santschi, *P. nimba* Bernard, and *P. batrachorum* Wheeler **stat. rev.**, which is removed from synonymy under *P. dea* and regains species status. The following new synonymy is proposed (senior synonym listed first): *P. pulchella* Santschi = *P. pulchella achantella* Santschi. The following seven species are described as new: *P. christinae* **sp. n..**, *P. darwini*, **sp. n.** *P. glabrella* **sp. n.**, *P. heliosa* **sp. n..**, *P. setosa* **sp. n.**, *P. semidea* **sp. n.**, and *P. rebeccae* **sp. n.** An illustrated key combining the two distinct worker subcastes is presented.

Keywords: Myrmicinae, *Pheidole*, new species descriptions, *Pheidole pulchella* group, Africa, Congo-Guinean rainforest belt, taxonomic revision

Introduction

The ant genus *Pheidole* Westwood (1839) is an evolutionary success story, both ecologically and in terms of species diversity. With more than 1100 valid species names it represents the ant genus with the highest species richness worldwide (Longino, 2009). Taxonomic interest in this genus increased relatively recently, especially within the last decade. Wilson's (2003) monograph on the New World fauna was particularly important since it more than doubled the number of described *Pheidole* species for the New World. However, recent material from Central America made an updated taxonomic treatment necessary, which was provided by Longino (2009). Different oriental faunas were revised by Eguchi and colleagues (Eguchi, 2000, 2001a, 2001b, 2008; Eguchi & Bui, 2005; Eguchi et al., 2007), and Sarnat (2008) provided a taxonomic treatment of the *P. roosevelti* group from Fiji.

In most ecological studies within the tropics, *Pheidole* is one of the most abundant and diverse ant taxa (Ward, 2000; Wilson, 2003). Especially in Africa, it is also one of the genera with very high rates of unidentifiable morphospecies (Belshaw & Bolton, 1993; Deblauwe & Dekoninck, 2007; Fisher, 2004; Hita Garcia et al., 2009). For the Afrotropical region, this is due to both a large number of undescribed species, and a lack of modern revisionary treatments and identification keys for described species. In an attempt to revise the *Pheidole megacephala* group, Emery (1915) tried to shed light on the unclear taxonomic situation in this confusing network of different species, subspecies and variations, but with very limited success. Since then, Afrotropical *Pheidole* have been neglected by ant taxonomists. Instead, tri- and quadrinoms assigned to many valid biological species remain unchanged, frustrating attempts to identify specimens based on taxonomic literature. In addition, the majority of African *Pheidole* was described between 150 to 50 years ago, mostly by A. Forel, F. Santschi, G. Mayr and C. Emery, at a time when subspecies and infra-subspecific taxa were still frequently used in ant taxonomy. Forel and Santschi alone, the two most productive taxonomists for the Afrotropical region, described more than half of their 95 *Pheidole* taxa as varieties, subspecies and races. Unfortunately, a lot of the descriptions are no longer sufficient for accurate species diagnosis. In several cases the differences between subspecies are poorly documented whereas in others different subspecies possess relatively little resemblance with each other. The last species in the Afrotropical region were described by Bernard (1953). Arnold (1960) described a new variation of *Pheidole shultzei*, and since then, one junior homonym was renamed by Wilson (1984).

The long neglect of the African *Pheidole* fauna and the large amount of new material and undescribed taxa calls for a comprehensive taxonomic treatment in order to provide the identification tools needed to promote and facilitate ecological, biogeographical and evolutionary studies. These studies are strongly underrepresented and comparatively rare on the African continent. Without a good taxonomic knowledge of Afrotropical species, it will remain difficult to gain any qualified information about endemism, species turnover, evolutionary patterns, and biogeographical patterns for this remarkable and important ant genus. For other African and Malagasy ant taxa, the taxonomic situation improved considerably during the last decades (Ward, 2010) owing in large part to Bolton's extensive taxonomic treatments (listed in Bolton, 2003; and Bolton & Fisher, 2008a, 2008b, 2008c, 2011). Other authors followed his efforts and several revisions for the two regions have been published in the last few years, showing that the interest in Afro-Malagasy ant taxonomy is undiminished (Blaimer, 2010; Fisher, 2009; Fisher & Smith, 2008; Heterick, 2006; Hita Garcia et al., 2010; LaPolla et al., 2010; Yoshimura & Fisher, 2007; 2009). Nevertheless, the way towards a comprehensively documented ant fauna of the world is still long and full of challenges, especially in the case of the three largest and hyperdiverse genera *Pheidole*, *Camponotus* and *Crematogaster* (Wilson, 1976).

This paper provides a brief outlook on the opportunities and challenges in the taxonomy of African *Pheidole* and a first revisionary treatment for species of the Afrotropical zoogeographic region. Five species groups are defined with the help of type material and additional material collected from localities and countries across sub-Saharan Africa. These groups will have to be validated with additional material in future revisions. Although the general utility of defining species groups within Pheidole has been questioned (Moreau, 2008), we consider them a necessary tool for analysing and categorizing the African fauna as a whole. The few Afrotropical species included in Moreau's analysis were unidentified species from Ghana, Ivory Coast and Madagascar. Thus, the phylogenetic justification of our proposed species groups remains untested. Although the proposed species groups are not necessarily representing close genealogical relationships or monophyletic lineages, we predict that results from genetic research will support our diagnostic decisions. The *P. pulchella* group currently contains 11 species, seven of which are described here as new on the basis of the available material. We also provide an illustrated identification key combining the minor and major worker subcastes.

Material and Methods

All observations and measurements were taken at 32x to 90x magnification with an Olympus SZX12 dissecting microscope and a dual-axis micrometer, at an accuracy of approximately 0.006 mm (half a scale mark). Minimal and maximal values, as well as the arithmetic mean in parentheses, are listed in the measurements, which are presented in mm units with three decimal digits. Most of the material is located at the BMNH, CASC and ZFMK entomological collections. All images were made with a QImaging Micropublisher 5.0 RTV camera on a Leica Z6 APO stereomicroscope in combination with Syncroscopy Auto-Montage software (version 5.03), and are online available at Antweb (http://www.antweb.org). The general morphological terminology follows Bolton (1994), Longino (2009) and Serna & Mackay (2010). Special terminology used in this revision includes the following: 'lateral clypeal carinae' for the outmost longitudinal carinae at the sides of clypeus near the antennal insertions, 'metapleural gland scrobe' (Serna & Mackay, 2010), referring to the ventral-most longitudinal carina near the metapleural gland bulla, and 'metapleural carina(e)', which are situated above the metapleural gland scrobe.

Measurements and indices

HL	*head length*: maximum distance from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin of the head, measured in full-face view; in majors from midpoint of tangent between anterior-most position of clypeus to midpoint of tangent between posterior-most projection of the vertex.
HW	*head width*: measured at widest point of the head, in full-face view behind eye-level.
SL	*scape length*: maximum scape length, excluding basal condyle and neck.
EL	*eye length*: maximum diameter of compound eye measured in oblique lateral view.

FL	*metafemur length*: measured from the junction with the trochanter to the junction with the tibia.
MTL	*metatibia length*: measured from the junction with femur to the junction with first tarsal segment.
MFL	*mandible length*: maximum length, measured in oblique frontolateral view, from apex to lateral base.
PW	*pronotal width*: maximum width of pronotum measured in dorsal view.
WL	*Weber's length*: diagonal length of mesosoma in lateral view from the anterior point of the pronotal slope and excluding the neck, to the posteroventral margin of the propodeum.
PSL	*propodeal spine length*: in dorsocaudad view, with the apex of the measured spine, its base, and the center of the propodeal concavity between the spines in focus: measurement is taken from apex to base along the one axis of a dual-axis micrometer, which is aligned along the length of the spine, crossing the second axis at the base of the measured spine, and the latter connecting the base with the center of the propodeal concavity (Fig. 4.1).
PTL	*petiole length*: maximum diagonal length of petiole, measured in lateral view, from most anteroventrad point of the peduncle to most posterodorsad point at the junction to first helcial tergite.
PTH	*petiolar node height*: maximum height of petiolar node measured in lateral view from the highest (median) point of the node, orthogonally, to the ventral outline of the node.
PTW	*petiolar node width*: maximum petiolar node width, measured in dorsal view.
PPL	*postpetiole length*: maximum length of postpetiole, measured in lateral view, from anterior beginning of the dorsal slope to the posterior juncture of postpetiole and second helcial tergite.

PPH	*postpetiole height*: maximum height of postpetiole, measured in lateral view, from the highest (median) point of the node to the lowest point of the ventral process, often in an oblique line.
PPW	*postpetiole width*: maximum width of postpetiole, measured in dorsal view.

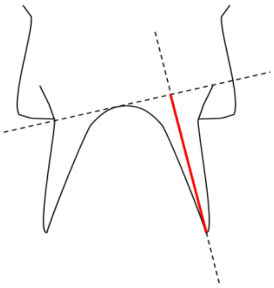

Figure 4.1 Measurement of propodeal spine length (PSL) in oblique fronto-dorsal view (dorsocaudad).

Indices

CI	*cephalic index*: HW / HL 100
EI	*eye index*: EL / HW 100
SI	*scape index*: SL / HW100
MDI	*mandible index*: ML / HW 100
PSLI	*propodeal spine index*: PSL / HW 100
PWI	*pronotal width index*: PW / HW 100
FI	*metafemur index*: FL / HW 100.
PeI	*petiole index*: PTW / PW 100 (major only)
PpI	*postpetiole index*: PPW / PW 100 (major only)
PpWI	*postpetiole width index*: PPW / PTW 100
PpLI	*postpetiole length index*: PTL / PPL 100

Taxonomy of Afrotropical *Pheidole* and preliminary species groups

The Afrotropical *Pheidole* fauna is unlikely as species rich as the New World or Oriental faunas. Currently, 136 valid taxa are listed for the African continent (Bolton & Alpert, 2009). This number does not include the Malagasy region, which hosts its own unique and species rich fauna (Brian Fisher, pers. communication). Nevertheless, the actual number of species in the Afrotropical region is estimated to be significantly higher. Most of the tropical forests and other species rich habitats remain unsampled, and museum collections already store many undescribed species.

Diagnostic definitions for 5 preliminary species groups are provided based on morphological analysis of type and non-type material. Species within these groups share important characteristics in shape and proportions of head and mesosoma, relative length of appendages in general, and scape and metafemur length in particular. These are related to life history traits and ecology of the species (Weiser & Kaspari, 2006). Furthermore, important diagnostic characters include postpetiole proportions and modifications (i.e. ventral and lateral processes), and the overall pattern of body sculpture. The latter is generally variable within species groups and between species, ranging from densely punctate to almost completely smooth and shiny. Nevertheless, intraspecifically the sculpture-patterns are consistent, except for some minor and sporadic differences in the expression among different populations. Pilosity is another good diagnostic character, and is suitable for the division of species into groups with major differences in length, thickness, and overall abundance of hairs. Please note that the following species group definitions are of provisional nature and that more groups are likely to emerge with more examined material. Until now, not all of the type material has been checked, except for the *excellens* group, where many of the described species have been examined already. The preliminary species groups are:

***P. excellens* group:**

This group can be subdivided into two different complexes, one with small species (*katonae* complex; minnow worker HW: 0.57-0.63 (n=8), possessing short legs and spines, and relatively larger eyes [*katonae* Forel*, sculpturata zambeziana* Forel]. The other complex consists of bigger species (*excellens* complex; minor worker HW: 0.69-0.93 (n=24), which possess longer legs and spines, and relatively smaller eyes [*excellens* Mayr, *liengmei* Forel, *njassae* Viehmeyer, *sculpturata* Mayr*, sculpturata welgelengensis* Forel]. Minor workers: characterized by wide, square head with straight posterior margin and subangulate to angulate corners, relatively short scape, barely to moderately exceeding occipital margin; postpetiole very short, lower than petiole, about as wide as long; body often deeply punctate-rugulose/rugose [e.g. *excellens*, *liengmei*], but some species mostly smooth [*excellens rhodesiana*] usually with coarse ridges along dorsopropodeum, to superficially sculptured [*sculpturata*]; high amount of very thin moderately short body pilosity, often pelt-like, at least at the head; spines short to long, linearly spinose. Major workers: pilosity and sculpture as in minor workers, head usually elongate, much longer than wide, or at least square-like with parallel to subparallel sides, sometimes anteriad wider than posteriad, high promesonotal dome, spines quasi-vertical, often thick, blunt or truncated; postpetiole laterally with an (often strongly) extended, wing-like, posteriad-curved process. The described species belonging to this group are: *Pheidole arnoldi* Forel*, Pheidole excellens* Mayr, *Pheidole excellens weissi* Santschi, *P. katonae* Forel*, P. liengmei* Forel, *Pheidole liengmei micrartifex* Forel, *Pheidole liengmei shinsendensis* Forel, *P. njassae* Viehmeyer, *P. sculpturata* Mayr, *Pheidole sculpturata areolata* Forel, *Pheidole sculpturata berthoudi* Forel, *Pheidole sculpturata dignata* Santschi, *Pheidole sculpturata rhodesiana* Forel, *P. sculpturata welgelengensis* Forel, *P. sculpturata zambeziana* Forel. Several probably undescribed morphospecies are located in the collections of BMNH, CASC and ZFMK.

P. megacephala **group:**

Relatively small species (minor: ML 0.51-0.66 mm (n=19) with relatively short appendages and spines (SI: 100-110, FI: 106-129), posterior head margin weakly rounded in the minor workers, eyes with eight or more ommatidia in the longest row, promesonotum without mesonotal process and often smoothly declining towards metanotal groove, relatively short petiole, enlarged postpetiole with ventral process in minor and major workers. A number of described species and infraspecific taxa exist for this group (*Pheidole megacephala costauriensis* Santschi, *P. megacephala duplex* Santschi, *P. megacephala ilgi* Forel, *P. megacephala impressifrons* Wasmann, *P. megacephala melancholica* Santschi, *P. megacephala nkomoana* Forel, *P. megacephala rotundata* Forel, *P. megacephala rotundata* Forel, *P. megacephala scabrior* Forel, *P. megacephala speculifrons* Stitz, *P. megacephala talpa* Gerstäcker, *P. picata* Forel, *P. picata bernhardae* Emery, *P. picata gietleni* Forel, *P. punctulata* Mayr, *P. punctulata atrox* Forel, *P. punctulata spinosa* Forel) which is in high need of revision.

P. nigeriensis **group:**

Small species (minor: HW: 0.41-0.46 mm), with short scapes and legs (SI: 89-102, FI: 95-122) posterior head margin straight to weakly concave, eyes small with a maximum of six ommatidia in the longest row, promesonotal dome large, propodeum relatively short, petiole relatively long, postpetiole not significantly enlarged and without ventral process. The group contains *Pheidole nigeriensis* Santschi and several morphospecies, collected from different localities.

P. aurivillii **group:**

Larger species (minor: ML > 0.850mm) with longer appendages (SI: 107-145, FI: 142-247), in minor workers posterior head margin rounded to almost straight, mesonotal process absent or inconspicuous, with uniform sculpture at mesosoma, mesopleuron and propodeum, and pilosity long, erect and flexous. Major workers with head rugose-punctate, frontal carinae and antennal scrobe absent or inconspicuous, mesonotal process and postpetiole ventral process present, pilosity as in minor and very abundant. Four described subspecies (*Pheidole aurivillii* Mayr, *P. aurivillii attenuata* Santschi, *P. aurivillii kasaiensis* Forel, *P. aurivillii rubricalva* Forel), plus other probably related species and several undescribed morphospecies.

***P. speculifera* group**:

Can be subdivided into *prelli* complex and *speculifera* complex, the first with slightly smaller species (minor: ML < 1.005 mm), which possess relatively large eyes (minor: EI > 30) and including species like *P. prelli* Forel, *P. caffra* Emery, and subspecies of both. The *speculifera* complex includes slightly to considerably larger species (ML: > 0.967 mm) with smaller eyes (EI: 22-28), for example *P. crassinoda* Emery, *P. occipitalis* André, *P. speculifera* Emery, and several subspecies. Minor workers: long antennal scapes, surpassing the occipital margin by about ¼ of their length; posterior head margin compressed, weakly rounded [*prelli* complex] to evenly rounded [*crassinoda*, *speculifera*]; postpetiole large and voluminous, as long as [*prelli* complex] or longer [*crassinoda*, *speculifera*] than petiole and more than twice as wide; pilosity moderately abundant, either short and stout, with blunt or split apices [*crassinoda*, *prelli*] or longer and flexous [*speculifera*]. Major workers: head massive and thick, either sculpture variable and frontal carinae & antennal scrobes absent [*crassinoda*, *speculifera*] or head with strong longitudinal and transverse rugose-punctate sculpturation and long, curved and broadly extended frontal carinae [*prelli* complex]; spines thick and short, almost lobate; postpetiole very massive, in dorsal view about 2-3 times wider than petiole, with a conspicuously spiked lateral process. Several described species and subspecies (*Pheidole caffra* Emery, *P. caffra abyssinica* Forel, *P. caffra amoena* Forel, *P. caffra bayeri* Forel, *P. caffra montivaga* Santschi, *P. caffra senilifrons* Wheeler, *P. crassinoda* Emery, *P. crassinoda pluto* Arnold, *P. crassinoda ruspolii* Emery, *P. crassinoda sordidula* Santschi, *P. occipitalis* André, *P. occipitalis adami* Santschi, *P. occipitalis neutralis* Santschi, *P. prelli* Forel, *P. prelli ingenita* Santschi, *P. prelli redbankensis* Forel, *P. speculifera* Emery, *P. speculifera ascara* Emery, *P. speculifera bispecula* Santschi, *P.*

speculifera cubangensis Forel) and undescribed species belong to this group with new material from different localities in the collections of BMNH, CASC and ZFMK.

Definition of the *P. pulchella* group

The *Pheidole pulchella* species group was defined in the process of our identification efforts of very distinct groups of specimens from the Kakamega Forest in Western Kenya and from the Budongo and Rabongo Forests in Uganda. Both were at first identified as *P. pulchella*. Comparison with type material later revealed the dark colored morphospecies, to be conspecific with *P. dea* Santschi from the Democratic Republic of Congo. We are now able to describe the previously unknown major workers. The orange colored specimens from Budongo Forest belong to a previously undescribed species and are predicted to be closely related to *P. pulchella*. In subsequent type material examinations and museum visits, additional undescribed material was found from the Ivory Coast in the west along the equatorial rain forest belt to Gabon, Central African Republic and Tanzania in the East. In their general morphology the species in this group are well separated from those of other groups by the following character combinations:

Diagnostic characters of minor workers

Head: Shape in full-face view variable among species, but never square with angulate posterolateral corners, from short-rounded (CI: 85-98) with sides of head strongly convex and convex [*dea*], or almost straight [*rebeccae*] posterior margin to long-elliptical (CI: 73-84), sub-angular at eye level and posteriad elongate towards occipital carina [*christinae*, *heliosa*]. Mandibles smooth and shiny, sometimes with very superficial rugulae, laterally with weak longitudinal rugulae. Eyes situated near midlength of the head, of medium size (EI: 19-29). Scapes moderately to very long (SI: 114-174) and surpassing occiput by one quarter to approximately one third of their length. Occipital carina always conspicuous in full-face view.

Mesosoma: Mesonotal declivity interrupted by promesonotal process, followed by a smaller process between promesonotal process and metanotal groove. The second, smaller, process is reduced and less conspicuous in some species. Propodeal spines long and spinate, much longer than distance between their bases (PSLI: 21-40), curved posteriad towards petiole, rarely straight. Promesonotum, in lateral view, with angulate to subangulate edges, pronotal dorsum flat to weakly rounded, never strongly convex.

Metasoma: Petiole longer than postpetiole (PpLI: 117-223), and in dorsal view usually about half as wide (PpWI: 152-232). Postpetiole also with well-developed convex ventral process and about as high as long, with subglobular to globular shape in profile. In dorsal view postpetiole about as long as wide, with a roughly trapezoidal shape.

Pilosity: With few to many long acute standing hairs, some species with hair apices truncate (or bifurcate), but in some species almost completely absent from dorsum of head, meso- and metasoma. Mesonotum and propodeum often with shorter, suberect to subdecumbent hairs. Standing hairs never very short and stiff. Between long erect hairs on head, often shorter suberect to subdecumbent hairs present.

Sculpture: Variable between species, with relatively little intraspecific variation, from completely and strongly punctate [*nimba*] to mostly smooth and shiny [*rebeccae*], but mesonotum and propodeum never completely smooth and shiny, at least partly punctate.

Diagnostic characters of major workers

Head: About as wide as long (CI: 96-105), broadest always between eye level and occipital margin, frons and sides of head rugose-punctate to varying degrees. Posterolateral lobes often differently sculptured. Dorsal surface of mandible smooth, laterally longitudinally rugulose. Clypeus with median longitudinal carina present. Scapes moderately long (SI: 49-58).

Hypostomal margin always with two inner and two outer submedian teeth present, median process absent to inconspicuous. In full-face view, and for all species but *Pheidole heliosa*, head margin without projecting hairs of any kind, only with relatively short appressed pilosity and long erect hairs, that are visible in lateral view. Pilosity on scape appressed to subdecumbent.

Mesosoma: Humeral area laterally not or weakly produced, mesonotal process always developed and with posterior steep declivity towards metanotal groove, which, in lateral view, is barely to broadly impressed. Propodeal spines relatively long and spinate, longer than distance between their bases.

Metasoma: Petiole longer than postpetiole (PpLI: 131-176). Postpetiole considerably wider than petiole (PpWI: 177-252), wider and higher than long, in lateral view with anteriorly produced ventral process.

General ecology of the *P. pulchella* group

Most of the collection localities for species of the *P. pulchella* group are in rainforests, habitats of a few are not indicated on the labels. Specimens were caught in pitfall-traps, leaf-litter extractions, by beating of the lower vegetation, or by hand-collection. Thus, the species in this group are most likely forest specialists living and/or foraging on the ground and in the lower vegetation. Their conspicuous morphology with the relatively large size, long spines and appendages, and well-developed eyes indicates that these species are not living within, but rather upon or above the leaf-litter layer. They possibly nest in dead wood, because several of the specimens, especially the more rarely observed majors, were collected from rotten logs. Still, the biology of this species group is largely unknown and there are no records or observations known, other than the collection data mentioned on the labels.

Synopsis of *P. pulchella* group species of the Afrotropical region

Pheidole batrachorum Wheeler 1922 **stat. rev.**

Pheidole christinae Fischer, Hita Garcia & Peters 2011 **sp. n.**

Pheidole darwini Fischer, Hita Garcia & Peters 2011 **sp. n.**

Pheidole dea Santschi 1921

Pheidole glabrella Fischer, Hita Garcia & Peters 2011 **sp. n.**

Pheidole heliosa Fischer, Hita Garcia & Peters 2011 **sp. n.**

Pheidole nimba Bernard 1953

Pheidole pulchella Santschi 1910

= *Pheidole niapuana* (Wheeler 1922)

= *Pheidole pulchella var. achantella* (Santschi 1939) **syn. n.**

Pheidole rebeccae Fischer, Hita Garcia & Peters 2011 **sp. n.**

Pheidole semidea Fischer, Hita Garcia & Peters 2011 **sp. n.**

Pheidole setosa Fischer, Hita Garcia & Peters 2011 **sp. n.**

Key to species of the *P. pulchella* group (minors and majors combined)

1a. **Minor:** In full-face view lateral head margin with abundant projecting hairs, both anteriad and posteriad of eye-level (Fig. 4.2A). **Minor and major:** Color yellow to orange. …..… 2

1b. **Minor:** In full-face view either without laterally projecting hairs at head margin (Fig. 4.2C), or if present, then only posteriad of eyes (Fig. 4.2B). **Minor and major:** Color light, reddish brown to very dark brown, sometimes black. ……………………………………………………………….… 4

FIGURE 4.2 A) *P. christinae* sp. n., **B)** *P. batrachorum* Wheeler, **C)** *P. glabrella* sp. n. Full-face view of minor workers: examples of laterally projecting hairs anteriad and posteriad of eye-level (A), posteriad of eye-level only (B) and completely without (C).

