GROUND-DWELLING ARTHROPODS IN A BIOSPHERE RESERVE: PATTERNS OF DIVERSITY AND CONSERVATION IMPLICATIONS.

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Thohoyandou

I swept the ground with the beam from my headlamp for signs of life, and found – diamonds! At regular intervals of several meters, intense pinpoints of white light winked on and off with each turning of the lamp. They were reflections from the eyes of wolf spiders, members of the family Lycosidae, on the prowl for insect prey. When spotlighted the spiders froze, allowing me to approach on hands and knees and study them almost at their own level. I could distinguish a wide variety of species by size, color and hairiness. It struck me how little is known about these creatures…Today a riot of diverse forms [of Lycosidae] occupy the whole world, of which this was only the minutest sample, yet even these species turning about now to watch me from the bare yellow clay could give meaning to the lifetime of many naturalists.

The Diversity of Life
E.O. Wilson

DECLARATION

I, Colin Schoeman, declare that this thesis is my own work and has not been submitted to another institution for a degree or any other qualification. I have followed the rules concerning referencing and citation in scientific writing.

Colin Schoeman

Date

DEDICATION

To my late grandmother, Marie "Miemie" Beukes who passed away on 18 February 2018, during the final stages of the preparation of this thesis.

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CONTENTS

ABSTRACT

Invertebrate diversity is often neglected in conservation planning initiatives. There are also very few large-scale diversity studies in Africa, with most studies being restricted to single properties and spatial extents that are on average not much larger than 30 km^2. Here, we provide a comparative regional assessment, two orders of magnitude larger than usual (30 000 km^2), of epigeal spider, beetle and millipede diversity in the Vhembe Biosphere Reserve – the largest biosphere reserve in South Africa, and one of the largest in Africa. Firstly we aim to provide an evaluation of the ability of a range of broad and fine scale predictors to explain the variation in the diversity of these taxa. Secondly, we measured cross-taxon congruence between our selected invertebrate taxa and woody vegetation, and within-taxon surrogate efficiency. Thirdly we evaluated performance of existing and proposed zonations in representing regional invertebrate species diversity. Finally, to aid in the development of species conservation profiles for lesser known taxa, annotated check lists are provided for two neglected but dominant epigeal beetle families, Tenebrionidae and Carabidae. Vegetation units explained the largest and most significant component of beetle and spider diversity (richness and complementarity of alpha and beta diversity). Elevation and mean annual temperature played a lesser but still significant role. Overall, woody vegetation was a poor surrogate, especially for millipedes which have several localized endemics. The use of higher taxa (genus and tribe in particular) shows the greatest potential for conservation planning. The current zonation of the Vhembe Biosphere Reserve performed significantly better than expected in representing invertebrate diversity across the region. The reality though is that conservation decision-making is largely informed by knowledge on the distribution of rare, localized or endangered species, for which detailed species inventories are

required. Though a coarse filter approach is recommended, the augmentation of species level data provides an extra filter, and contributes to our knowledge of what taxa are in urgent need of protection. Targeting rare and endangered species in transition zones and developing conservation assessments and plans for these in relatively small areas would compliment existing conservation initiatives in the VBR. Annotated check lists ofTenebrionidae of the Vhembe Biosphere suggest that the family is particularly speciose, the assemblage being comprised of an east African and a Kalahari element which contributes significantly to local endemicity, and yielded three new species, one of which is described in the revision to the genus *Anaxius*, a group largely restricted to the mountainous areas of Limpopo Province. Carabidae were also found to be speciose, with the assemblage comprised of a large proportion of stenotypic species. There is support for the use of vegetation types in conservation plans but these should be augmented with species level conservation initiatives that target particularly transition and buffer zones.