2a. **Minor:** Head evenly rounded at sides and posterior margin (CI 82-90); pilosity on scape and metatibia decumbent (Fig. 4.3A). **Major:** Antennal scrobe conspicuous; sides of head without laterally projecting hairs in full-face view (Fig. 4.3B). (Congo, Gabon). …….. *P. pulchella* Santschi

2b. **Minor:** Sides of head posteriad of eyes sublinear and elongated; head relatively longer (CI 73-84); pilosity on scape and metatibia suberect-erect (Figure 4.3C). **Major:** Antennal scrobe absent or inconspicuous; head in full-face view with laterally projecting hairs (Figure 4.3D). 3

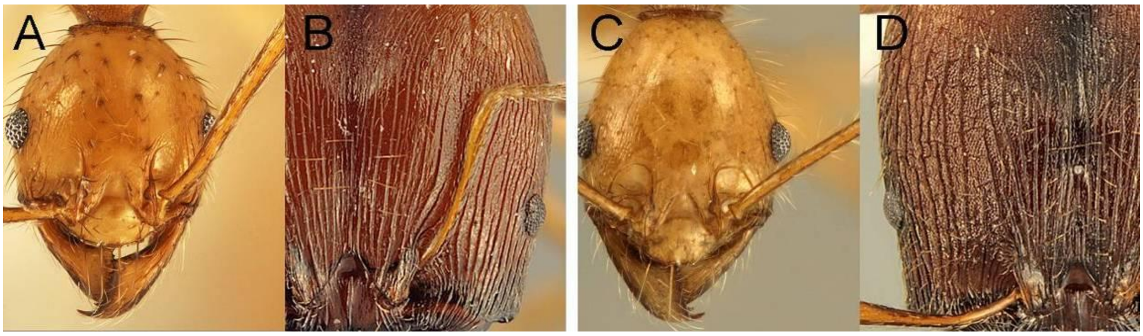

FIGURE 4.3 A, B) *P. pulchella* Santschi. Full face view of minor and major worker: showing sides of head rounded towards posterior head margin in the minor (A), and presence of antennal scrobe and absence of laterally projecting hairs in the major (B). **C, D)** *P. heliosa* sp. n. Full face view of minor and major worker: illustrating elongated posterior sides of head in the minor worker (C), and absence of antennal scrobe and presence of laterally projecting hairs in major worker (D).

3a. **Minor**: Head, scapes and legs very long (CI 73-76, SI 162-174, FI: 206-213); occipital carina broadly extended and collar-like; standing hairs acute and very abundant (Figure 4.4A), present also at lower meso- and metapleuron, visible in dorsal view. **Major:** Head without antennal scrobe; in full-face view hairs projecting beyond lateral margin. (Ivory Coast, Cameroon). .... *P. heliosa* sp. n.

3b. **Minor:** Head, scape and legs relatively shorter (CI 79-84, SI: 143-164, FI: 175-198); occipital carina narrow, not collar-like; standing hairs often apically truncated or split, generally less abundant (Figure 4.4B), absent at lower meso- and metapleuron. **Major:** Unknown. (Uganda, Gabon, D.R. Congo). .... *P.christinae* sp. n.

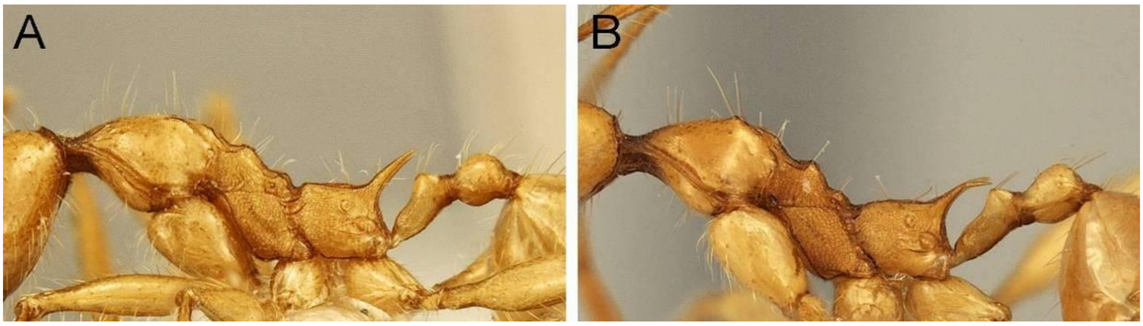

FIGURE 4.4 A) *P. heliosa* sp. n. lateral view of minor worker, illustrating mesosoma with long second mesonotal process, highest point of dorsopropodeum immediately at metanotal groove and metasoma with spheroidal postpetiole. **B)** *P. christinae* sp. n. with shorter second mesonotal process, highest point of dorsopropodeum midway between metanotal groove and postpetiole not spheroidal.

4a. **Minor:** Head with several relatively long, laterally projecting hairs posteriad of eye-level (Fig. 4.5A). **Major**: Either posterolateral lobes partly smooth and shiny and scape with erect hairs in addition to decumbent pilosity (Fig. 4.5B), or posterolateral lobes uniformly punctate with weak rugulae and posterior dorsopropodeum with oblique to longitudinal rugulae (Fig. 4.5C). ……….. 5

4b. **Minor:** Head completely without or at most with one or two moderately long projecting hairs near eyes or towards posterior margin (Fig. 4.5D). **Major:** Head sculpture various; scape never with several erect hairs in addition to appressed or decumbent pilosity (Fig. 4.5E); sculpture on posterior dorsopropodeum transversely rugulose, punctate or smooth, and never with oblique or longitudinal rugulae (Fig. 4.5F). ……………………………………………………………………….. 7

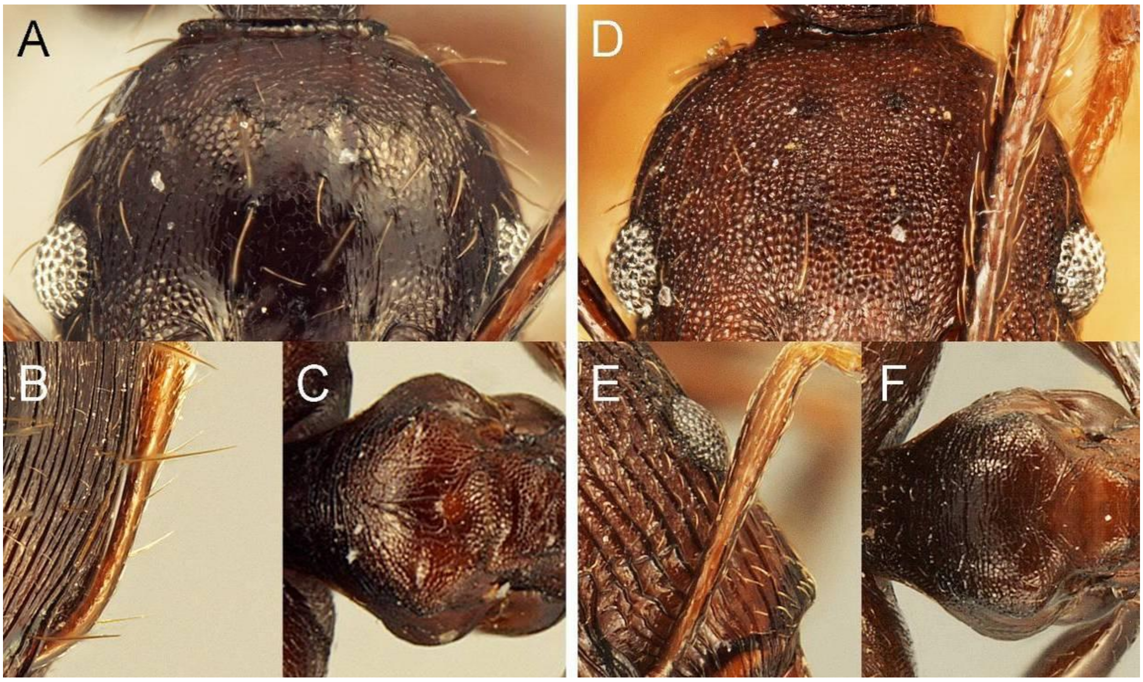

FIGURE 4.5: A) *P. setosa*, sp. n. minor worker in full-face view: illustrating head margin with several laterally projecting and long hairs; **B)** *P. darwini*, major worker in oblique fronto-lateral view: scape with erect, long hairs additionally to decumbent pilosity; **C)** *P. batrachorum* Wheeler, major worker in dorsal view: pronotum with several oblique to longitudinal rugulae. **D)** *P. nimba* Bernard, minor worker in full-face view: illustrating head margin with a maximum of two laterally projecting and short hairs; **E, F)** *P. glabrella* sp. n., major worker in oblique full-face view and in dorsal view: illustrating uniform scape pilosity without additional erect hairs (E) and transverse rugulae at dorsal pronotum (F).

5a. **Minor:** Head shape elliptical (CI: 79-89); posterior margin relatively narrow and not compressed; occipital carina with weak median impression; scapes moderately long (SI: 139-172), with pilosity uniformly suberect or decumbent (Figure 4.6A). **Major**: Posterolateral lobes partly smooth and shiny and scape with erect hairs in addition to decumbent pilosity, or posterolateral lobes uniformly punctate with weak rugulae and posterior dorsopropodeum with oblique to longitudinal rugulae. …………………………………………...…………………………………….…… 6

5b. **Minor:** Head shape broadly rounded, compressed at posterior margin (CI: 87-90); occipital carina without median impression; scapes relatively shorter (SI: 129-135); scape pilosity decumbent with additional suberect hairs on outer edge (Figure 4.6B). **Major:** Unknown. (D.R. Congo). ……………………………………………………………........................ *P. setosa* sp. n.

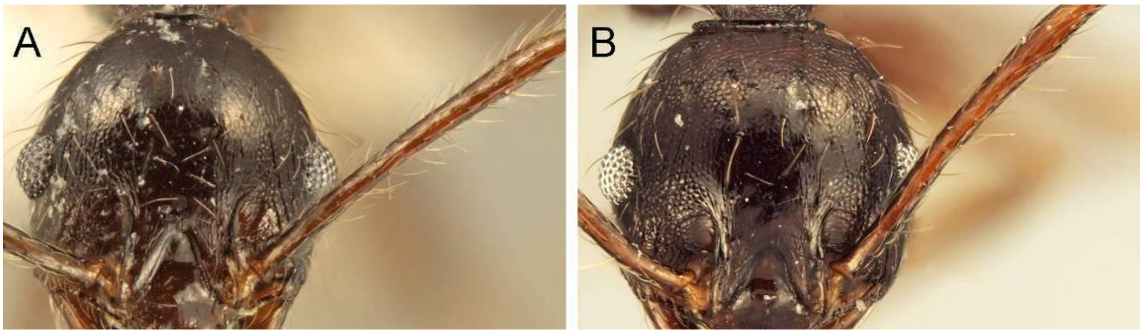

FIGURE 4.6: A, B) *P. darwini* sp. n. and *P. setosa* sp. n., full-face view of minor workers: illustrating narrow posterior head margin and uniformly subdecumbent to suberect scape pilosity (A) versus wider posterior head margin and scape with erect to suberect hairs additional to decumbent pilosity (B).

6a. **Minor:** Head shape relatively narrow (CI: 79-86); scapes long (SI: 153-172); scape pilosity uniformly decumbent; face almost completely and distinctly punctate (Figure 4.7A). **Major:** Posterolateral lobes uniformly punctate with some weak rugulae; scape with uniformly appressed to decumbent pilosity; posterior dorsopropodeum with oblique to longitudinal rugulae (Figure 4.7B). (Central African Republic, D.R. Congo, Gabon). …. *P. batrachorum* Wheeler

6b. **Minor:** Head shape relatively wider (CI: 84-89); scapes slightly shorter (SI: 139-160); scape pilosity uniformly subdecumbent to suberect; face smooth and shiny, hexagonally to very faintly punctate (Figure 4.7C). **Major:** Posterolateral lobes partly smooth and shiny; scape with some erect hairs additional to decumbent pilosity; posterior dorsopropodeum weakly to superficially rugulose-punctate (Figure 4.7D). (Cameroon, Central African Republic, Gabon). …… *P. darwini* sp. n.

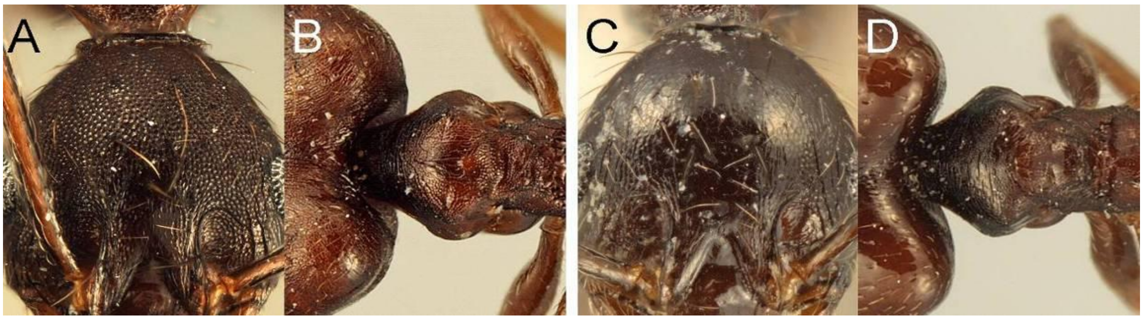

FIGURE 4.7: A, B) *P. batrachorum* Wheeler, full face view of minor and major worker: showing distinctly punctate face of the minor worker (A) and head with distinctly sculptured postolateral lobes, and posterior dorsopronotum with longitudinal rugulae for the major worker (A). **C, D)** *P. darwini* sp. n., full face view of minor and major worker: illustrating superficially punctate (hexagonally microsculptured) face in the minor worker (C) and head with smooth & shiny postolateral lobes, and posterior dorsopronotum without longitudinal, or oblique rugulae for the major worker (D).

7a. **Minor:** Sculpture variable, but head and mesosoma never completely and coarsely punctate; at least medially between eyes and at posterior dorsopronotum superficially sculptured to smooth and shiny (Figure 4.8A). **Major:** Head sculpture variable, but never distinctly punctate at frons; vertex and posterolateral lobes, gaster never entirely shagreened. ……… 8

7b. **Minor:** Head and mesosoma almost completely and coarsely punctate (Figure 4.8B). **Major:** Unknown. (Guinea). ……………………………………………………………………………… *P. nimba* Bernard

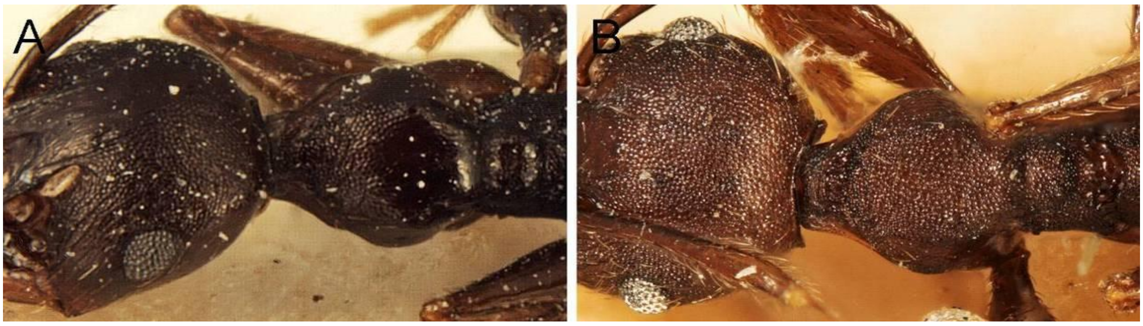

FIGURE 4.8: A, B) *P. dea* Santschi and *P. nimba* Bernard, minor workers, dorsal view of head and promesonotum: illustrating smooth to superficially punctate areas medially between eyes and posteriad at dorsal promesonotum (A) versus uniformly expressed sculpture in face and on promesonotum (B).

8a. **Minor:** Head longer than wide (CI: 85-95), posterior margin rounded to slightly compressed (Figure 4.9A); scapes and mandibles moderately long (SI: 123-150, MDI: 72-79). **Major:** Posterolateral lobes variably sculptured, never smooth and shiny; face with distinct and moderately long to long rugae; dorsal promesonotum mostly weakly to superficially sculptured (Figure 4.9B). ……… 9

8b. **Minor:** Head almost as wide as long (CI: 94-98), posterior margin compressed, almost straight (Figure 4.9C); scapes and mandibles shorter (SI: 114-121, MDI: 69-73). **Major:** Posterolateral lobes smooth and shiny; face with weak and relatively short rugae; dorsal promesonotum mostly smooth and shiny, with superficial rugulae anteriorly (Figure 4.9D). (Ghana, Ivory Coast). ………………………………………………………………………………… *P. rebeccae* sp. n.

FIGURE 4.9: A, B) *P. glabrella* sp. n., full-face view of minor worker (A): showing rounded head shape and rounded occipital margin; dorsal view of major worker (B): illustrating obliquely rugulose-punctate sculpture at postolateral lobes, and regular transversely rugulose-punctate sculpture at dorsopronotum. **C, D)** *P. rebeccae* sp. n., full-face view of minor worker (C): showing wider head shape and compressed head margin; dorsal view of major worker (D), illustrating smooth and shiny postolateral lobes, and dorsopronotum with superficially rugulose anterior to mostly smooth & shiny posterior surface.

9a. **Minor:** Long or moderately long hairs completely absent on mesosoma and waist segments; petiole and postpetiole without laterally projecting hairs in dorsal view; scape pilosity appressed to decumbent; metatibia pilosity appressed; second mesonotal process and sculpture at propodeum reduced; metanotal groove wide in profile (Figure 4.10A); spines long (PSLI: 28-40). **Major:** Scape and metatibia pilosity fine and inconspicuous, mostly fully appressed; long standing hairs absent on promesonotum; dorsopropodeum distinctly shorter than base of the spines (Figure 4.10B). (Cameroon, Central African Republic, Gabon). .... *P. glabrella* sp. n.

9b. **Minor:** Moderately long hairs at least present on waist segments, sometimes also on promesonotum; at petiole and / or postpetiole some laterally projecting hairs in dorsal view; scape and metatibia pilosity decumbent; second mesonotal process and sculpture at propodeum not reduced; metanotal groove relatively narrow in profile (Figure 4.10C); spines slightly shorter (PSLI: 25-35). **Major:** Scape and metatibia pilosity conspicuous and decumbent; standing hairs often present on promesonotum; dorsopropodeum at least as long as base of the spines or longer (Figure 4.10D). 10

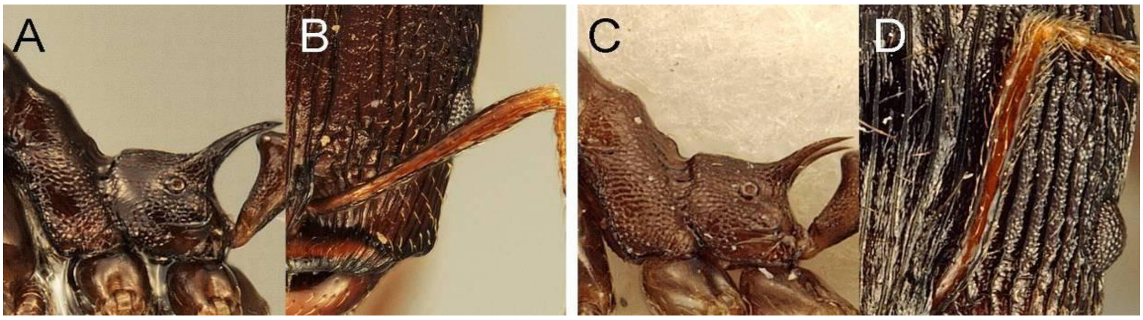

FIGURE 4.10: A, B) *P. glabrella* sp. n., dorsal view of minor worker (A): waist segments without long standing or laterally projecting hairs, only with short decumbent pubescence present; full-face view of major worker (B): scape pilosity appressed. **C, D)** *P. dea* Santschi, dorsal view of minor worker (C): illustrating waist segments with long standing and laterally projecting hairs present; full-face view of major worker (D): showing decumbent scape pilosity.

10a. **Minor:** Posterior head margin roundly convex; face and dorsal promesonotum mostly superficially punctate to punctate; second mesonotal process not raised above the level of dorsopropodeum (Figure 4.11A); postpetiole relatively short (PpLI: 155-223). **Major:** Posterolateral lobes of head longitudinally rugose (Figure 4.11B), with spaces between rugae weakly to superficially punctate; second mesonotal process at same level as dorsopropodeum (D.R. Congo, Kenya, Tanzania, Uganda). …………………….. *P. dea* Santschi

10b. **Minor:** Posterior head margin weakly compressed; face and promesonotum smooth and shiny, with very few superficial punctures; in lateral view second mesonotal process distinctly raised above the level of dorsopropodeum (Figure 4.11C); postpetiole relatively longer (PpLI: 126-167). **Major:** Posterolateral lobes of head punctate, overlain by oblique and superficial rugulae (Figure 4.11D); in lateral view second mesonotal process raised above level of dorsopropodeum (Nigeria) ....……. *P. semidea* sp. n.

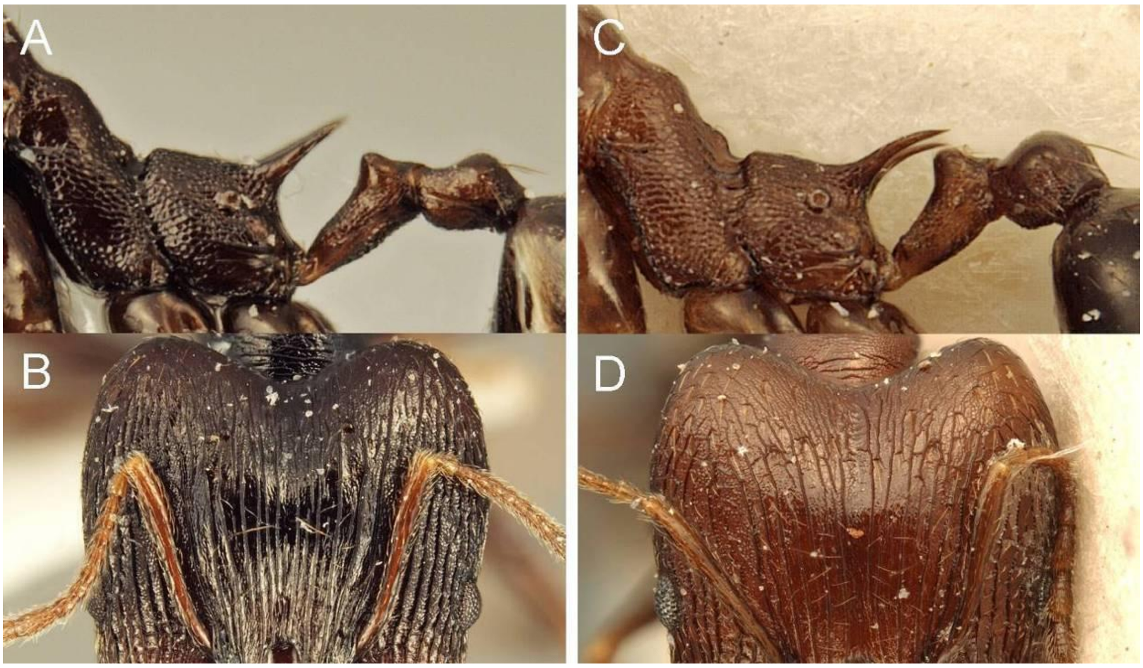

FIGURE 4.11: A, B) *P. dea* Santschi, lateral view of minor worker (A): second mesonotal process at same level as dorsopropodeum, postpetiole relatively small in relation to petiole; full-face view of major worker (B): vertex without cross-meshes and postolateral lobes longitudinally rugose. **C, D)** *P. semidea* sp. n., lateral view of minor worker (C): second mesonotal process raised at slightly higher level than dorsopropodeum, postpetiole relatively larger in relation to petiole; full-face view of major worker (D): vertex with cross-meshes and postolateral lobes obliquely and irregularly rugulose.

Review of species

Pheidole batrachorum **Wheeler 1922 stat. rev.**

(Figures 4.12 - 4.17)

Pheidole batrachorum Wheeler, W.M. 1922: 128. Syntype major workers (2) and minor workers (3). D.R. CONGO: Akengi (*H.O. Lang*); stomach *Bufo polycerus;* Akenge (*Lang*); stomach *Arthroleptis variabilis* (NMNH) [examined]. [Previously synonymised with *Pheidole dea* by Santschi, 1930a: 59.] **Stat. rev.**

Diagnosis: Both castes reddish brown to dark brown. Minor workers: Head shape elliptical and relatively narrow (CI: 79-86); antennal scapes long (SI: 153-172); head margin posteriad of eye-level with laterally projecting hairs; frons, vertex and most of mesosoma uniformly punctate, except smooth spots medially between eyes and on posterior lateropronotum; head and body with long standing and shorter decumbent to subdecumbent hairs, scape and metatibia pilosity mostly decumbent. Major workers: Head sculpture rugose-punctate with relatively long rugae; scape relatively long; sculpture at anterior portion of dorsopropodeum transversely rugulose-punctate, posteriad with obliquely curved or longitudinal rugulae and superficial punctures to partly smooth; long standing hairs present on promesonotum, scape and metatibia pilosity appressed to decumbent. [**Geographic Range:** Central African Republic, D.R. Congo, Gabon]

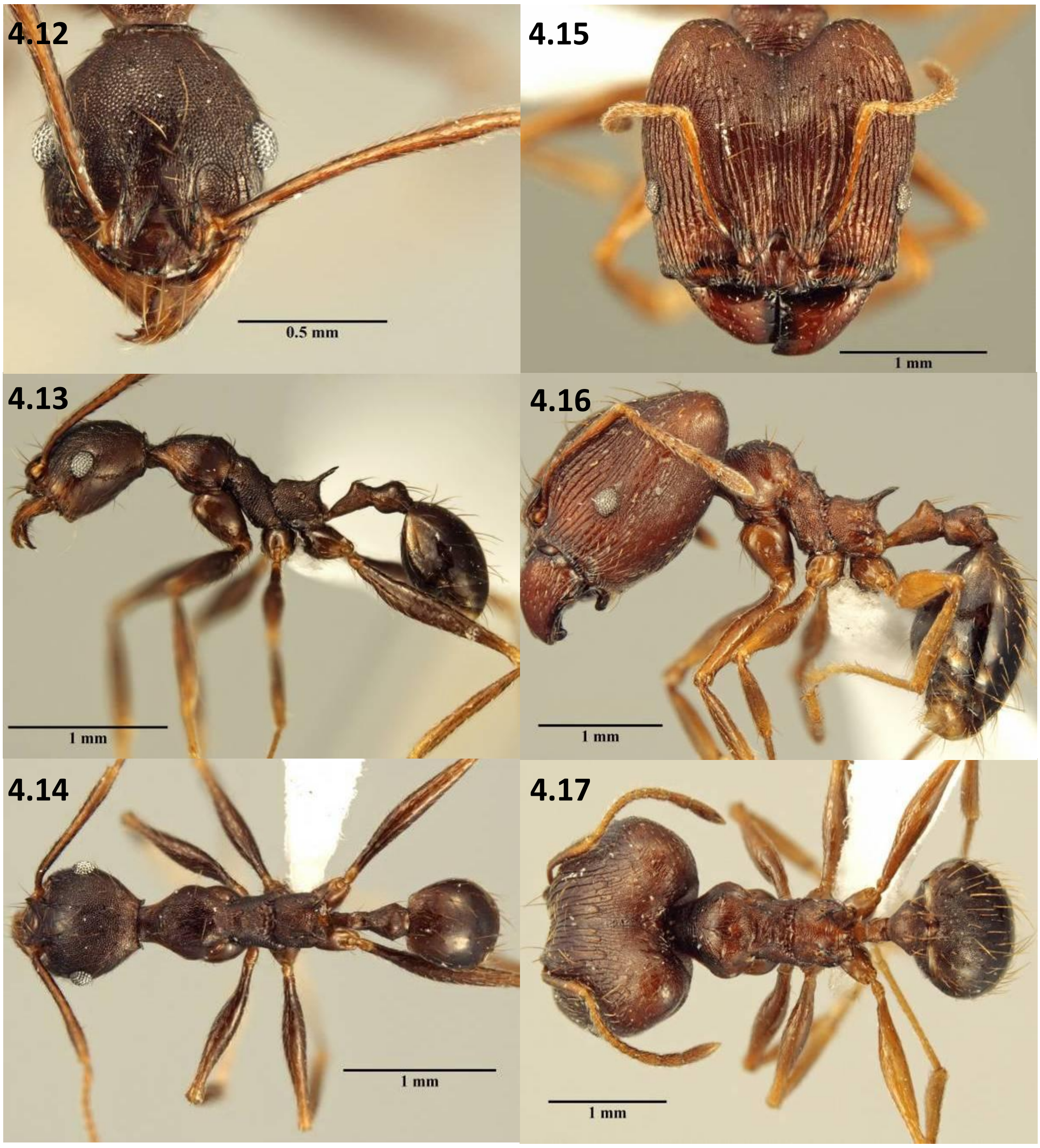

Fig. 4.12 - 4.17 *P. batrachorum* Wheeler: full-face, lateral & dorsal view of minor (**4.12 - 4.14**) and major worker (**4.15 - 4.17**).

Description of minor worker: Measurements (2 cotypes): HW: 0.656-0.744 (0.700), HL: 0.800-0.867 (0.833), SL: 1.089-1.133 (1.111), MDL: 0.522-0.556 (0.539), EL: 0.183-0.189 (0.186), FL: 1.286-1.381 (1.333), TL: 0.989-1.078 (1.033), ML: 1.111-1.206 (1.159), PSL: 0.211-0.244 (0.228), PTH: 0.167-0.178 (0.172), PPH: 0.211-0.233 (0.222), PTL: 0.311-0.322 (0.317), PPL: 0.222-0.256 (0.238), PTW: 0.111-0.133 (0.122), PPW: 0.211-0.244 (0.228), PW: 0.456-0.478 (0.467); CI: 82-86

(84), SI: 152-166 (159), MDI: 75-80 (77), PSLI: 26-28 (27), PWI: 64-69 (67), FI: 186-196 (191), PpWI: 183-190 (187), PpLI: 126-140 (133)

Measurements (n=14): HW: 0.589-0.722 (0.676), HL: 0.682-0.867 (0.817), SL: 0.900-1.122 (1.085), MDL: 0.456-0.567 (0.541), EL: 0.156-0.183 (0.177), FL: 1.011-1.317 (1.266), TL: 0.789-1.033 (0.968), ML: 0.956-1.167 (1.120), PSL: 0.144-0.244 (0.213), PTH: 0.144-0.189 (0.174), PPH: 0.172-0.233 (0.214), PTL: 0.256-0.367 (0.330), PPL: 0.178-0.267 (0.234), PTW: 0.100-0.133 (0.120), PPW: 0.189-0.244 (0.227), PW: 0.400-0.511 (0.463); CI: 79-86 (83), SI: 153-172 (160), MDI: 77-83 (80), PSLI: 15-21 (26), PWI: 67-72 (68), FI: 172-195 (187), PpWI: 181-200 (189), PpLI: 125-160 (141)

Head shape in full-face view elliptical (CI: 79-86), head margin posteriad of eye-level rounded towards well-developed occipital carina, with weak to absent medial impression; mandible dorsally unsculptured and smooth; clypeus smooth or superficially punctate, median carina absent to inconspicuous, nasal carinae weak and irregular; most of face uniformly punctate, except smooth to superficially sculptured central spot at eye-level; malar area punctate, overlain by some irregular rugulae, ending at posterior eye level; scapes long (SI: 152-172), pilosity decumbent to subdecumbent. Promesonotal outline in lateral view subangular; dorsopronotum flat; first and second mesonotal process conspicuously produced and subangular; mesosoma mostly punctate, save for smooth central area at lateropronotum; punctures on anteropronotum partly overlain with weak irregular transverse to diagonal rugulae, posteriad sometimes with weak longitudinal rugulae; propodeal spines relatively short (PSLI: 21-29); metafemur long (FI: 172-196); metatibia with decumbent pilosity. Petiole and postpetiole densely punctate, weaker dorsally than ventrally; anterior margin at gaster weakly shagreened, rest smooth and shiny. Standing hairs on head, pronotum and waist segments moderately long and acute, longer on gaster; face with four to five pairs of long standing hairs, additionally with shorter subdecumbent hairs, in full-face view, laterally projecting over head margin posteriad of eye-level; one hair immediately above eye curved in weak S-shape; mesonotum, propodeum and waist segments with short subdecumbent hairs. Color dark brown, mandibles and appendages lighter colored.

Description of major worker: Measurements (cotype): HL: 2.000, HW: 2.040, SL: 1.133, MDL: 0.944, EL: 0.278, FL: 1.700, TL: 1.302, ML: 1.700, PSL: 0.322, PTH: 0.378 , PPH: 0.456, PTL: 0.511, PPL: 0.389, PTW:0.278 , PPW: 0.511, PW: 0.889; CI: 98, SI: 57, MDI: 47, PSLI: 16, PWI: 44, FI: 85, PeI: 31, PpI: 58, PpWI: 184, PpLI: 131

Measurements (n=5): HL: 1.860-1.920 (1.888), HW: 1.800-1.880 (1.860), SL: 1.011-1.089 (1.053), MDL: 0.889-1.000 (0.951), EL: 0.233-0.267 (0.247), FL: 1.476-1.603 (1.546), TL: 1.111-1.254 (1.181), ML: 1.444-1.587 (1.508), PSL: 0.278-0.322 (0.304), PTH: 0.300-0.344 (0.324), PPH: 0.367-0.422 (0.394), PTL: 0.511-0.567 (0.542), PPL: 0.333-0.378 (0.358), PTW: 0.222-0.244 (0.233), PPW: 0.483-0.556 (0.514), PW: 0.800-0.844 (0.820); CI: 97-100 (99), SI: 55-58 (57), MDI: 49-53 (51), PSLI: 14-17 (16), PWI: 44-45 (44), FI: 79-85 (83), PeI: 27-30 (28), PpI: 60-66 (63), PpWI: 212-235 (221), PpLI: 144-160 (152)

Frons longitudinally rugose-punctate, some rugae moderately long, others shorter and irregular, posterolateral lobes weakly rugulose-punctate; sides laterad of antennal scrobe and posteriad of eye-level irregularly rugose-reticulate, with punctate ground sculpture, scape pilosity shorter than maximum scape diameter, appressed-decumbent. Pronotal outline in profile relatively rounded to subangular, in dorsal view laterally angulate and weakly produced; promesonotal and mesonotal declivity steep; mesonotal process right-angled; second mesonotal process small and dorsally narrow, sometimes only a short median tip, but usually raised above level of dorsal propodeum; anteropronotum transversely rugulose-punctate; posteropronotum with irregular oblique to longitudinal rugulae and superficial to smooth ground-sculpture; posterior lateropronotum with smooth central area; meso- and metapleuron punctate, except smooth areas around metapleural carinae and metapleural gland scrobe; dorsopropodeum anteriorly punctate, grading from weak to superficial punctures posteriorly, transverse rugulae in dorsal view visible between spines and on posteropropodeum, metatibia pilosity appressed to decumbent. Petiole and postpetiole densely punctate, sides of postpetiole in dorsal view angulate, posteriorly with a conspicuous flange; punctures on posterodorsal face partly overlain by short oblique to longitudinal rugulae; anterior half of first gastral tergite weakly punctate, posterior half shagreened or microsculptured. Standing hairs of moderate length, relatively stiff and truncated, on mesonotum and propodeum short, subdecumbent to decumbent. Color reddish brown to brown, gaster darker.

Discussion: Santschi synonymized *Pheidole batrachorum* with *P. dea*, yet the similarities are superficial (see below), which is the reason why species status is revived in this revision. Another species with a high amount of punctate sculpture is *P. nimba*. Both, *P. dea* and *P. nimba* were described only from minor workers. These two species are best separated from *P. batrachorum* by their wider heads and more rounded posterior head margins (CI: 86-93 [*dea*] and CI: 90 [*nimba*] versus CI: 79-86 [*batrachorum*]), at most one or two laterally projecting hairs at eye-level or posterior margin versus several, and significantly shorter antennal scapes (SI: 134-147 and SI: 129 versus SI: 153-172). A unique character for *P. nimba* is the uniformity and strength of its punctate sculpture without any superficially punctate or smooth dorsal surfaces at the head, mesosoma and metasoma. In the Central African Republic *P. batrachorum* co-occurs with *P. darwini*, from which major workers are separated by shorter spines (PSLI: 29-35 versus PSLI: 21-29), slightly longer scapes (SI: 153-172 versus SI: 139-160), a narrower head (CI: 79-86 versus CI: 84-89) in the minor worker caste, and slightly shorter scapes (SI: 49-53 versus SI: 55-58), mandibles (MDI: 42-51 versus MDI: 47-53) and metafemur (FI: 75-80 versus FI: 79-85), and significantly more sculpture in the face and at the dorsopronotum in both worker castes. *Pheidole batrachorum* types have been collected at Akenge in the D.R. Congo. Wheeler described this species from four major and twenty-one minor workers, found in stomachs of toads and frogs in the rainforest. Of the eight minor and two major workers loaned from the

NMNH, the two majors are concordant with Wheeler's description, but only three of the minors are, the rest belong to *P. glabrella* and are treated as such. The non-type material is conspecific with the types and was collected in Gabon and the Central African Republic, from within rotten logs and sifted leaf-litter in rainforest habitat.

Type material examined: D.R. CONGO: (2 major workers, cotypes) Akengi (*H.O. Lang*); stomach *Bufo polycerus;* (3 minor workers, cotypes) Akenge (*Lang*); stomach *Arthroleptis variabilis.*

Other material examined: CENTRAL AFRICAN REPUBLIC: (1 minor worker) Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 03° 00.27' N, 16° 11.55' E, 420 m, 11-17.v.2001 (*S. van Noort*); (1 minor worker) P.N. Dzanga-Ndoki, 21.4 km 53° NE Bayanga 03° 02.01' N, 16° 24.57' E, 510 m, 1-7.v.2001 (*S. van Noort*); (1 minor worker) P.N. Dzanga-Sangha, 38.6 km 173° S Lidjombo, 02° 21.60' N, 16° 03.20' E, 350 m, 21-27.v.2001 (*S. van Noort*); (4 major workers, 13 minor workers) Res. Dzanga-Ndoki, Mabea Bai, 21.4 km 53° NE Bayanga, 03° 02' N, 16° 25' E, 510 m, 1-07.v.2001 (*B.L. Fisher*); (1 minor worker) Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 03° 00' N, 16° 12' E, 470 m, 10-17.v.2001 (*B.L. Fisher*); (2 major workers, 6 minor workers) Res. Dzanga-Ndoki, Mabea Bai, 21.4 km 53° NE Bayanga, 03° 02' N, 16° 25' E, 510 m, 1-07.v.2001 (*B.L. Fisher*); GABON: (4 minor workers) Prov. Woleu-Ntem, 31.3 km 108° ESE Minvoul, 02° 04.8' N, 12° 24.4' E, 600 m, 11.ii.1998 (*B.L. Fisher*); (1 major worker) Prov. Woleu-Ntem, 31.3 km 108° ESE Minvoul, 02° 04.8' N, 12° 24.4' E, 600 m, 7.ii.1998 (*B.L. Fisher*)

Pheidole christinae sp. n.

(Figures 4.18 - 4.20)

Diagnosis: *Pheidole christinae* is known from minor workers only. Color orange. Head elliptical, posteriad of eye-level slightly elongated (CI: 79-84); occipital carina very narrow; scape relatively long (SI: 143-164) and with erect to suberect pilosity. Promesonotum at humeri with small dent, in lateral view slightly raised above dorsal outline; spines and metafemur long (PSLI: 26-36, FI: 175-198); metatibia with pilosity at inner edge subdecumbent, at outer edge subdecumbent to suberect. Standing hairs of variable lengths, mostly ending bluntly or truncated. [**Geographic Range:** D.R. Congo, Gabon, Uganda]

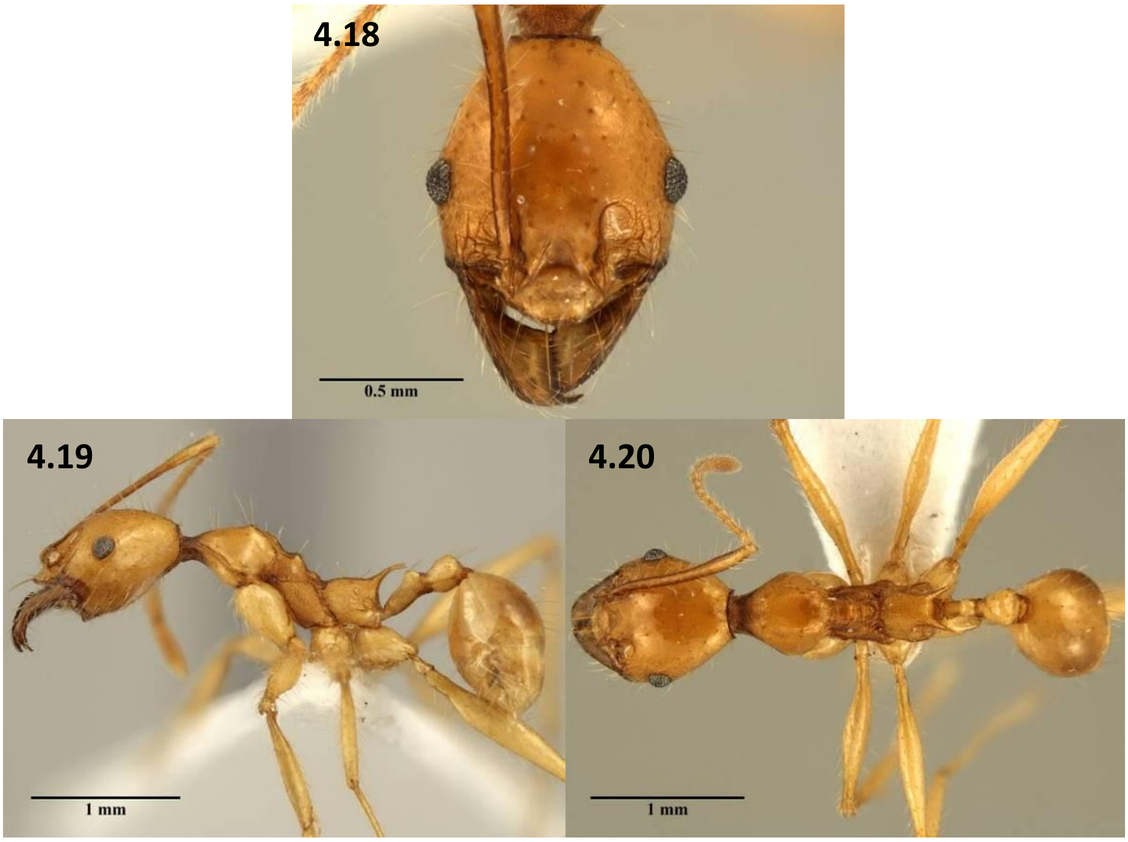

Fig. 4.18 - 4.20: *P. christinae* sp. n.: full-face, lateral & dorsal view of minor worker.

Description of minor worker: Measurements (holotype): HL: 0.989, HW: 0.811, SL: 1.302, MDL: 0.633, EL: 0.167, EW: 0.133, FL: 1.508, TL: 1.167, ML: 1.286, PSL: 0.278, PTH: 0.178, PPH: 0.244, PTL: 0.367, PPL: 0.256, PTW: 0.122, PPW: 0.256, PW: 0.533, CI: 82, SI: 160, MDI: 78, PSLI: 28, PWI: 66, FI: 186, PpWI: 209, PpLI: 143

Measurements (n=21): HW: 0.733-0.833 (0.798), HL: 0.878-1.022 (0.977), SL: 1.100-1.349 (1.244), MDL: 0.578-0.678 (0.643), EL: 0.156-0.178 (0.166), FL: 1.333-1.635 (1.497), TL: 1.044-1.333 (1.187), ML: 1.144-1.556 (1.315), PSL: 0.256-0.344 (0.304), PTH: 0.144-0.206 (0.188), PPH: 0.222-0.267 (0.247), PTL: 0.333-0.411 (0.378), PPL: 0.233-0.278 (0.254), PTW: 0.122-0.133 (0.129), PPW: 0.222-0.267 (0.251), PW: 0.489-0.567 (0.538); CI: 79-84 (82), SI: 143-164 (156), MDI: 77-83 (81), PSLI: 26-36 (31), PWI: 64-70 (67), FI: 175-198 (188), PpWI: 182-209 (195), PpLI: 136-168 (149)

Head elongated elliptical, about 1.2 times longer than wide (CI: 79-84), with sides posteriad of eye-level elongate, converging evenly towards posterior margin; occipital carina narrow; clypeus smooth, carinae absent; face smooth, only malar area weakly punctate and irregularly rugulose near antennal insertion, with some cross-meshes present, rugulae ending at anterior eye-level; hairs at face relatively slender and of varying lengths, longer and shorter hairs uniformly distributed, often apically truncated or split; scapes long (SI: 143-164), in full face view and when laid back, surpassing occiput by about one third of its length, pilosity erect to suberect, almost twice as long as maximum scape diameter. Promesonotum anteriorly punctate towards neck, at humeri with a tiny, prominent peak, in profile, representing highest point of pronotum, smooth and shiny to superficially punctate, anteriad to neck weakly punctate, posteriad to mesonotum superficially punctate; pronotal declivity long, midway between humeral peak and mesonotal process obtusely angular, smooth; mesonotal process conspicuously produced, dorsal face often marginate and smooth or weakly and irregularly rugulose-punctate; second mesonotal process conspicuously produced, similarly shaped and sculptured; metanotal groove in lateral view shallowly to conspicuously impressed, highest point of dorsopropodeum at about midlength towards base of propodeal spines; mesopleuron and propodeum weakly punctate, spines long, slender (PSLI: 26-36), and strongly curved posteriorly; metafemur long (FI: 175-198); pilosity of metatibia at inner edge subdecumbent, outer edge with subdecumbent to suberect hairs and slightly longer hairs. Color yellow to light orange.

Discussion: *Pheidole christinae* is a readily recognizable species by its color, head shape and pilosity. In color it is similar to *P. pulchella* and *P. heliosa*, and in general appearance it is very close to the latter and with an intermediate head shape (CI: 79-84 [*christinae*], versus CI: 82-90 [*pulchella*] and CI: 73-76 [*heliosa*]). From *P. heliosa* it can be separated best by its shorter appendages, a significantly narrower occipital carina, less abundant pilosity (especially by its lack of laterally projecting hairs ventrad at meso- and metapleuron), different kinds of metatibial pilosity at inner and outer egdes, and asymmetrically shaped postpetiole in lateral view. From *P. pulchella* it can be distinguished by longer propodeal spines (PSLI: 26-36 versus 25-29), erect versus decumbent scape pilosity, the small peaks at the humeri which are raised above the pronotal outline, and the shape of the dorsopropodeum in profile view, which has its highest point at about midlength versus immediately at the metanotal groove in *P. pulchella*. The population in Gabon differs from the Ugandan *P. christinae* type specimens in a deeper, conspicuously impressed, metanotal groove, and longer, more spinose, propodeal spines. The minor workers of *P. christinae* were collected in the Budongo Forest, Uganda, in Gabon and in D.R. Congo from sifted leaf-litter, pitfalls and hand-collections. Majors have not yet been collected.

Etymology: This species is named after my wife Christina, who is simply the best.

Type material examined: UGANDA: Holotype (minor worker): 01° 45' N, 31° 34' 59'' E, Budongo Forest Reserve, 900 m, 30.vi.2004 (*M. Peters*) (ZFMK: CASENT0227935); Paratypes: (6 minor workers) same data as holotype (ZFMK: CASENT0227936, CASENT0227937, CASC: CASENT0227938, CASENT0227939, BMNH: CASENT0227940, CASENT0227941); (3 minor workers) 01° 43' N, 31° 33' E, Bunyoro District, Budongo Forest, 1000 m, hand collection, 30.vi.2004 (*M. Peters*) (ZFMK: CASENT0227942, CASENT0227943, CASENT0227944).

Other material examined: GABON: (18 minor workers) Prov. Woleu-Ntem, 31.3km, 108° ESE Minvoul, 2°04.8'N, 12°24.4'E, 600m, 7.ii.1998 (*B.L. Fisher*); UGANDA: (1 minor worker) 01°

43.583' N, 31° 33.142' E, Budongo Forest FS, 1081 m, 08.vii.09 (*W. Freund & T. Klug*); D.R. CONGO: (1 minor worker) Epulu, 01° 23' N, 28° 35' E, 750 m, xi.1995 (*S.D. Torti*)

***Pheidole darwini* sp. n.**

(Figures 4.21 - 4.26)

Diagnosis: Color medium to dark brown, appendages slightly lighter. Minor worker: Head shape elliptical (CI: 84-89); posteriad of eye-level with laterally projecting hairs; posterior margin relatively narrow; vertex smooth; scapes moderately long (SI: 139-160) with suberect pilosity; dorsopronotum punctate anteriorly, partly overlain with irregular rugulae, posteriad smooth; spines relatively long (PSLI: 29-35); metatibia pilosity subdecumbent. Major worker: Head sculpture weakly rugose-punctate, with moderately long rugae; postolateral lobes smooth and shiny; scape with appressed to decumbent pilosity plus a few erect hairs along outer edge; dorsopropodeal sculpture weakly and irregularly transversely rugulose-punctate; in profile dorsopropodeum shorter than or of same length as base of spines; standing hairs long and thick, present everywhere except propodeum; metatibia pilosity appressed to decumbent with additional subdecumbent to suberect hairs along outer edge. [**Geographic Range:** Cameroon, Central African Republic, Gabon]

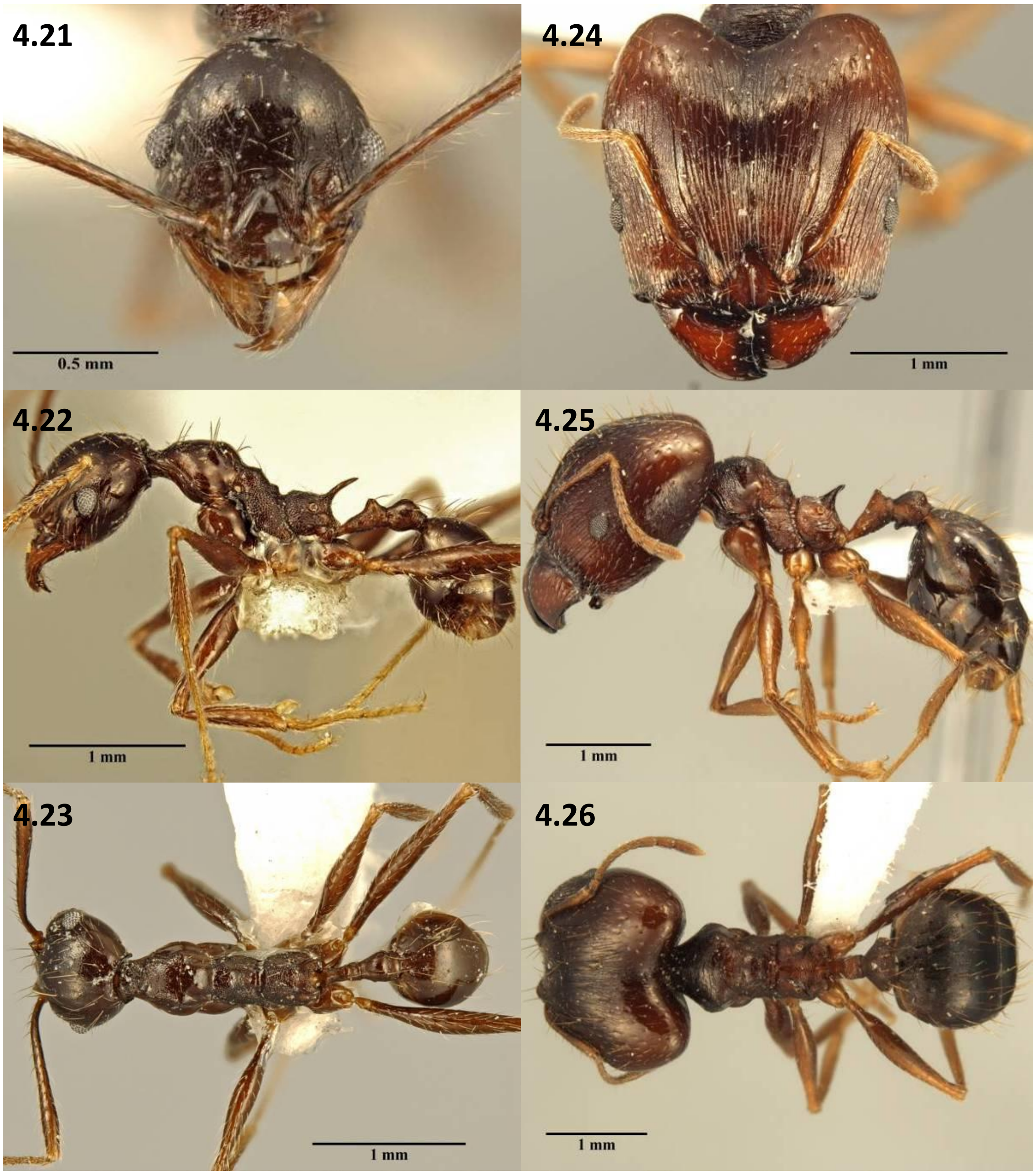

Fig. 4.21 - 4.26: *P. darwini* sp. n.: full-face, lateral & dorsal view of minor (**4.21 - 4.23**) and major worker (**4.24 - 4.26**).

Description of minor worker: Measurements (n=17): HL: 0.772-0.878 (0.838), HW: 0.667-0-756 (0.721), SL: 0.989-1.206 (1.076), MDL: 0.522-0.611 (0.562), EL: 0.161-0.189 (0.171), FL: 1.133-1.381 (1.277), TL: 0.878-1.067 (0.981), ML: 1.078-1.254 (1.163), PSL: 0.244-0.300 (0.271), PTH: 0.167-0.189 (0.179), PPH: 0.189-0.222 (0.210), PTL: 0.300-0.356 (0.332), PPL: 0.189-0.244 (0.220), PTW: 0.106-0.128 (0.118), PPW: 0 211-0.256 (0.225), PW: 0.444-0.511 (0.484); CI: 84-89

(86), SI: 139-160 (149), MDI: 75-82 (78), PSLI: 29-35 (32), PWI: 66-68 (67), FI: 169-189 (177), PpWI: 165-211 (191), PpLI: 135-176 (151)

Head elliptical, longer than wide (CI: 84-89), with sides of head rounded towards relatively narrow posterior margin; occipital carina conspicuous, medially with a weak concavity in full face view; dorsum of head smooth and shiny, hexagonally micropunctate to very faintly punctate; malar space with few short carinae next to antennal insertion ending at posterior eye level; scapes moderately long (SI: 139-160), pilosity basally subdecumbent to decumbent, apically subdecumbent to suberect. Dorsopronotum in lateral view flat, anteriad towards neck weakly punctate, partly overlain by some weak irregular rugulae, posteriad grading to smooth and relatively steep posterior declivity; lateropronotum partly to completely smooth and shiny; both metanotal processes conspicuous and well-developed, sharply angulate, metanotal groove deep and broad; mesopleuron and propodeum uniformly punctate; dorsopropodeum in lateral view level to declining gently towards base of spines,; propodeal spines moderately long (PSLI: 29-35). Petiole and postpetiole punctate, dorsally superficially and partly smooth. Gaster smooth and shiny, anteriorly with superficially punctate central area, in size not bigger than dorsal surface of postpetiole. Pilosity generally abundant, long erect setae and shorter suberect to subdecumbent hairs present, head margin posteriad of eye-level in full-face view with laterally projecting hairs. Metatibia with appressed to decumbent pilosity at inner edge, subdecumbent at outer edge. Color medium to dark brown.

Description of major worker: Measurements (holotype): HL: 1.960, HW: 1.960, SL: 1.044, MDL: 1.000, EL: 0.239, FL: 1.571, TL: 1.190, ML: 1.476, PSL: 0.356, PTH: 0.322, PPH: 0.400, PTL: 0.556, PPL: 0.356, PTW: 0.222, PPW: 0.500, PW: 0.878; CI: 100, SI: 53, MDI: 51, PSLI: 18, PWI: 45, FI: 80, PeI: 25, PpI: 57, PpWI: 225, PpLI: 156

Measurements (n=9): HL: 1.980-2.200 (2.099), HW: 1.960-2.225 (2.120), SL: 1.011-1.133 (1.056), MDL: 0.944-1.056 (1.011), EL: 0.239-0.267 (0.251), FL: 1.556-1.714 (1.623), TL: 1.206-1.667

(1.293), ML: 1.492-1.651 (1.570), PSL: 0.333-0.389 (0.354), PTH: 0.322-0.378 (0.341), PPH: 0.367-0.467 (0.422), PTL: 0.544-0.667 (0.590), PPL: 0.333-0.389 (0.360), PTW: 0.211-0.267 (0.236), PPW: 0.467-0.589 (0.546), PW: 0.856-0.978 (0.931); CI: 99-104 (101), SI: 49-53 (50), MDI: 42-51 (48), PSLI: 16-18 (17), PWI: 43-45 (44), FI: 75-80 (77), PeI: 24-27 (25), PpI: 55-63 (59), PpWI: 219-252 (231), PpLI: 151-176 (164)

Frons and sides of head weakly to superficially rugose-punctate, grading weaker at anterior posterolateral lobes, posteriad smooth and shiny, median excavation with a narrow superficially sculptured strip; laterally and in profile view smooth area extending anteriad, almost towards eye-level; pilosity on scape basally appressed, apically decumbent, additionally with three to five erect hairs, distributed along outer edge. Promesonotal outline slightly rounded; mesonotal process subangulate, with relatively steep posterior declivity; second process inconspicuous, weakly raised carina or narrow acuteness present instead; pronotum transversely to irregularly rugulose-punctate, posterodorsad less rugulose, punctures either slightly weaker or superficial; posterolaterad smooth and shiny or superficially punctate-rugose; humeral area slightly processed to subangulate laterally; promesonotal declivity smooth, with hexagonal microsculpture; meso- and metapleuron punctate, dorsopropodeum weakly punctate, in profile mostly shorter than base of spines; area between spines and posteropropodeum punctate or weakly punctate, overlain by weak or superficial transverse rugulae, also posterolateral rugae towards metapleural carinae present. Petiole and postpetiole densely punctate, except smooth anterodorsal petiole; postpetiolar ventral process significantly anteriorly produced. Punctures at anterior half of first gastral tergite grading to hexagonal microsculpture at second half. Long standing, often truncated, hairs relatively abundant on dorsal body, but absent from propodeum. Metatibia with appressed to decumbent pilosity and additionally with subdecumbent to suberect hairs along outer edge. Color brown to dark brown, appendages lighter.

Discussion: *P. darwini*, *P. batrachorum*, and *P. setosa* are the only darkly colored species with minor workers possessing several laterally projecting hairs at the head margin posteriad of the eye-level. *Pheidole darwini* can be distinguished from *P. batrachorum* by the following characters: lack of [*darwini*] versus presence of [*batrachorum*] conspicuously impressed punctures at frons and vertex, wider head, shorter scapes, and longer spines (CI: 84-89, SI: 139-160, PSLI: 29-35 [*darwini*] versus CI: 79-86, SI: 153-172, PSLI: 21-29 [*batrachorum*]). From minor workers of *P. setosa* it is separated by: significantly narrower head margin; mostly decumbent to subdecumbent scape pilosity versus decumbent pilosity with additional erect to suberect hairs along outer edge, metatibia pilosity with subdecumbent hairs along outer edge versus uniform pilosity without subdecumbent hairs and metafemur marginally longer (FI: 169-189 versus 167-168). The major workers are unique in their combination of diagnostic characters, in particular, by the three to five erect hairs at the outer edge of the scape. *Pheidole darwini* occurs in Cameroon, Central African Republic and Gabon. The specimens have been collected from sifted leaf-litter and rotten logs.

Type material examined: GABON: Holotype (major worker): Prov. Woleu-Ntem, 31.3 km 108° ESE Minvoul, 02° 04.8' N, 12° 24.4' E, 600 m, 7.ii.1998 (*B.L. Fisher*) (CAS: CASENT0218307); Paratypes: (8 major workers) same data as holotype (CAS: CASENT0218300, CASENT0218301, CASENT0218302, CASENT0218303, CASENT0218304, CASENT0218306, CASENT0218308); (12 minor workers) Prov. Woleu-Ntem, 31.3 km 108° ESE Minvoul, 02° 04.8' N, 12° 24.4' E, 600 m, 11.ii.1998 (*B.L. Fisher*) (CAS: CASENT0218311, CASENT0218313, CASENT0218315, CASENT0218316, CASENT0218317, CASENT0218318, CASENT0218319); (18 minor workers) Prov. Woleu-Ntem, 31.3 km 108° ESE Minvoul, 02° 04.8' N, 12° 24.4' E, 600 m, 12.ii.1998 (*B.L. Fisher*) (CAS: CASENT0218324, CASENT0218325, CASENT0218326, CASENT0218327, CASENT0218328).

Other material examined: CAMEROON: (2 minor workers) Nkormvon, 1980, M175 (*D. Jackson*); (2 minor workers) Prov. Sud P.N. Campo, 43.3 km 108° ESE Campo, 290 m, 7.iv.2000, 02° 17.0’ N, 10° 12.4' E (*B.L. Fisher*); CENTRAL AFRICAN REPUBLIC: (1 major worker, 2 minor workers) Res. Dzanga-Ndoki, 37.9 km 169° S Lidjombo, 02° 22' N, 16° 10' E, 360 m, 21.v.2001 (*B.L. Fisher*); GABON: (2 minor workers, 2 major workers) Prov. Ogooue Maritime, Res. Monts Doudou, 24.3 km 103° NW Doussala, 02° 13.4' S, 10° 24.4' E, 6-11.iii.2000, 375 m (*B.L. Fisher*); (3 minor workers) Prov. Woleu-Ntem, 31.3 km 108° ESE Minvoul, 02° 04.8' N, 12° 24.4' E, 600 m, 12.ii.1998 (*B.L. Fisher*); (4 major workers) Prov. Ogooue Maritime, Res. Monts Doudou, 24.3 km 103° NW Doussala, 02° 13.4' S, 10° 24.4' E, 6.iii.2000, 375 m (*B.L. Fisher*); (3 minor workers) Prov. Ogooue Maritime, Res. Monts Doudou, 24.3 km 303° WNW Doussala, 02° 14.0' S, 10° 23.9' E, 18.iii.2000, 630 m (*B.L. Fisher*).

Pheidole dea **Santschi 1921**

(Figures 4.27 - 4.29, 4.30 - 4.35)

Pheidole dea Santschi, 1921c: 115. Syntype worker (1). D.R. CONGO [examined]. [Previously senior synonym of *P. batrachorum*: Santschi, 1930a: 59]

Diagnosis: Color brown to dark blackish brown. Minor workers: Head shape broadly rounded (CI: 86-93), posterior head margin evenly rounded to weakly compressed; central area between eyes and posterior pronotum smooth and shiny to superficially punctate or hexagonally microsculptured; scape and metafemur moderately long (SI: 134-147, FI: 158-174), pilosity decumbent to subdecumbent. Mesopleuron and propodeum uniformly punctate; edge of first mesonotal process in lateral view rounded; second process not higher than level of dorsopropodeum; metanotal groove narrow; postpetiole relatively narrowly developed and relatively short (PpLI: 155-223). Standing hairs almost completely absent from mesosoma, but at least few scattered hairs at head and metasoma. Major workers: rugae in face very strong, almost parallel, some continuing uninterrupted towards posterior head margin. Mesonotal process, in lateral view, obtuse; second process conspicuous to reduced, not raised higher than level of dorsopropodeum, which is longer than the base of the spines; postpetiole relatively narrow, on average less than twice as wide as petiole (PpWI: 177-210). Standing hairs at pronotum mostly absent. [**Geographic Range:** D.R. Congo, Kenya, Tanzania, Uganda]

Fig. 4.27 - 4.29: *P. dea* Santschi holotype: full-face, lateral & dorsal view of minor worker.

Fig. 4.30 - 4.35: *P. dea* Santschi non-type: full-face, lateral & dorsal view of minor (**4.30 - 4.32**) and major worker (**4.33 - 4.35**).

Description of minor worker: Measurements (holotype): HL: 0.856, HW: 0.944, SL: 1.156, MDL: 0.667, EL: 0.200, FL: 1.444, TL: 1.100, ML: 1.333, PSL: 0.278, PTH: 0.200, PPH: (0.244), PTL: 0.367, (PPL: 0.222), PTW: 0.144, PPW: (0.244), PW: 0.567, CI: 91, SI: 135, MDI: 78, PSLI: 29, FI: 169, PWI: 66, FI: 169, PpWI: (169), PpLI: (165)

Measurements (n=32): HL: 0.733-0.922 (0.849), HW: 0.656-0.833 (0.759), SL: 0.944-1.144 (1.070), MDL: 0.500-0.611 (0.571), EL: 0.167-0.198 (0.179), FL: 1.089-1.397 (1.262), TL: 0.811-1.100 (0.968), ML: 1.011-1.317 (1.159), PSL: 0.200-0.278 (0.243), PTH: 0.156-0.200 (0.178), PPH: 0.156-0.222 (0.195), PTL: 0.256-0.367 (0.318), PPL: 0.144-0.200 (0.182), PTW: 0.106-0.135 (0.121), PPW: 0.167-0.233 (0.204), PW: 0.422-0.533 (0.487); CI: 86-93 (89), SI: 134-147 (141), MDI: 72-79 (75), PSLI: 25-32 (29), PWI: 61-67 (64), FI: 158-174 (166), PpWI: 152-191 (169), PpLI: 156-223 (175)

Head shape broadly rounded (CI: 86-93), convex sides evenly rounding into uncompressed or weakly compressed posterior margin; occipital carina narrow; face distinctly to superficially punctate, mediad at eye level smooth, hexagonally microsculptured; punctures laterad at malar area and near eyes slightly stronger, malar carinae long, often faintly continuing towards posterolateral head margin, ending between latter and eye-level; scape moderately long, in full face view and when laid back, surpassing occiput by about one third of its length (SI: 134-147), pilosity decumbent to subdecumbent. Pronotal outline in lateral view slightly angulate; humeral area flat to faintly convex; first mesonotal process obtusely angulate to weakly flattened, subangulate and appearing worn; second process small to almost inconspicuous, with angle at same level as anterior dorsopropodeum; metanotal groove conspicuous, narrowly impressed; anteropronotum punctate or weakly punctate; dorsopronotum, lateropronotum and mesonotum mostly smooth, hexagonally microsculptured; mesopleuron and propodeum punctate; dorsopropodeum flatly declining to base of spines; propodeal spines relatively short (PSLI: 25-32) and often weakly curved or almost straight; metafemur moderately long (FI: 158-174); metatibia with decumbent pilosity. Petiole and postpetiole lateroventrally and posterodorsally weakly to superficially punctate, upper dorsum smooth. Gaster smooth and shiny, anteriad with small shagreened to microsculptured spot. Standing hairs moderately long and scarce, sometimes missing at mesosoma, rarely completely absent from dorsal surfaces, except at end of first gastral tergite and posteriad; also with few shorter subdecumbent hairs on waist segments; in every specimen except holotype, petiole and postpetiole in dorsal view with short, laterally projecting hairs present. Color medium to dark blackish brown.

Description of major worker: Measurements (n=7): HL: 1.760-1.980 (1.867), HW: 1.780-1.980 (1.873), SL: 1.011-1.089 (1.046), MDL: 0.822-1.000 (0.888), EL: 0.222-0.244 (0.232), FL: 1.460-1.603 (1.515), TL: 1.111-1.254 (1.172), ML: 1.460-1.587 (1.519), PSL: 0.294-0.356 (0.326), PTH: 0.267-0.322 (0.307), PPH: 0.322-0.378 (0.347), PTL: 0.456-0.567 (0.507), PPL: 0.289-0.333 (0.309), PTW: 0.200-0.244 (0.222), PPW: 0.378-0.500 (0.431), PW: 0.800-0.878 (0.830); CI: 99-102 (100), SI: 54-57 (56), MDI: 42-51 (47), PSLI: 16-19 (17), PWI: 43-46 (44), FI: 79-83 (81), PeI: 25-29 (27), PpI: 46-58 (52), PpWI: 177-210 (194), PpLI:155-176 (164)

Face rugose-punctate, with long, subparallel and uninterrupted rugae, continuing (more weakly) to posterolateral lobes; laterad of frons punctures weak, grading to superficial at frons and corners of lobes; scape pilosity decumbent. Promesonotal outline rounded dorsally, weakly subangulate posteriad to pronotal declivity; anteropronotum irregularly and weakly rugose-punctate, grading to superficially sculptured or almost smooth at posteropronotum and pronotal declivity; posterior lateropronotum smooth and shiny; first mesonotal process strongly produced, obliquely angulate; dorsal mesonotum partially to completely smooth, or faintly rugulose on posterior mesonotal process; second mesonotal process in some specimens low and conspicuous, in others short and reduced to a weakly raised carina; metanotal groove narrow and conspicuously impressed; dorsopropodeum with smooth medial area; posteropropodeum weakly to superficially transversely rugulose-punctate, in lateral view about as long or slightly longer than basal width of spines; propodeal spines strongly and massively developed; punctures on mesopleuron and metapleuron weak to superficial; posterior metapleuron ventrad of spiracle smooth; metapleural gland scrobe and carinae weak; metatibia pilosity relatively short, appressed to decumbent. Smooth median strip on anterodorsal petiole very narrow; postpetiole usually relatively narrow (PpWI: 177-210), on average almost twice as wide as petiole, laterally weakly angulate to rounded, posterolateral flange narrow to inconspicuous; ventral process short and weakly developed. Gaster anteriorly, near articulation to postpetiole, weakly punctate or shagreened, rest smooth and shiny, hexagonally microsculptured. Long standing hairs present on head, postpetiole, and gaster, absent to almost absent on mesosoma, rarely with one pair present on posterolateral dorsopronotum, absent on petiole.

Discussion: *Pheidole dea* was described from two minor workers, one of which is destroyed except for the postpetiole and gaster. This is the first publication describing the major workers for this species and new material from three East African countries, revealing distinct variations in the expression of head sculpture between the different localities. In this character the *P. dea* type specimen most closely resembles the minor workers from Tanzania. Both possess the same distinct punctures (excluding the smooth central area at eye-level) in the face on frons and vertex, in which they differ from the minor workers found in Kenya and Uganda, with only weak to superficial sculpture on frons and vertex. One unique feature of the *P. dea* type specimen is the almost complete lack of conspicuous pilosity, other than short decumbent to subdecumbent pubescence, and a few long hairs at the third gastral tergite. Although standing hairs in the new material of *P. dea* can be strongly reduced, some hairs usually remain at the head or first gastral tergite. And the waist segments are endowed with some shorter, posteriorly and laterally projecting hairs. These are also absent in the holotype. However, in a closer examination of the latter, the typical and faintly elevated punctures, where standing hairs are inserted, were found on head and mesosoma. This suggests the hairs were probably lost prior to or after its collection. Other significantly differentiating characters could not be observed. The species most similar to *P. dea* is *P. semidea*. Minor workers of the latter possess a relatively broader and longer postpetiole (PpWI: 173-200 and PpLI: 126-167 [*semidea*] versus PpWI: 152-191 and PpLI: 156-223 [*dea*]). In *P. semidea* the second mesonotal process in lateral view is slightly raised above the level of the dorsopropodeum, and usually up to three pairs of centrally inclined, moderately long hairs are found at the anterior, lateral and posterior corners of the promesonotal dorsum. The major workers of *P. semidea* possess an irregular pattern of longitudinal rugae at the frons, joined by a few cross-meshes at the vertex and oblique rugulose-punctate sculpture at the postolateral lobes versus regular longitudinal rugae from frons to vertex in *P. dea*. They also have a higher situated second mesonotal process and, on average, a slightly longer and wider postpetiole (PpLI: 154, PpWI: 211 versus PpLI: 164, PpWI: 194).

The new material of *P. dea* has been collected in four forests in Eastern Africa: Kakamega Forest in Western Kenya, Rabongo Forest and Budongo Forest in Uganda, and in Gombe, Tanzania. In Kakamega *P. dea* is among the more rarely collected *Pheidole* species, only found in 26 out of 800 pitfall-traps, where it constituted 2.2 % of all *Pheidole* individuals collected (in winkler samples 0.2 %). Stable isotope measurements of several Kakamega specimens revealed that *P. dea* had the highest d15N value among its congeners from the same location (unpublished). Its trophic position is in the third trophic level of the local food network, indicating that it is probably a more specialized predator than other *Pheidole* species. Details about its diet, however, remain unknown.

Type material examined: D.R. CONGO: (1 minor) Lugombe (*Gérard*).

Other material examined: KENYA: (4 major workers, 8 minor workers): Kakamega Distr.: Isecheno, Isecheno Forest Res., 1600 m 8.ii.2002 (*R.R. Snelling*); (1 minor worker + 1 major worker) Kakamega Forest, Colobus, 00° 21' 4.9'' N, 34° 51' 41.1'' E, 12.vi.2007, 1650 m (*M. Peters*); (1 minor worker, 1 major worker) Kakamega Forest, Buyangu, 00° 20' 53.6" N, 34° 51' 54.1" E, 12.vii.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Isecheno B, 00° 14' 52.3'' N, 34° 52' 5.3'' E, vi.2008, 1650 m (*F. Hita Garcia*); (1 minor worker) Kakamega Forest, Salazar, 00° 19' 36'' N, 34° 52' 14.6'' E, 21.vi.2007, 1650 m (*S. Maurer*); (1 minor worker) Kakamega Forest, Malawa East, 00° 27' 15.7" N, 34° 51' 48.8" E, 03.vii.2002, 1650 m (*M. Peters*);

(1 minor worker) Kakamega Forest, Yala, 00° 12' 9' 'N, 34° 52' 6' E, v.2008, 1650 m (*M. Peters*); (2 minor workers) Kakamega For., Udo´s camp, 00° 21’ 7.9'' N, 34° 52' 2.6'' E, 02.vii.2007, 1650 m (*G. Fischer*); (2 minor workers) Kakamega For., Malava West, 00° 27' 0.9'' N, 34° 50' 52.9'' E, 03.vii.2007, 1650 m (*G. Fischer*); (1 minor worker) Kakamega Forest, Kisere, 00° 23' 6.2'' N, 34° 53' 37.8'' E, 16.vii.2007, 1650 m (*F. Hita Garcia*); (1 minor worker) Kakamega Forest, Salazar, 00° 19' 36'' N, 34° 52' 14.6" E, 21.vi.2007, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Yala, 00° 12' 09.9" N, 34° 52' 52.6" E, 19.vi.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Salazar, 00° 19' 36'' N, 34° 52' 14.6'' E, 09.iii.2009, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Colobus, 00° 21' 05" N, 34° 51' 41" E, vii.2009, 1650 m (*G. Fischer*); (9 minor workers) Kakamega For., Malava East, 00° 27' 10.6'' N, 34° 51' 48.7'' E, 19.vi.2007, 1650 m (*G. Fischer*); (1 minor worker) Kakamega Forest, Kisere, 00° 23' 07" N, 34° 53' 32.7" E, 24.vi.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Malawa East, 00° 27' 13.8" N, 34° 51' 44.6" E, 26.vi.2002, 1650 m (*M. Peters*); (3 minor workers) Kakamega Forest, Yala, 00° 13' 15.5'' N, 34° 55' 52.3'' E, 23.viii.2007, 1650 m (*F. Hita Garcia*); (1 minor worker) Kakamega Forest, Colobus, 00° 21' 18.5'' N, 34° 51' 30.1'' E, 14.vi.2007, 1650 m (*M. Peters*); (1 minor worker) 00° 12' 58.5" N, 34° 55' 56.6" E, Kakamega Forest, Ikuywa, 20.vi.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Ikuywa, 00° 13' 13.8" N, 34° 55' 52.1" E, 20.vi.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, vi./vii.2002, 1653 m (*M. Peters*); Kakamega Forest, (2 minor workers) Kisere, 00° 23' 6.2'' N, 34° 53' 37.8'' E, 16.vii.2007, 1650 m (*F. Hita Garcia*); (1 minor worker) Kakamega Forest, Ikuywa, 20.vi.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Isecheno B, 00°15' 16.6" N, 34° 52' 06.1" E, 18.vi.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Isecheno B, 00° 14' 52.3'' N, 34° 52' 5.3'' E, vi.2008, 1650 m (*F. Hita Garcia*); (1 minor worker) Kakamega Forest, Kisere, 00° 23' 07" N, 34° 53' 32.7" E, 17.vi.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Kisere, 00° 23' 07" N, 34° 53' 32.7" E, 01.vii.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Kisere, 00° 23' 03.1" N, 34° 53' 38.8" E, 24.vi.2002, 1650 m (*M. Peters*); (6

minor workers) Kakamega Forest, Malawa East, 00° 27' 20.2" N, 34° 51' 39.1" E, 26.vi.2002, 1650 m (*M. Peters*); (5 minor workers) Kakamega Forest, Malawa East, 00° 27' 20.2" N, 34° 51' 39.1" E, 03.vii.2002, 1650 m (*M. Peters*); (2 minor workers) Kakamega Forest, Malawa East, 00° 27' 13.8" N, 34° 51' 44.6" E, 03.vii.2002, 1650 m (*M. Peters*); (1 minor worker) Kakamega Forest, Malawa East, 00° 27' 15.7" N, 34° 51' 48.8" E, 19.vi.2002, 1650 m, (*M. Peters*); TANZANIA: (3 major workers, 16 minor workers) Gombe Stream N.P., 04° 42' S, 29° 37' E, 790 m, 11.i.2010 (*R. O'Malley*); UGANDA: (3 minor workers) Bunyoro District, Budongo Forest FS, 01° 43.583' N, 31° 33.142' E, 1081 m, 08.vii.09 (*W. Freund & T. Klug*); (2 minor workers) Murchinson Falls NP, Rabongo Forest, 02° 04.431' N, 31° 51.974' E, 958 m, 11.vii.09 (*W. Freund & T. Klug*).

***Pheidole glabrella* sp. n.**

(Figures 4.36 - 4.41)

Diagnosis: Color reddish brown to dark brown. Minor workers: head shape broadly rounded, with rounded to slightly compressed posterior head margin (CI: 88-95); scapes short to moderately long (SI: 123-141), pilosity appressed to decumbent. Promesonotum and parts of meso- and metapleuron smooth and shiny to superficially punctate, spines relatively long and massive (PSLI: 28-40), pilosity on metatibia mostly appressed; second mesonotal process usually shallow; standing hairs scarce to practically absent from dorsum of entire body, completely absent from mesosoma. Major workers: head irregularly rugose-punctate, rugae of varying lengths, punctures weak to superficial with smooth areas between rugae; scapes relatively short (SI: 49-53), pilosity appressed. Pronotum irregularly and transversely rugulose, declivity smooth and shiny; metanotal groove broad; dorsopropodeum in lateral view shorter than base of spines; metatibia pilosity fully appressed. Standing hairs rare, absent from mesosoma. [**Geographic Range:** Cameroon, Central African Republic, D.R. Congo, Gabon]

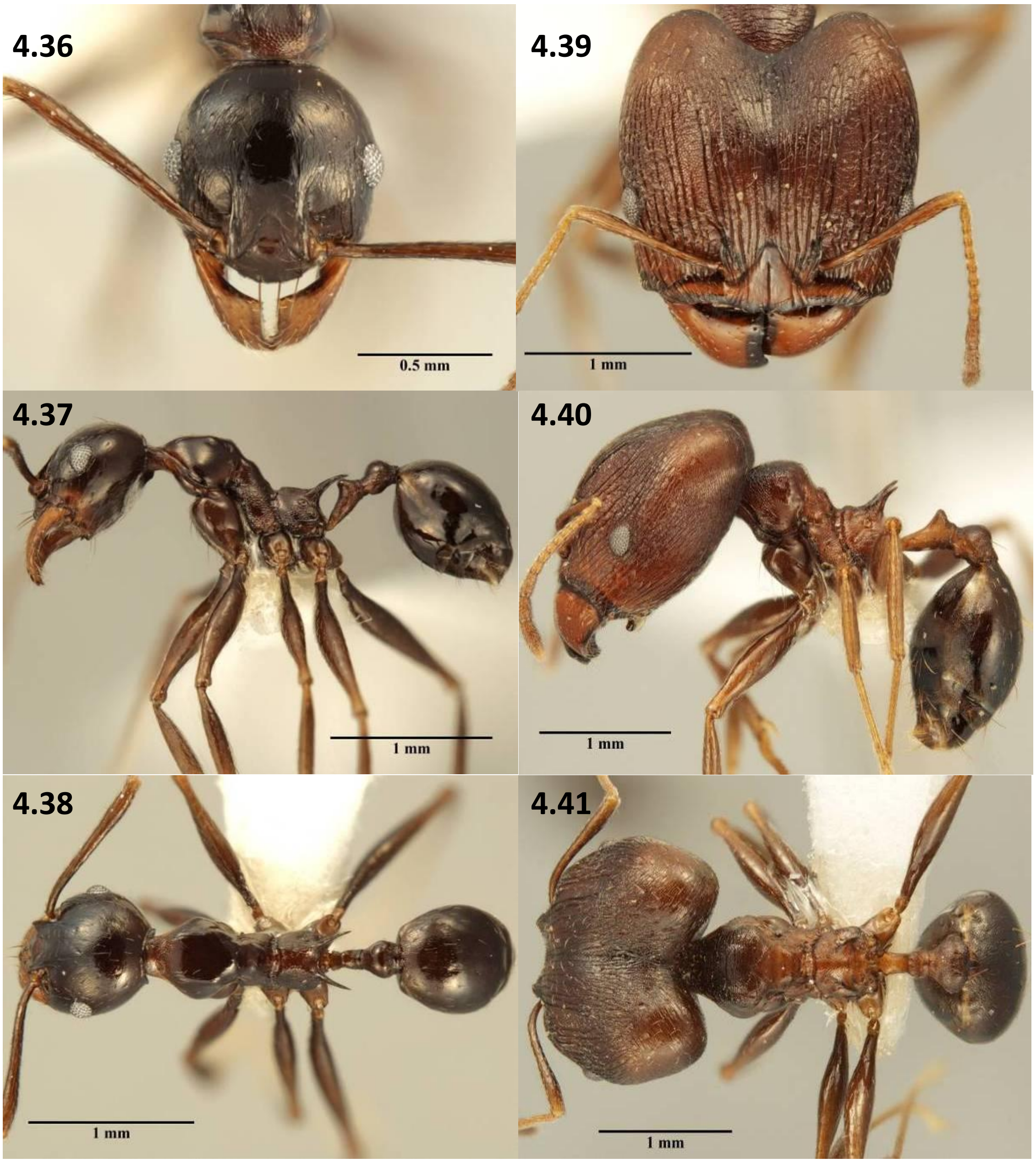

Fig. 4.36 - 4.41: *P. glabrella* sp. n.: full-face, lateral & dorsal view of minor (**4.36 - 4.38**) and major worker (**4.39 - 4.41**).

Description of minor worker: Measurements (n=26): HL: 0.722-0.922 (0.851), HW: 0.667-0.856 (0.779), SL: 0.876-1.133 (1.022), MDL: 0.511-0.633 (0.576), EL: 0.167-0.194 (0.181), FL: 1.044-1.349 (1.224), TL: 0.789-1.044 (0.951), ML: 1.011-1.286 (1.162), PSL: 0.200-0.356 (0.282), PTH: 0.167-0.206 (0.185), PPH: 0.183-0.239 (0.212), PTL: 0.267-0.367 (0.336), PPL: 0.178-0.233 (0.198), PTW: 0.106-0.133 (0.121), PPW: 0.183-0.267 (0.225), PW: 0.456-0.557 (0.506); CI: 88-95

(92), SI: 123-141 (131), MDI: 71-78 (74), PSLI: 28-40 (33), PWI: 61-68 (65), FI: 143-170 (157), PpWI: 165-210 (186), PpLI: 142-206 (170)

Head shape in full-face view posteriad of eyes roundly convex to compressed, posterior margin of vertex rounded to weakly flat (CI: 88-95); occipital carina narrow; mandibles smooth and shiny dorsally; clypeus without or rarely with short submedian carinae and with inconspicuous and short nasal carinae; face smooth with hexagonal microsculpture, weakly to superficially punctate laterally near eyes, malar carinae weak, disappearing posteriad of eyes; scape, when laid back, surpassing occiput by more than one quarter of its length (SI: 123-141), pilosity appressed to decumbent. Promesonotum in lateral view flat and subangular, completely smooth and shiny to superficially punctate; first mesonotal process conspicuously produced, with worn appearance, due to complete lack of sculpture, other than hexagonal microsculpture; second process shallow and worn, very rarely more conspicuous; mesopleuron and propodeum weakly to superficially punctate to almost smooth, intensity also varying with viewing-angle; episternum, anterior lateropropodeum, and dorsopropodeum often with smooth spots; metapleural carina and gland scrobe developed; spines mostly very long (PSLI: 28-40), relatively massive basally, short rugulae radiating mediad and posteroventrad from their bases; metanotal groove conspicuously U-shaped in lateral view; metafemur moderately to relatively long (FI: 143-170); metatibial pilosity appressed. Petiole and postpetiole punctate laterally and ventrally, peduncle and nodes dorsally polished smooth. First gastral tergite anteriorly shagreened, posteriad grading to smooth and shiny. Mesosoma lacking long standing hairs dorsally, but moderately long hairs at posterior end of gaster, in some specimens also at anterior gaster and at head; head or postpetiole or both with additional appressed inconspicuous pubescence, sometimes with very few short decumbent to subdecumbent hairs. Color reddish brown, appendages and head margin near lateral base of mandibles in lighter shade.

Description of major worker: Measurements (holotype): HL: 1.800, HW: 1.800, SL: 0.956, MDL: 0.778, EL: 0.222, FL: 1.397, TL: 1.067, ML: 1.349, PSL: 0.311, PTH: 0.300, PPH: 0.333, PTL: 0.489, PPL: 0.300, PTW: 0.200, PPW: 0.411, PW: 0.744; CI: 100, SI: 53, MDI: 43, PSLI: 17, PWI: 41, FI: 78, PeI: 27, PpI: 55, PpWI: 206, PpLI: 163

Measurements (n=5): HL: 1.820-2.125 (1.974), HW: 1.840-2.150 (2.015), SL: 0.944-1.078 (1.024), MDL: 0.778-0.967 (0.878), EL: 0.228-0.267 (0.246), FL: 1.429-1.635 (1.537), TL: 1.089-1.270 (1.192), ML: 1.381-1.619 (1.524), PSL: 0.311-0.367 (0.342), PTH: 0.300-0.356 (0.333), PPH: 0.344-0.444 (0.392), PTL: 0.467-0.567 (0.536), PPL: 0.311-0.344 (0.329), PTW: 0.200-0.261 (0.232), PPW: 0.428-0.544 (0.483), PW: 0.800-0.944 (0.880); CI: 99-105 (102), SI: 49-53 (51), MDI: 42-45 (44), PSLI: 16-18 (17), PWI: 42-44 (44), FI: 75-79 (76), PeI: 24-28 (26), PpI: 50-59 (55), PpWI: 186-222 (209), PpLI: 145-170 (163)

Some rugae at frons long and others short or interrupted; posterolateral lobes weakly and obliquely rugulose-punctate to smooth at corners or weakly reticulate; sides laterad of antennal scrobe weakly rugose-reticulate or irregularly rugose, punctures weak to superficial and sometimes smooth areas present between sculpture; scapes relatively short (SI: 49-53), with appressed pilosity. Promesonotum in lateral view in some specimens short, dorsally nearly flat and posteriorly slightly compressed, with steep and long declivity, in other speciemens longer and rounding into posterior declivity; anteropronotum dorsally and laterally with irregularly distributed transverse rugulae, in between with weak to superficial punctures, grading to smooth and shiny promesonotal declivity dorsally and posteropronotum laterally; humeral area laterally weakly processed and angulate; mesonotal process shallow to well-produced, dorsally smooth, with oblique angle or right-angled and steeply declining; second mesonotal process inconspicuous, at most visible as weak carina; metanotal groove broad and shallow; dorsopropodeum very short, significantly shorter than base of spines in lateral view, weakly punctate, but with dense punctures lateroventrally; meso- and metapleuron weakly to superficially punctate, smooth and shiny around metapleural carina, metapleural gland scrobe absent or inconspicuous; transverse rugula(e) present posteriorly between spines, posteropropodeum otherwise weakly punctate; metatibia with fully appressed pilosity. Petiole (except anterodorsally) and postpetiole punctate to weakly punctate, the latter posterodorsally with weak irregular rugulae. First gastral tergite shagreened, posteriorly hexagonally microsculptured. Long standing hairs very rare on head, postpetiole and dorsal gaster, their apices blunt or truncate, on mesosoma completely absent. Color reddish brown, gaster dark brown.

Discussion: Minor and major workers show a relatively great degree of variability in size and sculpture, especially between the type specimens from Cameroon and the material from the Central African Republic and Gabon. Minors from the Central African Republic differ from the types in a more variable sculpture at the mesonotum, mesopleuron and propodeum. The latter is almost smooth in some specimens versus strongly punctate in others. The minor workers of the type series possess a smooth mesonotum and superficially sculptured mesopleuron and propodeum. Majors from Gabon are differentiated from the type majors by the absence of punctate sculpture between the rugae at the head, and, in lateral view, a longer, rounded promesonotum. They are also more than 10 percent larger than the majors from the type series, although the indices are not significantly different between the two populations. Other than these differences, all specimens share the same morphometric profile and overall habitus. This and the fact that intermediate forms are present in the minor caste, is in support of a one-species hypothesis. Still, there is a small probability that the different populations could turn out to be heterospecific, if more material from other sites and particularly from the major worker caste becomes available.

The species most similar to *Pheidole glabrella* is *P. rebeccae*. The minor workers of the latter are separated from those of the former by a slightly more compressed posterior head margin, and shorter scapes (SI: 114-121 versus SI: 123-141), spines (PSLI: 25-30 versus PSLI: 28-40) and legs (FI: 133-139 versus FI: 143-170). The major workers of *P. rebeccae* differ from those of *P. glabrella* by longer and uninterrupted rugae on the face, a narrow versus broad metanotal groove, and significantly more standing hairs on all dorsal surfaces, except the propodeum. *P. glabrella* has a West to Central African distribution, from Cameroon to the D.R. Congo, where several minor workers were collected by the American Museum Congo Expedition together with and included in the type series of *P. batrachorum*. The other material has been collected in rainforests from sifted leaf-litter, rotten logs, and beating lower vegetation.

Type material examined: CAMEROON: Holotype (major worker): Ebodije, 4.xi.91 (*A. Dejean*) (BMNH: CASENT0227949); Paratypes (2 major workers, 6 minor workers): same data as holotype (BMNH: CASENT0227949, CASENT0227950, CASENT0227951).

Other material examined: CAMEROON: (4 minor workers) Prov. Ogooue Maritime, Res. Monts Doudou Moukalaba, 12.2 km 305° NW Doussala, 110 m, 02° 17.0' S, 10° 29.8' E, 24.ii.-3.iii.2000 (*B.L. Fisher*); (5 minor workers) Prov. Sud P.N. Campo, 43.3 km 108° ESE Campo, 290 m, 7.iv.2000, 02° 17.0’ N, 10° 12.4' E (*B.L. Fisher*); CENTRAL AFRICAN REPUBLIC: (1 minor worker) Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 03° 00.27' N, 16° 11.55' E, 420 m, 11-17.v.2001 (*S. van Noort*); (2 minor workers) P.N. Dzanga-Sangha, 38.6 km 173° S Lidjombo, 02° 21.60' N, 16° 03.20' E, 350 m, 21-27.v.2001 (*S. van Noort*); (1 minor worker) P.N. Dzanga-Ndoki, 21.4 km 53° NE Bayanga, 03° 02.01' N, 16° 24.57' E, 510 m, 3.v.2001 (*S. van Noort*); (5 minor workers) Res. Dzanga-Ndoki, Mabea Bai, 21.4 km 53° NE Bayanga, 03° 02' N, 16° 25' E, 510 m, 1-07.v.2001 (*B.L. Fisher*); (2 minor workers) Res. Dzanga-Ndoki, 37.9 km 169° S Lidjombo, 02° 22' N, 16° 10' E, 360 m, 21.v.2001 (*B.L. Fisher*); (1 minor worker) Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 03°00' N, 16° 12' E, 470 m, 10-17.v.2001 (*B.L. Fisher*); D.R. CONGO: (5 major workers, among cotypes of *P. batrachorum*) Akengi (*H.O. Lang*); GABON: (2 minor workers) Prov. Ogooue Maritime, Res. Moukalaba, 12.2 km 305° NW Doussala, 110 m, 02° 17.0' S, 10°29.8' E, 24.ii.2000

(*B.L. Fisher*); (2 minor workers) Prov. Sud P.N. Campo, 43.3 km 108° ESE Campo, 290 m, 7.iv.2000, 02° 17.0’ N, 10° 12.4' E (*B.L. Fisher*), (5 minor workers) Prov. Woleu-Ntem, 31.3 km 108° ESE Minvoul, 02° 04.8' N, 12° 24.4' E, 600 m, 12.ii.1998 (*B.L. Fisher*), (2 major workers) Prov. Ogooue Maritime, Res. Monts Doudou Moukalaba, 12.2 km 305° NW Doussala, 110 m, 02° 17.0' S, 10° 29.8' E, 24.ii.-3.iii.2000 (*B.L. Fisher*); (1 minor worker, 1 major worker) Prov. Ogooue Maritime, Res. Monts Doudou, 25.2 km, 304° NW Doussala, 02° 13.60' S, 10° 23.70' E, 14.iii.2000, 640 m (*B.L. Fisher*).

***Pheidole heliosa* sp. n.**

(Figures 4.42 - 4.47)

Diagnosis: *Pheidole heliosa* is the largest species in the *P. pulchella* group, with a long mesosoma and a wide pronotum. Color orange, major worker darker. Minor workers: head shape elongated, 1.25 times longer than wide; occipital carina strongly developed and relatively broad; scapes, legs and mandibles longest within the group; scape pilosity subdecumbent to suberect; highest number of standing hairs on head and mesonotum, also with laterally projecting hairs at meso- and metapleuron; a long and pronounced second metonotal process; postpetiole spheroidal in lateral view. Major worker: antennal scrobe absent; head margin with laterally projecting hairs; promesonotal dome lower and longer than in other species of this group, in lateral view almost continuous with mesonotal processes; propodeal spines straight, not curved posteriad, standing hairs abundant everywhere, including on dorsopropodeum and laterally at meso- and metapleuron. [**Geographic Range**: Cameroon, Ivory Coast]

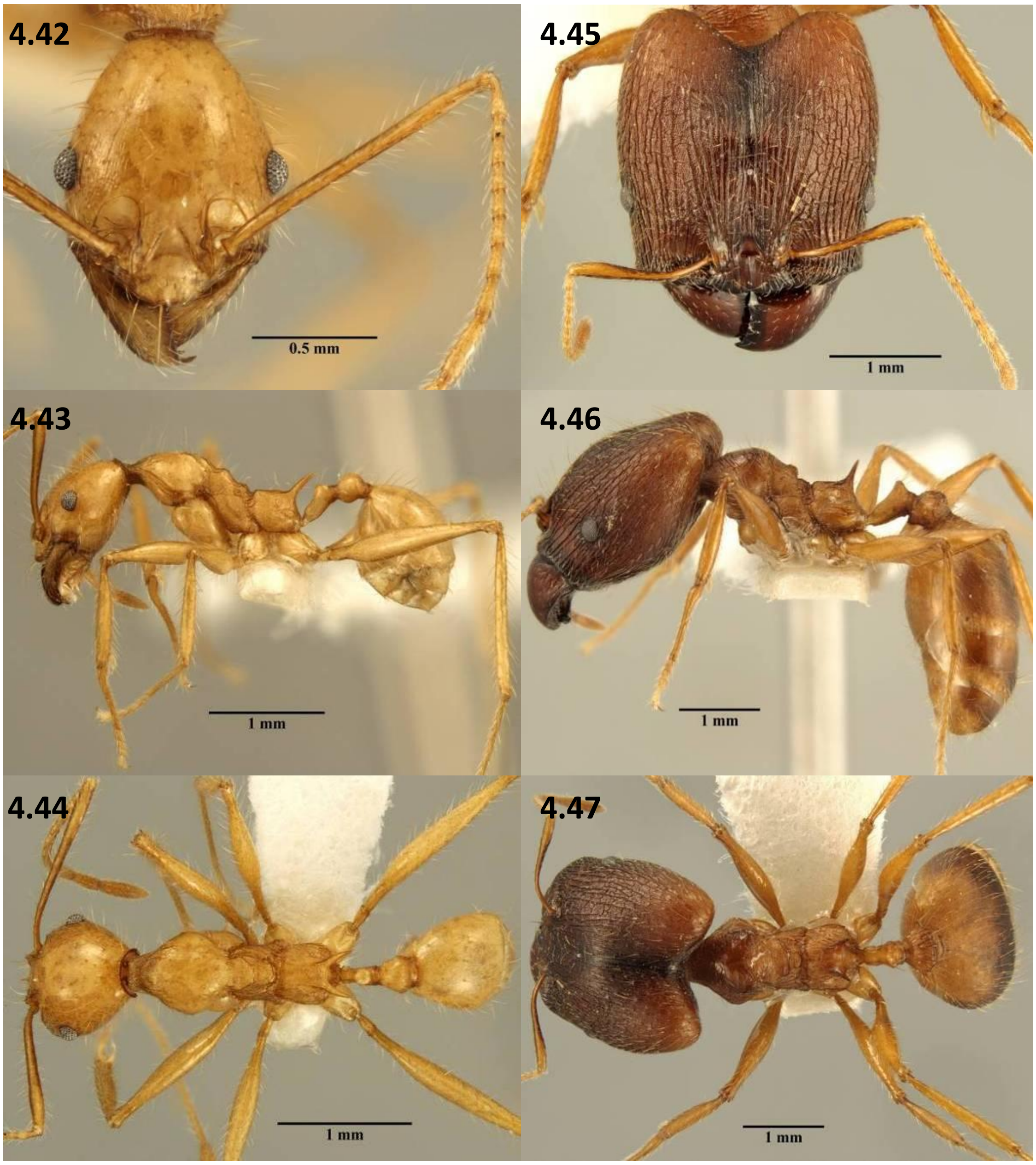

Fig. 4.42 - 4.47: *P. heliosa* sp. n.: full-face, lateral & dorsal view of minor (**4.42 - 4.44**) and major worker (**4.45 - 4.47**).

Description of minor worker: Measurements (n=8): HL: 1.056-1.089 (1.074), HW: 0.778-0.822 (0.798), SL: 1.302-1.429 (1.353), MDL: 0.639-0.800 (0.685), EL: 0.167-0.200 (0.176), FL: 1.600-1.740 (1.678), TL: 1.381-1.476 (1.427), ML: 1.600-1.740 (1.678), PSL: 0.294-0.400 (0.324), PTH: 0.189-0.211 (0.198), PPH: 0.233-0.278 (0.249), PTL: 0.367-0.422 (0.385), PPL: 0.267-0.283 (0.276), PTW: 0.122-0.133 (0.128), PPW: 0.261-0.300 (0.273), PW: 0.567-0.611 (0.594); CI: 73-76

(74), SI: 162-174 (170), MDI: 79-99 (86), PSLI: 28-37 (30), PWI: 73-76 (74), FI: 206-213 (210), PpWI: 200-232 (214), PpLI: 129-152 (140)

Head about 1.25 times longer than wide, longest within group (CI: 73-76), sides of head posteriad of eye level elongated and converging evenly towards posterior margin, occipital carina conspicuous and broad, almost collar-like; mandibles very long (MDI: 79-99), with strong rugulae laterally, grading to smooth masticatory margin; clypeus smooth with short to inconspicuous nasal carinae; face smooth, hexagonally microsculptured; malar carinae interrupted, ending posteriad of eye level; frontal carina developed but weak, ending at eye-level; space near antennal insertion surrounded by conspicuous carina; scape long, longest within group (SI: 162-174), in full face view, when laid back, surpassing occiput by more than one quarter to one third of its length, pilosity subdecumbent to suberect, about twice as long as scape diameter. Pronotum wide (PWI: 73-76), outline in lateral view elongate convex, rounded towards posterior declivity, smooth, only neck weakly punctured, humeral area laterally with short superficial carina, in dorsal view posteriad of highest point of pronotum lacking lateral process; mesonotal processes conspicuous and well-developed, second process almost as long as first; metanotal groove relatively narrow, conspicuously impressed; mesonotal process, mesopleuron and propodeum weakly punctate, dorsopropodeum with highest point immediately at metanotal groove, weakly declining towards base of spines; propodeal spines moderately long (PSLI: 28-37); metafemur very long (FI: 206-213); metatibial pilosity at inner edge subdecumbent, outer edge with longer suberect to subdecumbent hairs. Petiole and postpetiole smooth dorsally, weakly to superficially punctate ventrally; postpetiole in lateral view spheroidal and widest within *pulchella* group (PpWI: 200-232); gaster smooth, hexagonally micropunctate. Standing hairs very abundant, slender and acute, of varying lengths, at mesonotum, propodeum and waist segments relatively short; at mesosoma not restricted to dorsal surfaces, also abundantly present lateroventrally, best visible in oblique dorsolateral view. Color yellow to light orange.

Description of major worker: Measurements (holotype): HL: 2.450, HW: 2.350, SL: 1.238 MDL: 1.300, EL: 0.267, FL: 1.980, TL: 1.640, ML: 2.100, PSL: 0.272, PTH: 0.422, PPH: 0.544, PTL: 0.611, PPL: 0.422, PTW: 0.311, PPW: 0.700, PW: 1.067; CI: 96, SI: 53, MDI: 55, PSLI: 11, PWI: 45, FI: 84, PeI: 29, PpI: 66, PpWI: 225, PpLI: 145

Head longer than wide (CI: 96); mostly rugose-punctate; median ocellus developed, small; mandible relatively long (MDI: 55); median part of clypeus smooth, with conspicuous median and several weak submedian carinae; frons longitudinally rugose-punctate, spaces in between weakly punctate; rugae reaching posterior margin only at median emargination, grading from weak to superficial rugulae on posterolateral lobes; sides laterad of frons rugose-reticulate, punctate, in full-face view with several standing hairs projecting beyond lateral margin; frontal carinae inconspicuous and short; antennal scrobe absent to inconspicuous. Promesonotum, in lateral view elongated and medially raised, dorsally, antero- and dorsolaterally rugose-reticulate, mediodorsally and posterolaterally mostly smooth with few short rugae present; humeri weakly vertically processed, sharply marginate and rugose-reticulate; mesonotal process uniquely shaped, broadly and squarely raised above shallowly declining mesonotal declivity, marginate and partly punctate, partly rugose-reticulate; posteriad falling steeply to a shallow, but extensively produced, medially flexed, and posteriorly marginate second mesonotal process; metanotal groove very narrowly impressed in lateral view; meso- and metapleuron weakly punctate, with several weak to superficial irregular rugulae, metapleural carinae very conspicuous, flange-like produced laterad; dorsopropodeum weakly punctate, laterodorsad very densely punctate, in lateral view almost level and about as long as spines; propodeal spines relatively short (PSLI: 11), facing almost straight up, not curved posteriorly; posteropropodeum punctate, partly overlain by superficial rugulae. Petiole laterodorsally and ventrally densely punctate, smooth dorsal area at peduncle laterally marginate; postpetiole relatively wide compared to pronotal width (PpI: 66) and with strong ventral process, densely punctate, anterodorsally with short longitudinal, at highest point with interrupted longer transversal rugulae. First gastral tergite densely shagreened. Whole body with abundant, long, slender filiform standing hairs of varying lengths; head also with short appressed to decumbent pubescence and in frontal view with several laterally projecting hairs; lateroventrally at pronotum and laterodorsally at propodeum with abundant suberect hairs, best visible in dorsal view; scape with relatively short decumbent pilosity, metafemur with longer subdecumbent pilosity. Color reddish orange, antennae, mesosoma, metasoma and occipital corners orange, rest of head darker and red.

Discussion: The species most similar to *Pheidole heliosa* are *P. christinae* and *P. pulchella*, especially in color (yellow to orange). All of them share the laterally projecting hairs at the head margin anteriad and posteriad of eye-level, which separates them from the group of darkly colored species with laterally projecting hairs only posteriad of eye-level or completely without. *Pheidole christinae* and *P. pulchella* differ from *P. heliosa* in shape of the promesonotum, in lateral and dorsal view (PWI: 64-70 and 64-68 versus PWI: 73-76), especially in the development of the second mesonotal process, which in dorsal view is short and narrow [*christinae*] or inconspicuous [*pulchella*] versus long and broad [*heliosa*]. *Pheidole pulchella* differs from the other two orange colored species in scape and metafemur pilosity, which is short and decumbent [*pulchella*] versus longer and subdecumbent to erect [*christinae* and *heliosa*]. The *P. heliosa* type series has been collected in the Ivory Coast, additional minor workers are from Cameroon and were found in sifted leaf-litter.

Type material examined: IVORY COAST: Holotype (major worker): vic. Abidjan, 1976, no. 10 (*T. Diomande*) (BMNH: CASENT0227945); Paratypes (8 minor workers, 2 queens): same data as holotype (BMNH: CASENT0227945, CASENT0227946, CASENT0227947, CASENT0227948).

Other material examined: CAMEROON: (1 minor worker) Prov. Sud Ouest, Korup NP, 6.9 km 417° NW Mundemba, 19.iv.2000, 110 m, 05° 1.0' N, 8° 51.8' E (*B.L.Fisher*).

Pheidole nimba **Bernard 1953**

(Figures 4.48 - 4.50)

Pheidole nimba Bernard, 1953b: 224, fig. 8. Syntype worker (1) [examined]. GUINEA.

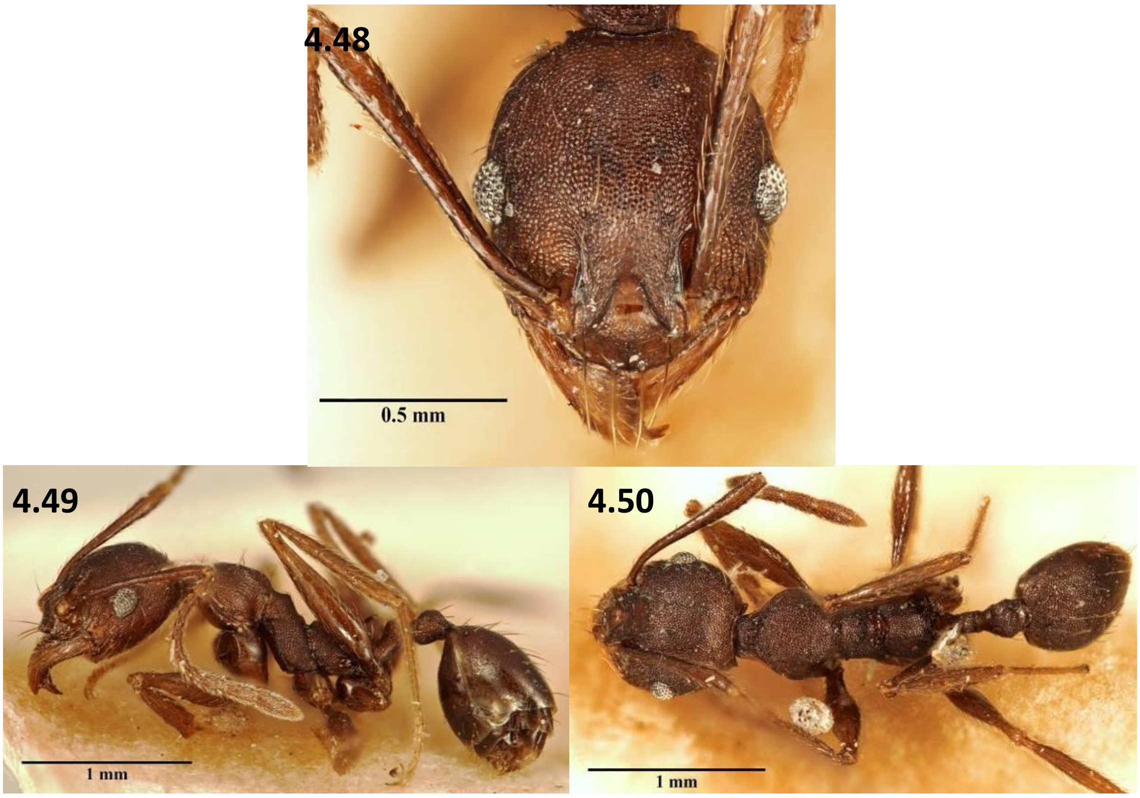

Fig. 4.48-4.50: *P. nimba* Bernard: full-face, lateral & dorsal view of minor worker.

Diagnosis: *Pheidole nimba* is the species with the highest amount of sculpture in this group. Color is dark brown. Minor worker: Head shape rounded (CI: 90), with medially impressed occipital carina; uniformly and coarsely punctate on all dorsal surfaces from clypeus to anterior half of first gastral tergite, except smooth triangular spot between frontal carinae, and spaces between cross-ribs of metanotal groove. Standing hairs present on head, meso- and metasoma, moderately long and stiff; scape and metatibia pilosity decumbent. [**Geographic Range:** Guinea]

Description of minor worker: Measurements (syntype): HL: 0.856, HW: 0.767, SL: 0.989, MDL: 0.578, EL: 0.189, FL: 1.133, TL: 0.889, ML: 1.156, PSL: 0.233, PTH: 0.178, PPH: 0.211, PTL: 0.356, PPL: 0.233, PTW: 0.122, PPW: 0.222, PW: 0.517; CI: 90, SI: 129, MDI: 75, PSLI: 27, PWI: 67, FI: 148, PpWI: 182, PpLI: 152

Head longer than wide (CI: 84-90), almost elliptical, with posterior margin weakly compressed; face strongly punctate; median part of clypeus weakly punctate, median carina conspicuous and short, nasal carinae well-developed; punctures at malar area overlain by weak to irregular rugulae, ending at eye-level; occipital carina narrow, medially conspicuously impressed; scapes relatively short (SI: 129), with decumbent pilosity. Promesonotal outline weakly convex in lateral view, subangulate towards posterior declivity; mesonotal process flatly produced, angulate, declivity long and straight; second mesonotal process more shallowly produced, similar in shape to first process; metanotal groove conspicuous and deep; dorsopropodeum in lateral view distinctly declining towards propodeal declivity; mesosoma strongly punctate except small superficially sculptured spot at posterior lateropronotum; punctures at anteropronotum overlain with weak and irregular transverse rugulae; propodeal spines and metafemur moderately short (PSLI: 27, FI: 148); metatibia with decumbent pilosity. Petiole and postpetiole densely punctate dorsally, except anterodorsal surface of petiole ventrally punctate; anterior half of first gastral tergite punctate, posterior half shagreened. Standing hairs moderately long and stiff, partly with blunt to truncate apices and relatively scarce on head and at pronotum; pilosity at mesonotum and propodeum subdecumbent and shorter; additional short decumbent to subdecumbent pubescence present. Color uniformly brown.

Discussion: In habitus and amount of punctate sculpture *Pheidole dea* is the species that most closesly resembles *P. nimba*. However, the clypeus, central area at frons, and posterior dorsopropodeum are smooth to superficially punctate, and standing hairs are relatively rare to almost absent in *P. dea*. *Pheidole nimba* was found in the Mount Nimba Nature Reserve in

Guinea, close to the border to the Ivory Coast, at the Nion crest and at an altitude of 1300 m. It was described on the basis of four minor workers, two of which were used for this redescription (one was without head, and thus was not measured). Major workers remain unknown, but one specimen from Ghana, which did not match with any of the other species presented here, might be conspecific with *P. nimba*, although the differences in sculpture to the type specimen are relatively strong. Until additional material from the different localities becomes available the description of major workers will not be possible.

Type material examined: GUINEA: (1 minor worker) Nion, 1300 m, maqun crête lamothe (*F. Bernard*); No. 228 types.

***Pheidole pulchella* Santschi 1910**

(Figures 4.51 - 4.56)

Pheidole pulchella Santschi, 1910: 360. Syntype major workers (2) and syntype minor workers (4). CONGO [examined]. [Misspelled as *P. putchella* by Emery, 1921: 89.]

Pheidole niapuana Wheeler 1922: 136, fig. 34. Syntype major workers (7) and syntype minor workers (5). D. R. CONGO [examined]. Junior synonym of *P. pulchella*: Santschi, 1930a: 59.

Pheidole pulchella var. achantella Santschi 1939: 242. Holotype major worker (1). CONGO [examined]. **syn. n.**

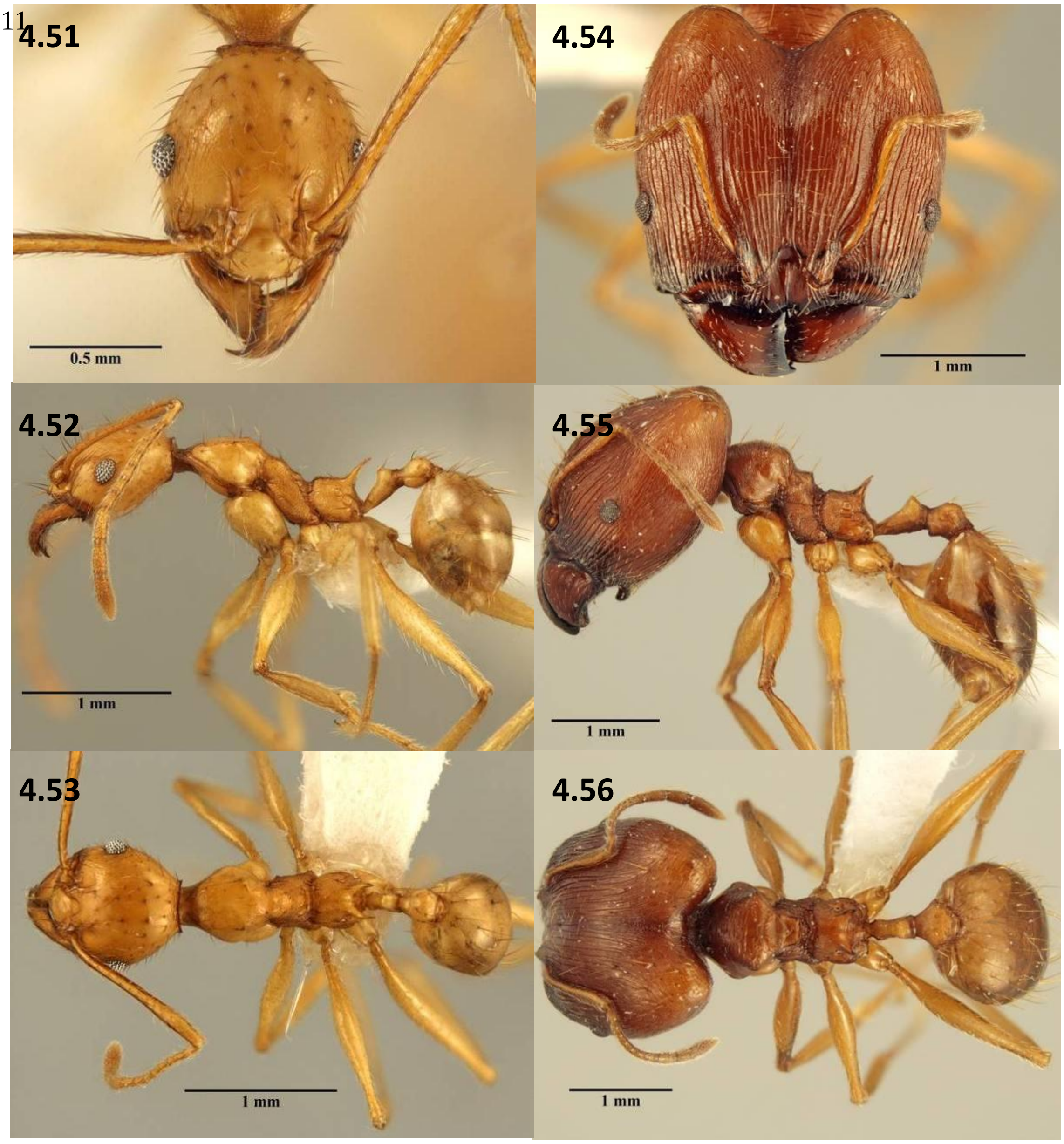

Fig. 4.51 - 4.56: *P. pulchella* Santschi: full-face, lateral & dorsal view of minor (**4.51 - 4.53**) and major worker (**4.54 - 4.56**).

Diagnosis: Color orange (minor) to dark orange with lighter appendages (major). Minor workers: head shape rounded and relatively wide (CI: 82-90); occipital carina narrow; scape and metafemur relatively long (SI: 147-161, FI: 169-194), pilosity decumbent. Promesonotal outline in lateral view flat, without raised peak at humeri; mesonotal processes relatively shallow; metanotal groove broad and deep in lateral view; dorsopropodeum straight; propodeal spines relatively short (PSLI: 25-29). Standing hairs comparatively thick. Major workers: frontal carinae and antennal scrobes present, rugae in face of varying lengths, grading into weak oblique rugulae at posterolateral lobes, ground sculpture weakly to superficially punctate; dorsal promesonotum transversely rugulose and weakly punctate, posteriad towards mesonotum partly smooth and shiny; mesonotal process strongly produced, right-angled; dorsopropodeum longer than base of spines; petiole and postpetiole moderately wide (DPeI: 38-40, DPpI: 127-151). Standing hairs relatively long and thick, absent from propodeum. [**Geographic Range:** Congo, D.R. Congo, Gabon]

Description of minor worker: Measurements (n=15): HL: 0.856-0.944 (0.895), HW: 0.733-0.800 (0.766), SL: 1.133-1.254 (1.192), MDL: 0.578-0.644 (0.610), EL: 0.167-0.189 (0.173), FL: 1.317-1.508 (1.414), TL: 1.056-1.133 (1.092), ML: 1.156-1.317 (1.258), PSL: 0.222-0.267 (0.244), PTH: 0.172-0.211 (0.190), PPH: 0.206-0.244 (0.221), PTL: 0.289-0.389 (0.347), PPL: 0.211-0.256 (0.237), PTW: 0111-0.133 (0.122), PPW: 0.222-0.267 (0.235), PW: 0.478-0.544 (0.506); CI: 82-90 (86), SI:147-161 (156), MDI: 75-83 (80), PSLI: 25-29 (27), PWI: 64-68 (66), FI: 169-194 (185), PpWI: 182-218 (193), PpLI: 117-175 (147)

Head longer than wide (CI: 82-90), with sides posterior of eye-level evenly rounded towards posterior margin; occipital carina conspicuous, medially and laterally faintly impressed; mandibles of moderate length (MDI: 75-83), dorsally smooth to superficially rugulose; clypeus smooth, median and submedian carinae absent, nasal carinae conspicuous, sometimes short; frons and vertex smooth, hexagonally micropunctate; superficial punctures at malar area and near eyes; malar carinae weak and interrupted, disappearing at posterior eye-level; standing hairs relatively stiff, long and acute or truncated; scape relatively long (SI: 147-161) in full face view and when laid back surpassing occiput by more than one third of its length, pilosity decumbent. Promesonotal outline in lateral view flat, obtusely angulate at posterior declivity; first and second mesonotal process weakly produced, at edges slightly rounded, not marginate dorsally; humeri with small, weakly marginate angle, not peaked in lateral view; pronotal and mesonotal declivities shallow and flatly declining towards deeply and broadly impressed metanotal groove; promesonotum anteriad at neck weakly punctate, with short to moderately long, irregular rugulae, remainder smooth and shiny to superficially punctate; mesonotum dorsally smooth to superficially punctate; mesopleuron and propodeum weakly punctate, with superficially sculptured or almost smooth spots on anepisternum, katepisternum, and posterior dorsopropodeum; spines relatively short (PSLI: 25-29), in dorsal view, at apices almost parallel; metafemur relatively long (FI: 169-194); metatibia pilosity decumbent. Petiolar node and postpetiole weakly punctate lateroventrally and ventrally, dorsum with superficially punctate to smooth and shiny area, peduncle also weakly to superficially punctate dorsally, without smooth strip medially. First gastral tergite smooth and shiny, except very narrow, superficially punctate anterior strip. Standing hairs relatively stiff and of varying lengths, longest hairs at pronotum, gaster and head; mesonotum and propodeum with shorter subdecumbent hairs, also present at head and projecting beyond lateral margin anteriad and posteriad of eye-level. Color yellow to light orange.

Description of major worker: Measurements (n=13): HL: 1.940-2.225 (2.140), HW: 2.000-2.275 (2.162), SL: 1.056-1.167 (1.134), MDL: 0.900-1.111 (1.016), EL: 0.233-0.256 (0.243), FL: 1.667-1.840 (1.738), TL: 1.286-1.429 (1.353), ML: 1.397-1.740 (1.651), PSL: 0.244-0.378 (0.316), PTH: 0.333-0.389 (0.357), PPH: 0.367-0.500 (0.443), PTL: 0.533-0.644 (0.594), PPL: 0.333-0.411 (0.378), PTW: 0.200-0.267 (0.240), PPW: 0.422-0.611 (0.524), PW: 0.811-1.033 (0.950); CI: 98-103 (101), SI: 51-56 (53), MDI: 43-50 (47), PSLI: 11-17 (15), PWI: 39-47 (44), FI: 76-90 (80), PeI: 22-29 (25), PpI: 47-61 (55), PpWI: 200-239 (218), PpLI: 141-167 (157)

Head about as long as wide (CI: 98-103); frontal carinae and antennal scrobes conspicuous; frons longitudinally rugose, with irregular pattern of moderately long to shorter rugae, spaces between rugae weakly punctate to almost smooth, rugae grading weaker posteriad and curving towards posterolateral lobes, or replaced by oblique, weak, rugulose-punctate sculpture; scape pilosity appressed. Promesonotal outline, in lateral view, rounded or very weakly subangulate; dorsally and anterolaterally with transverse and irregular rugulose and weakly punctate sculpture; posterolaterad with smooth area; posterodorsad towards well-produced, right-angled mesonotal process weakly sculptured and partly smooth, at its edges weakly marginate, steeply declining towards small or inconspicuous second mesonotal process, terminating in narrow and short transverse carina; metanotal groove in lateral view narrow and shallow; dorsopropodeum weakly to superficially punctate, and in lateral view about as long as base of spines; propodeal spines weakly curved posteriad; posteropropodeum with weak transverse rugulae overlaying punctures; punctures at mesopleuron and metapleuron weak and dense, posterobasad around long and conspicuous metapleural carina and gland scrobe superficial to smooth and shiny; metatibia with short appressed pilosity; metatibia pilosity appressed to decumbent. Petiole and postpetiole very densely punctate, anterodorsal petiole superficially sculptured, posterodorsal postpetiole with short irregular rugulae. Anterior half of first gastral tergite shagreened, posterior half smooth and hexagonally microsculptured. Long standing hairs acute, relatively slender, abundantly present on dorsal head, promesonotum, waist segments, and gaster; additionally with short appressed pubescence. Color orange to darker orange, legs lighter.

Discussion: Type specimens of the three synonyms *Pheidole pulchella, P. pulchella achantella* and *P. niapuana* are conspecific. All of them were collected from only two different localities in Congo and in the D.R. Congo. As they share the same morphometric and diagnostic characters, measurement values for the junior synonym specimens were combined with those for the *P. pulchella* types and the new material from Gabon. The latter was collected in rainforest habitat from sifted leaf-litter. Minor workers of *P. pulchella* can be differentiated easily from those of *P. christinae* and *P. heliosa* by the relatively wider, more circular, head (CI: 82-90 [*P. pulchella*] versus CI: 79-84 [*P. christinae*] and CI: 73-76 [*P. heliosa*]), less abundant and thicker standing hairs, short, decumbent scape and metatibia pilosity versus suberect to erect hairs, and shorter propodeal spines (PSLI: 25-29 versus PSLI: 26-36 and PSLI: 28-37). Major workers of *P. pulchella* are separated from those of *P. heliosa* by presence of frontal carinae and antennal scrobes. They have a less coarsely, sculptured face and promesonotum, a mesonotal processes which is separated from the pronotum by an obtuse angle, and curved versus straight propodeal spines. Majors from the *P. niapuana* types and the newer material from Gabon differ slightly in coloration from the *P. pulchella* and *P. pulchella achantella* type material. The latter are somewhat darker which might be a result of age or former storage conditions. Most of the material from Gabon was collected from pitfall traps and sifted leaf-litter within rainforests.

Type material examined: CONGO: (*P. pulchella*: 4 minor workers, 2 major workers, syntypes) Brazzaville, 1907, (*A. Weiss*); (*P. pulchella achantella*: 1 major worker, holotype) Brazzaville, 1907, (*A. Weiss*); D.R. CONGO (*P. niapuana*: 7 major workers, 5 minor workers, syntypes) Niapu, Nov. 1913, (*H.O. Lang*).

Other material examined: GABON: (1 major worker, 2 minor workers) La Makande, Foret des Abeilles, i-ii.1999 (*S. Lewis*); (2 major workers, 2 minor workers) Prov. Ogooue Maritime, Res. Monts Doudou, 24.3 km 103° NW Doussala, 02° 13.4' S, 10° 24.4' E, 6-11.iii.2000, 375 m (*B.L. Fisher*); (3 minor workers) Prov. Woleu-Ntem, 31.3 km 108° ESE Minvoul, 02° 04.8' N, 12° 24.4' E, 600 m, 12.ii.1998 (*B.L. Fisher*); (1 major worker, 1 minor worker) Prov. Woleu-Ntem, 31.3 km 108° ESE Minvoul, 02° 04.8' N, 12° 24.4' E, 600 m, 11.ii.1998 (*B.L. Fisher*).

Pheidole rebeccae **sp. n.**

(Figures 4.57 - 4.62)

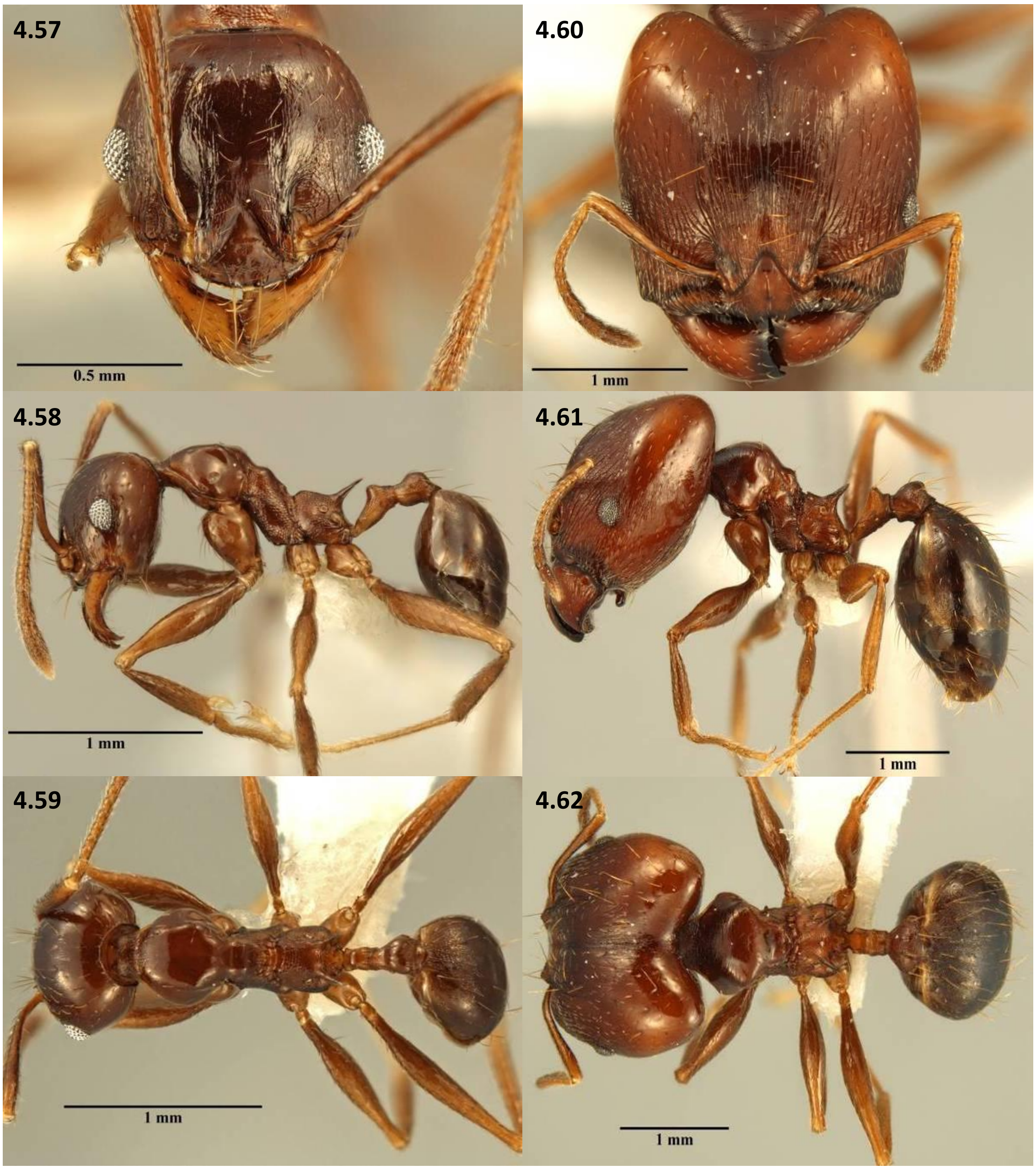

Fig. 4.57 - 4.62: *P. rebeccae* sp. n.: full-face, lateral & dorsal view of minor (**4.57 - 4.59**) and major worker (**4.60 - 4.62**).

Diagnosis: Color reddish brown (major) to brown (minor). Minor workers: head shape rounded, almost as broad as long (CI: 94-98), posterior margin compressed to almost straight; scapes short (SI: 114-121), pilosity mostly decumbent; most dorsal surfaces superficially punctate (sides of head, propodeum, anterior gaster) to smooth and shiny (posterior head margin, promesonotum, waist segments partly); legs short (FI: 133-139); metatibia pilosity decumbent. Major workers: head and promesonotum with short and weak superficial rugulation, posteriad largely smooth and shiny, sculpture on meso- and metapleuron also reduced, with several smooth spots; metanotal groove barely impressed in lateral view; dorsopropodeum about as long as base of spines; standing hairs abundant, absent from propodeum, sometimes also from rest of mesosoma. [**Geographic Range:** Ivory Coast, Ghana]

Description of minor worker: Measurements (n=11): HL: 0.756-0.811 (0.785), HW: 0.717-0.778 (0.754), SL: 0.856-0.900 (0.885), MDL: 0.511-0.556 (0.531), EL: 0.167-0.178 (0.171), FL: 0.967-1.067 (1.024), TL: 0.756-0.867 (0.809), ML: 1.011-1.078 (1.035), PSL: 0.194-0.233 (0.217), PTH: 0.167-0.178 (0.170), PPH: 0.183-0.206 (0.194), PTL: 0.267-0.333 (0.303), PPL: 0.189-0.222 (0.197), PTW: 0.106-0.111 (0.110), PPW: 0.189-0.217 (0.204), PW: 0.456-0.500 (0.475); CI: 94-98 (96), SI: 114-121 (117), MDI: 69-73 (70), PSLI: 25-30 (28), PWI: 62-64 (63), FI: 133-139 (136), PpWI: 170-195 (185), PpLI: 133-176 (154)

Head shape in full-face view compactly rounded, posterior margin of head compressed to almost straight; occipital carina narrow; mandibles relatively short (MDI: 69-73); clypeus smooth, with two very faint median carinae, nasal carinae usually more strongly developed; face smooth and shiny with faint hexagonal microstructure; malar carinae short, ending at midlevel of eyes; scapes relatively short, shortest within group (SI: 114–121), pilosity decumbent, partly subdecumbent to suberect apically. Promesonotum smooth and shiny, without sculpture, mostly without standing hairs, but occasionally with two pairs of long, bluntly ending hairs on anterior corners of humeral area or one pair at humeri; pubescence short and appressed to decumbent; meso- and metapleuron weakly to superficially punctate, katepisternum and anterior metapleuron with smooth central spots; first mesonotal process conspicuous, roundly angulate; second process reduced to shallow, obliquely angulate projection; metanotal groove wide and deep; dorsopropodeum weakly punctate, descending smoothly from highest point after metanotal groove towards propodeal declivity; propodeal spines relatively short (PSLI: 25-30) and slender, almost straight to well-curved posteriad; metafemur relatively short, shorter than in other species from this group (FI: 133-139); metatibial pilosity decumbent. Petiole and postpetiole weakly punctate laterally and ventrally, dorsally smooth and shiny. Anterior half of first gastral tergite shagreened, rest smooth, hexagonally microsculptured or whole gaster weakly punctate. Long standing hairs often truncated, present on head, postpetiole and gaster, number on dorsal head variable, up to five pairs, absent to very scarce on mesosoma and petiole, both usually with shorter decumbent hairs; pubescence inconspicuous, fine and appressed. Color brown, mandibles and appendages lighter.

Description of major worker: Measurements holotype: HL: 1.960, HW: 1.980, SL: 0.978, MDL: 0.911, EL: 0.250, FL: 1.476, TL: 1.133, ML: 1.556, PSL: 0.278, PTH: 0.333, PPH: 0.411, PTL: 0.556, PPL: 0.344, PTW: 0.239, PPW: 0.522, PW: 0.900; CI: 101, SI: 49, MDI: 46, PSLI: 14, PWI: 45, FI: 75, PeI: 27, PpI: 58, PpWI: 219, PpLI: 161

Measurements (n=3): HL: 1.820-1.980 (1.900), HW: 1.860-1.960 (1.927), SL: 0.944-0.967 (0.956), MDL: 0.833-0.889 (0.859), EL: 0.233-0.267 (0.256), FL: 1.476-1.556 (1.503), TL: 1.078-1.122 (1.104), ML: 1.444-1.524 (1.487), PSL: 0.244-0.300 (0.278), PTH: 0.322-0.344 (0.337), PPH: 0.361-0.400 (0.378), PTL: 0.467-0.500 (0.489), PPL: 0.311-0.356 (0.330), PTW: 0.211-0.233 (0.226), PPW: 0.456-10.533 (0.493), PW: 0.856-0.900 (0.881); CI: 99-103 (102), SI: 49-51 (50), MDI: 42-45 (44), PSLI: 13-16 (15), PWI: 45-46 (46), FI: 75-84 (78), PeI: 25-26 (26), PpI: 53-59 (56), PpWI: 210-229 (218), PpLI: 141-161 (149)

Frons with relatively weak, irregular, very short or interrupted rugae, spaces between rugae superficially punctate, only narrow, sculptured strip continuing towards median emargination of posterior margin, posterolateral lobes and sides of head posteriad of eye-level smooth and shiny, at most hexagonally microsculptured; scape pilosity appressed. Pronotum anteriorly weakly to superficially and transversely rugulose-punctate and posteriorly smooth, or in some specimens with superficial punctures and/or with weak to superficial rugulae; humeri with weak and subangulate lateral process; pronotal declivity rounded to subangulate; mesonotal process almost right-angled, second metanotal process inconspicuous, at most represented as weak, quasi-vertical carina; metanotal groove forming broad constriction between mesonotum and propodeum in dorsal view, shallow to unimpressed in profile; meso- and metapleuron weakly to superficially punctate, with several smooth spots (extent of sculpture strongly varies with viewing-angle); dorsopropodeum in lateral view short, shorter than base of spines, in dorsal view anteromedially smooth, lateraloventrad densely punctate, posteriad between spines transversely and weakly rugulose; posteropropodeum weakly transversely rugose-punctate, laterally with vertical curved rugae from spines towards metapleural carina(e); metatibial pilosity appressed. Anterior face of petiole broadly smooth and shiny, rest of petiole and postpetiole densely punctate, postpetiole with short irregular rugulae posterodorsally and conspicuous lobate flange posterolaterally. Gaster weakly punctate. Long standing hairs acute, present everywhere, except propodeum; mesonotum with shorter subdecumbent hairs, sometimes mesosoma completely without hairs other than short appressed pubescence.

Discussion: *Pheidole rebeccae* specimens were collected in the Ivory Coast and in Ghana. The minor workers from Ghana differ slightly from those from the Ivory Coast in the extent of sculpture at the first gastral tergite. Minor workers of *P. rebeccae*, in overall habitus and reduced body sculpture, are closest to those of *P. glabrella*, and best differentiated from the latter by wider head shape (CI: 94-98 [*rebeccae*] versus CI: 88-95 [*glabrella*]); shorter scapes, propodeal spines and metafemur (SI: 114-121, PSLI: 25-30, FI: 133-139 versus SI: 123-141, PSLI:

28-40, FI: 143-170), and more abundant standing hairs. Major workers of *P. rebeccae* are distinctively separated from those of other species by the short and weak longitudinal rugulae in face, largely smooth and shiny surfaces on the posterior half of face and pronotum, and reduced sculpture on meso- and metapleuron. Major workers of *P. darwini* also feature a reduced punctate sculpture in face and on posterior pronotum and partly smooth posterolateral lobes, but the longitudinal rugae are longer and more conspicuous, the punctures between the rugae are stronger, smooth surfaces at the head and mesosoma are restricted to significantly smaller areas and promesonotal standing hairs are long and erect versus shorter and decumbent in *P. rebeccae*. A unique character in *P. darwini* is the small number of erect hairs in combination with the appressed to decumbent pilosity along the outer edge of the scape, that is absent in the majors of *P. rebeccae*.

Etymology: This species is named after my daughter Rebecca, the most delightful and curious little person in the world.

Type material examined: IVORY COAST: Holotype (major worker): vic. Abidjan, 1976, no. 15 (*T. Diomande*) (CAS: CASENT0227952); Paratypes (3 major workers, 8 minor workers): same data as holotype (CAS: CASENT0227952, CASENT0227953, CASENT0227954, CASENT0227955, CASENT0227956).

Other material examined: GHANA: (3 minor workers) Atewa For. Res., nr. Kibi, 26.ii.1992 (*R. Belshaw*).

***Pheidole semidea* sp. n.**

(Figures 4.63 - 4.68)

Fig. 4.63 - 4.68: *P. semidea* sp. n.: full-face, lateral & dorsal view of minor (**4.63 - 4.65**) and major worker (**4.66 - 4.68**).

Diagnosis: Color light to dark brown. Minor workers: head shape rounded (CI: 85-89), with medially impressed occipital carina; dorsal surfaces of head, promesonotum and metasoma smooth, at most superficially punctate; second mesonotal process in lateral view distinctly raised above level of anterior dorsopropodeum; petiole relatively short (PpLI: 126-144). Major workers: frons with moderately long rugae; vertex weakly rugose-reticulate; oblique rugulae at posterolateral lobes. Mesonotal process in lateral view almost right-angled, second process very shallow and raised above level of dorsopropodeum; dorsopropodeum in profile longer than base of spines; postpetiole moderately wide (PWI: 192-221). Standing hairs at pronotum medially inclined. [**Geographic Range:** Nigeria]

Description of minor worker: Measurements (n=5): HL: 0.778-.0811 (0.796), HW: 0.689-0.722 (0.697), SL: 0.967-1.033 (0.989), MDL: 0.533-0.544 (0.542), EL: 0.156-0.189 (0.169), FL: 1.111-1.190 (1.149), TL: 0.900-0.911 (0.904), ML: 1.044-1.111 (1.084), PSL: 0.206-0.233 (0.222), PTH: 0.167-0.172 (0.168), PPH: 0.178-0.200 (0.192), PTL: 0.256-0.289 (0.276), PPL: 0.189-0.222 (0.207), PTW: 0.111-0.122 (0.114), PPW: 0.200-0.222 (0.211), PW: 0.467-0.478 (0.475); CI: 85-89 (88), SI: 134-150 (142), MDI: 75-79 (78), PSLI: 26-29 (28), PWI: 68-69 (69), FI: 160-173 (165), PpWI: 173-200 (185), PpLI: 126-144 (134)

Head shape in full-face view slightly elliptical with roundly convex posterior margin (CI: 85-89); occipital carina conspicuous and medially impressed; clypeus smooth, nasal carinae weak; face smooth, except hexagonal microsculpture, superficially punctate laterally towards eyes; malar rugulae well-developed, disappearing posteriad of eyes; scape surpassing occiput by about one third of its length (SI: 134-150), pilosity decumbent, apically some hairs Subter.decumbent. Promesonotum in lateral view flat, Subter.angular, anterodorsad towards neck weakly punctate, rest smooth; first mesonotal process obtusely angulate, dorsally smooth; second process conspicuous and distinctly raised above level of dorsopropodeum; metanotal groove asymmetrically impressed, posteriorly more shallowly; mesopleuron and propodeum punctate, with superficially sculptured spots on katepisternum and posterior dorsopropodeum; spines moderately long (PSLI: 26-35), posteriad strongly curved; metafemur long (FI: 158-173);

metatibial pilosity decumbent. Petiole punctate laterally and ventrally, dorsolateral postpetiole and ventral process weakly punctate, dorsum of both waist segments smooth, partly micropunctate. Gaster smooth, anteriorly near insertion of postpetiole superficially punctate. Standing hairs on head, postpetiole and gaster long and acute, on petiole short and on promesonotum mostly moderately long and Subter.decumbent, directed towards center or dorsopronotum. Body surface also with several short and relatively long appressed hairs. Color light to dark brown, gaster darker, mandibles partly transparent.

Description of major worker: Measurements (holotype): HL: 1.800, HW: 1.760, SL: 0.978, MDL: 0.833, EL: 0.222, FL: 1.444, TL: 1.078, ML: 1.429, PSL: 0.300, PTH: 0.333, PPH: 0.367, PTL: 0.500, PPL: 0.311, PTW: 0.222, PPW: 0.467, PW: 0.800; CI: 98, SI: 56, MDI: 47, PSLI: 17, PWI: 45, FI: 82, PeI: 28, PpI: 58, PpWI: 210, PpLI: 161

Measurements (n=3): HL: 1.619-1.860 (1.705), HW: 1.635-1.820 (1.724), SL: 0.922-1.000 (0.975), MDL: 0.722-0.833 (0.792), EL: 0.211-0.222 (0.215), FL: 1.349-1.444 (1.393), TL: 1.000-1.111 (1.061), ML: 1.286-1.476 (1.365), PSL: 0.244-0.306 (0.285), PTH: 0.250-0.311 (0.285), PPH: 0.311-0.406 (0.357), PTL: 0.489-0.556 (0.515), PPL: 0.333-0.344 (0.336), PTW: 0.200-0.233 (0.211), PPW: 0.383-0.500 (0.447), PW: 0.711-0.800 (0.764); CI: 98-106 (101), SI: 55-58 (57), MDI: 43-48 (46), PSLI: 15-18 (16), PWI: 39-47 (44), FI: 79-83 (81), PeI: 25-30 (28), PpI: 50-66 (579, PpWI: 192-221 (212), PpLI: 147-161(153)

Face entirely rugose-punctate, rugae relatively long and sometimes interrupted at frons, posteriad with some weak cross-meshes, disappearing towards obliquely and weakly rugulose-punctate posterolateral lobes, outer corners of posterolateral lobes and spaces between rugae at frons superficially punctate; laterad of antennal scrobe irregularly rugose-reticulate; scape with decumbent pilosity. Promesonotum in lateral view short, posteriorly subangulate, declivity short, anterodorsally and anterolaterally weakly and irregularly rugulose-punctate, grading to superficially punctate posteriad at dorsopronotum, lateropronotum and mesonotum; first mesonotal process right-angled, with a steep declivity; second process small or reduced to short, narrowly raised carina, but raised above level of dorsopropodeum; meso- and metapleuron punctate, with smooth area at katepisternum and posteroventral metapleuron; metapleural carina relatively short and weak, gland scrobe weak to inconspicuous; dorsal and posterior propodeum smooth to superficially punctate, with transverse rugula(e) between spines and moderately developed, longitudinal rugula(e) posteriad along spines. Petiole and postpetiole punctate, except medial area of anterodorsal petiole. First gastral tergite shagreened, posteriad slightly weaker. Metatibia with appressed pilosity. Acute, long standing hairs present on head, postpetiole, dorsal gaster and pronotum, at the latter medially inclined. Color reddish brown, gaster darker.

Discussion: *Pheidole semidea*, in morphometrics and overall habitus, is closest to *P. dea*, but differentiated from the latter by the following characters: (minor workers) sculpture in face strongly reduced to mostly smooth and shiny versus weakly to superficially punctate in *P. dea*, higher situated second mesonotal process that is raised above dorsopropodeal outline, more strongly curved spines and a shorter petiole and longer postpetiole (PpLI: 126-144 versus PpLI: 156-223); (major workers) rugae at frons and vertex moderately long, posterolateral lobes with oblique rugulae versus very long, longitudinal and subparallel rugae from frons to head margin, postpetiole on average wider (PpWI: 192-221 [*P. semidea*]) versus relatively narrow (PpWI: 177-210 [*P. dea*]), and first gastral tergite almost completely shagreened versus only anteriorly shagreened in *P. dea*. Given the relatively minor differences between minor workers of the two species, it is possible that they are conspecifics and that intermediate forms exist within or between the West and East African populations. Yet, we propose that *P. semidea* and *P. dea* should be considered separate species until additional data from future sampling proves otherwise. The *P. semidea* types were collected from a log at Gambari, Nigeria, and another major was collected from Ibadan, Nigeria.

Type material examined: NIGERIA: Holotype (major worker): Gambari, 22.vii.69, in log (*B. Bolton*) (BMNH: CASENT0227957); Paratypes (2 major workers, 5 minor workers): same data as holotype (BMNH: CASENT0227957, CASENT0227958, CASENT0227959).

Other material examined: NIGERIA: (1 major worker): Ibadan, Ilta, 18.v.81, no. 16 (*A. Russel-Smith*).

Pheidole setosa **sp. n.**

(Figures 4.69 - 4.71)

Fig. 4.69 - 4.71: *P. setosa* sp. n.: full-face, lateral & dorsal view of minor worker.

Diagnosis: Color brown. Major unknown. Minor worker: Head shape broadly elliptical (CI: 87-90), with relatively wide, slightly compressed occipital margin; in full-face view laterally projecting hairs at head margin posteriad of eye-level present; punctures in face variable: absent to superficial medially between eyes, stronger and more conspicuous in rest of face; scape and metafemur moderately long (SI: 141-145, FI: 167-168); scape pilosity decumbent with additional erect to suberect hairs at outer edges; metatibia pilosity appressed. Posterior and lateral pronotum smooth, rest of mesosoma with distinct punctures. Standing hairs coarse and moderately long and truncated, present on all dorsal surfaces. [**Geographic Range:** D.R. Congo]

Description of minor worker: Measurements (holotype): HL: 0.856, HW: 0.744, SL: 1.078, MDL: 0.578, EL: 0.178, FL: 1.254, TL: 0.989, ML: 1.133, PSL: 0.300, PTH: 0.178, PPH: 0.222, PTL: 0.367, PPL: 0.222, PTW: 0.122, PPW: 0.233, PW: 0.489; CI: 87, SI: 145, MDI: 78, PSLI: 35, PWI: 66, FI: 168, PpWI: 191, PpLI: 165

Measurements (n=1): HL: 0.867, HW: 0.778, SL: 1.100, MDL: 0.567, EL: 0.178, FL: 1.302, TL: 1.033, ML: 1.167, PSL: 0.267, PTH: 0.178, PPH: 0.233, PTL: 0.378, PPL: 0.211, PTW: 0.122, PPW: 0.233, PW: 0.511; CI: 90, SI: 141, MDI: 73, PSLI: 31, PWI: 66, FI: 167, PpWI: 191, PpLI: 172

Head longer than wide (CI: 87-90); sides roundly convex, with laterally projecting hairs posteriad of eye-level; posterior margin broadly developed and compressed to almost flat; occipital carina narrow; clypeus smooth, with conspicuous long median carina and short or inconspicuous submedian carinae; frons smooth, hexagonally microsculptured; weakly to conspicuously punctate areas posteriad, about halfway between posterior eye-level and occipital margin, laterad towards eyes, and anteriad towards malar space, malar carinae ending at posterior eye-level; scapes moderately long (SI: 141-145), pilosity decumbent, with additional erect to suberect hairs along outer edge; head margin in full-face view and posteriad of eye-level with laterally projecting hairs. Promesonotal outline angulate, dorsopronotum flat, pronotal and mesonotal declivities obtuse-angled, edges in lateral view almost straight and long; second mesonotal process small, subangular and distinctly raised above level of dorsopropodeum; metanotal groove conspicuous; dorsopropodeum flat; spines relatively long and curved (PSLI: 31-35), about as long as height of posteropropodeum; anterior dorsopronotum punctate, grading to smooth or superficially punctate posterodorsad and on posterior declivity; lateropronotum mostly smooth, except superficial sculpture anteriad and dorsad; mesopleuron, metanotal process and propodeum uniformly punctate, except narrow, smooth strip between spines on dorsopropodeum; metatibia with appressed to decumbent pilosity. Petiole and postpetiole weakly punctate laterally and ventrally, dorsum partly smooth and hexagonally micropunctate. Gaster smooth and shiny. Standing hairs stiff, of moderate length, apically truncated or split. Color brown.

Discussion: The description of *P. setosa* is based on 2 minor workers from a single leaf-litter collection event in a rainforest in the D.R. Congo. The major is unknown. In habitus and amount of sculpture the minors are comparable to those of *P. batrachorum.* But the punctures in face and on dorsopronotum are much less distinct in *P. setosa* and the head is both, absolutely and relatively wider (CI: 87-90 [*P. setosa*] versus CI: 79-86 [*P. batrachorum*]). Scapes and legs are shorter in *P. setosa* than in *P. batrachorum* (SI: 141-145, FI: 167-168 versus SI: 152-172, FI: 172-196), the propodeal spines are significantly longer (PSLI: 31-35 versus PSLI: 21-29) and scape pilosity differs distinctly.

Type material examined: Holotype (minor worker): D.R. CONGO: Epulu, 01° 23' N, 28° 35' E, 750 m, xi.1995, Rainfor. (*S.D. Torti*) (CAS: CASENT0218297); Paratype (1 minor worker): same data as holotype (CAS: CASENT0218298).

Chapter 5:

General Discussion

Kakamega ant diversity

Before the start of the Biota project in 2001, a bit more than one hundred ant species in 38 genera and 8 subfamilies were known for the Kakamega Forest (Espira, 2001). This previous study in the north of the forest was restricted to a small area of the whole forest and collection methods were only pitfall traps and leaf-litter samples. By the year 2009 after many hundreds of analyzed samples from all different forest strata, this number had increased to already 288 species in 52 genera and 11 subfamilies (Hita Garcia et al., 2009). Presently, it has reached an astonishing 329 species in 55 genera, which is the currently the highest ant diversity found anywhere in the Afrotropical region (chapter 2). Part of the recent increase is due to an additional amount of leaf-litter samples which have been processed since, where previously undiscovered species occurred.

The high species-richness in the Kakamega ant fauna has been completely unexpected, due to the relatively high altitude of the plateau, where it is located (mostly between 1550 and 1750 m). It is generally accepted, that the highest ant diversity can be found in lowland tropical rainforests (Fisher, 2010). In all other studies published so far the ant diversity in these altitudes was strongly reduced and almost an order of magnitude lower than in low-land rainforests. The enormous disparity is most likely a combination of its unique geographic position (Hita Garcia et al., 2009), and the climate which seems to be advantageous compared to colder and wetter montane cloud forests at elevations above 1500 m in other regions. Brown (1973) observed that above the forests limit of mountainous regions, where it is usually warmer during the day than in the fog covered cloud forests below, ants are much more frequent than in the forests at slightly lower altitudes and suggested the climate as ultimate reason. Of equally high importance might be the high sampling intensity at the Kakamega Forest. In fact, new species records would be highly expected with further sampling activity as observed by another long-term ant sampling project at the La Selva Station in Costa Rica (Longino & Colwell, 2011). Although the accumulation curve for new ant species in Kakamega already slowed down, it is still without sign of saturation. Especially from the less intensively studied tree crown and underground strata several new species might be discovered (Brühl et al., 1998; Andersen & Brault, 2010). As for example members of the more rarely collected, but still relatively widespread, genera Asphinctopone Santschi, Amblyopone Erichson, Terataner Emery could be discovered in new samples. Also the genus Pheidole, which is taxonomically poorly resolved in Africa could be much more diverse than currently known, because some of its species seem to occur only in termite nests or in the higher vegetation, where they can become quite dominant in South American rainforests (Hölldobler & Wilson, 1990). Nevertheless, despite its high faunal and floral diversity the whole forest endures considerable human pressure, which is probably going to increase even further in the future (Bleher et al., 2006; Müller & Mburu, 2008). Firstly, it is only partially protected as a National Forest Reserve, which still suffers from illegal exploitation, although much less than the unprotected parts in the south (Bleher, 2006; FHG unpublished). Logging and fire-wood collection occur regularly and can pose serious threats to rare species and specialists that nest in dead branches, for example. Secondly, it might also become a problem if the climate changes to hotter and drier condition, and if the majority of rainforest species with Congo-Guinean distributions cannot adapt to or endure harsher climate conditions (Jenkins et al., 2011; Laurance et al., 2011). But another scenario could also be that the local climate remains largely unchanged because of its altitude, while the low-land forests further west would be become drier and hotter. Then the Kakamega Forest could become a refuge for its Congo-Guinean fauna and flora.

Biodiversity and ecosystem stability

The Kakamega Forest is, however, not only a diversity hotspot for Kenyan or Afrotropical ants and diversity in general, but also provides important services and functions to the human population surrounding the forest, for example crop pollination by bees on the farmlands near the forest (Kasina, 2007). In ecology there is a growing consensus that increasing habitat modification and degradation alter community composition and can lead to loss of functionally unique species and thus to degradation of ecosystem functions (Diáz et al., 2006; Hooper et al., 2005; O'Gorman et al., 2011; Peters & Okalo, 2009). In chapter 3 it was shown that the ant diversity inside the forest is on average 20 % (species diversity) to 40 % (species richness) higher than in intensive sugarcane agriculture, and that it also provides a higher amount of ecosystem functions, which is between 18 % (FD27 index) and 53 % (FAD index) higher, with many unique and ecologically specialized taxa. What also became clear is that not all ecosystem functions will get lost in the farmlands and that the scavenging rates in the baiting experiment were up to 57 % higher than in the forest. Predatory ants, for example the ponerines and army ants, were significantly less diverse and abundant in the farmlands, which could be a reason why trophic chain lengths of the local food webs decreased significantly (about ½ trophic level) in the subsistence farmland (Post & Takimoto, 2007). But intensive sugarcane agriculture ant communities showed a high range of values, with some as high as in the forest food webs. This indicates that other factors were probably more important for the height of the food webs. But, if it was compensation by unspecialized predators or increased intraguild predation within the ant community was not determined. The results of baiting experiments do not provide further insights to this question, as the species responsible for bait removal in the farmland were not the apical predators or even very high in the food chains, and because the baiting method is biased towards opportunistic foragers (Bestelmeyer et al., 2000; Fayle et al. 2011). The fact that long trophic chains occurred in the intensive sugarcane might, however, be related to the use of chemical fertilizers and enhanced primary production rates. Shorter trophic chain lengths are easier to explain, because the additional use of herbicides and insecticides in the high-intensity sugarcane production sites has high negative impact on predator communities, thus shortening the complete food web.

Sustainability and conservation versus deforestation

Diverse rainforest habitats are of high conservation value, also as an important insurance against the consequences of worldwide over-exploitation of natural resources in general (Balvanera et al., 2006; Diáz et al., 2006). They act as carbon sinks sequestering high amounts of CO2, water catchment areas, climate regulators, diversity conservatories and evolutionary experimentation grounds. They also provide rich income to the local human communities, if managed sustainably they can provide multiple benefits, such as plants for medicinal use, food, wood, and attractions for tourism. Thus, it also seems prudent to include the human population of an area in the conservation efforts and to find compromises that provide for the well-being of both, humans and natural ecosystems (Diáz et al., 2011). Yet agriculture is a serious threat for the survival of forest species and solutions must be found to provide a long-term protection for larger areas of natural habitats. And, in contrast to research about the influence of oil-palm plantations in South-East Asia (Brühl & Eltz, 2010; Fayle et al., 2010; Pfeiffer et al., 2008), relatively little is known about the effects of industrialized sugarcane production on ant species and functional diversity in the tropics. And although biofuel production in Africa is projected to be less important than on most other continents (FAO, 2011), the momentum of growing populations and the need for stable incomes might still be resulting in severe environmental effects for endangered ecosystems and habitats. Therefore, research on the functions provided by organismic diversity in natural and modified habitats might become highly important, because species richness numbers alone provide little indications of the processes and ecosystem services involved (Loreau & Hector, 2001; Tilman, 1997).

Further biodiversity research questions

The updated checklist, combined with the included eco-biogeographical distribution analyses in chapter 2 and with the analyses of human disturbances on several levels of biological diversity from chapter 3, provides a relatively strong argument for 1) the high conservation value of the Kakamega Forest flora and fauna, and 2) the need of basic diversity mapping in combination with applied research on general patterns across habitats, ecosystems and geographical or political barriers. These two parts of this dissertation are dedicated to increase the knowledge about African ants in general, as well as the historical background and the special ecological adaptations of a rainforest fauna that is unique in Kenya and maybe even in East Africa. It is also dedicated to raise a number of new questions and hypotheses, and to be an incentive for other researchers who are interested in African ant diversity, ecology and biogeographical patterns. For example, why is it that other studies in tropical mid-altitudinal forests found so much lower ant diversities? Is it the sampling intensity in the higher elevations, or is it the climate and the area-diversity relationship which caused these differences? And, will it be more efficient for biodiversity conservation, to strictly conserve natural habitats and rainforests under exclusion of human activities or to make compromises for a sustainable coexistence of humans and the more adaptable proportion of the natural biodiversity? These are important questions, apart from a multitude of unanswered ecological, eco-evolutionary and dispersal hypotheses that will need a lot more specific efforts, than could be covered in the time of this dissertational thesis.

Pheidole Taxonomy

The family of the ants evolved around 120 million years ago during the Cretaceous period, with the oldest fossils (Sphecomyrminae) found in French and Burmese ambers (Fisher, 2009). The oldest fossil of the genus Pheidole is from the late Eocene about 34 million years ago and molecular clock analyses for a relatively large subset of the genus estimated an age of around 60 million years (Moreau, 2008). With a known diversity of over 1000 extant species (Longino, 2009) the genus underwent a comparatively high number of speciation events, which is many times higher than for most other ant genera. This and their ecological variability and dominance in many habitats shows that the genus Pheidole is highly competitive and belongs to one of the winners on the playground of evolution. Thus, it is of importance to further our understanding of their biology, and to provide an in-depth species-level treatment of their taxonomy. The basis for that are modern revisions, providing the identification tools that can then be used for broad scale comparisons of ecological and distributional analyses, as well as for habitat monitoring and conservation purposes. In chapter 4 I provided the first revision for a subset of the Afrotropical Pheidole fauna, and the description of the pulchella group which contains the following seven new species: P. christinae sp. n., P. darwini sp. n., P. glabrella sp. n., P. heliosa sp. n., P. setosa sp. n., P. semidea sp. n., and P. rebeccae sp. n. I also revised the 4 earlier described species P. batrachorum Wheeler stat. rev. (earlier subspecies of P. dea), P. dea Santschi, P. nimba Bernard, and P. pulchella Santschi and proposed the subspecies P. pulchella achantella Santschi to be a synonym for P. pulchella Santschi. Based on a large amount of examined types, species and morphospecies from several localities and museum collections I also defined five preliminary species groups: Pheidole excellens group, P. megacephala group, P. nigeriensis group, P. aurivillii group and P. speculifera group. In comparison to how much of the African Pheidole fauna still needs to be revised, which will be at least another 132 valid species and subspecies and probably as many, or even more potentially new species, this may seem only a small accomplishment. And compared to the revisions that were already published for the New World (Wilson, 2003; Longino, 2009) and part of the South-East Asian Pheidole faunas (Eguchi, 2000; 2001a; 2001b; 2008; Eguchi & Bui, 2005; Eguchi et al., 2007; Sarnat, 2008) the taxonomic accomplishments for Africa are still highly under-represented. However, it is a first systematic attempt to provide a tool for both, experts and non-experts, with detailed descriptions, high-depth of focus images, a variety of measurements and an illustrated identification key for the two different worker castes. The Pheidole pulchella group is most certainly a group of related species that seems to be distributed over the large expanse of the Congo-Guinean rainforest system along the equator. It might also be interesting in future research and with newly collected material to find out about the exact distribution of this group, its history and biology. What we know is that some of these species are occurring in sympatry today, as for example Pheidole christinae and P. rebeccae in Budongo Forest in Uganda, or P. batrachorum and P. darwini in the Central African Republic. But it is not clear if these evolved in allopatric speciation, maybe during glacial-time forest isolations, and if they hybridize in their contact zones today, or if they are already genetically isolated. Species usually have geographically limited distributions for two reasons: either because they are adapted to narrow biological niches and ecologically limited in their distribution, or because they are spatially restricted from populating other areas by geographic barriers. This was for example observed in several endemic flightless montane insects, with some of them occurring just on a single mountain or in a mountain range, which is isolated from other montane forests (Brühl, 1997). These evolution-distribution relationships are not well investigated in ants and might be investigated in future phylogenetic studies.

Biodiversity conservation - conclusion

Modern organismal biology is dealing with a dilemma. On the one hand, new species are being discovered constantly and improved methods for their delimitation, which includes studies of their systematic relationships, contribute to a better identification and understanding of biodiversity in general. On the other hand biological diversity is disappearing at an alarming rate. Millions of species are probably undiscovered and waiting for scientific recognition, and there is still a high amount of uncertainty about the functions and processes that biodiversity performs in natural ecosystems. However, there is growing knowledge and understanding about the link(s) between species diversity and ecological processes and how important they are for the stability of natural ecosystems, and accordingly for the well-being of the human society. It seems that biodiversity conservation must find a way to provide both, protection of the few remaining undisturbed habitats from any human disturbance and protection of sustainably used low disturbance zones, where humans are able to interact with and profit from the services that nature provides, without endangering the functioning and the stability of its life-supporting processes. Finding the right balance will not be easy, but all hope is not lost.

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Scientific publications in peer-reviewed journals

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