SUMMARY (TSHIVENDA)

MAVU ANE A DZULA ZWI KOKONONO KHA SHANGO LA VHEMBE

MANWELEDZO

Mabuvhi, magonono na madongololo ndi tshigwada tsha phambano khulu tshi re na ngundo thukhu dzo itiwaho Afurika. Vhunzi ha ngudo dzo itwa vhuponi ho tsireledziwaho kana mabulasini. Hafha ri nea mbambedzo ya u sedzesa tshiimo tsha zwikokovhi zwi no fana na mabuvhi, magonono na madongololo o fhambanaho a vhupo ha tsireledzo ha Vhembe – vhupo ho tsireledziwaho vhuhulusa ha Afurika Tshipembe, ha dovha ha vha vhuhulusa na Afurika. Ho kuvhanganyiwa zwikokovhi zwi no fana na magonono ano dzula mavuni, mabuvhi na madongololo nga kha milindi ye ya vha yo bwiwa kha tshipida tshi no lingana mithara dza zwigidi zwa mahumi mararu nga u angaredza. Tsha u thoma ro linga khonadzeo ya tshishumiswa tshi no talutshedza phambano dzi re kha tshigwada tsha zwikhokhonono. Tshavhuvhili, ro kala zwino fana kha zwigwada zwo fhambanaho vhukati ha zwigwada zwe ra zwi nanga na madaka a miri, ra kala na khonadzeo ya u imelelwa nga zwigwada zwihulwane.

CHAPTER 1

INTRODUCTION

Invertebrate Diversity and Conservation

The invertebrates, known colloquially as 'animals without backbones' are the most diverse group of organisms on our planet, comprising approximately 80% of all known animals (Gaston, 1991; Scheffers *et al*., 2012). The fact that we know so little about them is in itself a threat (Cardoso *et al*., 2011), as the greater proportion of estimated extinctions are those of still-undescribed species (Samways, 2002).

Amongst the invertebrates, the members of the Phylum Arthropoda are the most diverse and conspicuous taxa. The Arthropoda, or simply arthropods, include those invertebrates that are bilaterally symmetrical, coelomate and display protostomic embryonic development, and have a so-called exoskeleton, a hardened cuticle that has to be shed in order for the animal to grow. The body and hence the cuticle is segmented, with each segment specialized to perform a certain function. All, or certain of these segments, depending on the Class, referred to as tagma, may bear jointed appendages. The appendages are usually biramous (two pairs of appendages per segment) or uniramous (one pair of appendages per segment) (Hickman *et al*., 2011). We focused on three classes of arthropod for this study, namely Diplopoda, Araneae and Insecta (Coleoptera), mainly because taxonomic expertise was available for these taxa.

Challenged with what Chapin *et al*. (2000) has termed the 6th extinction event, conservation efforts nationally and internationally have responded by establishing more protected areas, extending the boundaries of existing reserves, and introducing land use management practices (and policies, in cases where these become law) that aim to maintain the planet's biodiversity (McNeely & Mainka, 2009), especially the other 99%, meaning the inconspicuous invertebrates (Lydeard *et al*., 2004). Despite global efforts to halt biodiversity loss, insect abundances have plunged by three-quarters over the past 25 years in Europe (Hallmann *et al*. 2017). In tropical forests in South America, declines of 45% have been recorded (Dirzo *et al*., 2014). Invertebrate diversity worldwide is threatened by a suite of drivers: global climate change, invasive alien species, pollution, and habitat degradation (Samways, 2007). The effect of drivers acting together can be greater than the sum of their parts and are thus synergistic (Schoeman & Samways, 2013). Most affected are specialists that require specific breeding conditions, localized food plants and narrow temperature ranges. Certain invertebrates, such as members of the Class Insecta within the Phylum Arthropoda, on which many of these studies are based because of their conspicuity, are responding to global climate change by shifting ranges polewards, and elevationally; in addition, phenological changes have also been observed in recent years (Parmesan, 2006; Perissinotto *et al*., 2011). Geographic shifts, which can otherwise facilitate the survival of species, are hindered through barriers of agricultural land-use, roads and urbanization. This has potentially catastrophic results for humanity because invertebrates maintain soil fertility, pollinate crops and maintain other important ecosystem services and functions.

Plant diversity and composition and arthropod diversity

Plant species diversity and composition maintains invertebrate species diversity (Blake *et al*., 2003; Schaffers *et al*., 2008; Uchida *et al*., 2016; De Palma *et al*., 2017), and is closely associated with habitat heterogeneity (Qian & Ricleffs, 2012). Habitat heterogeneity refers to plant architecture and form and floristic composition. Heterogeneity provides for niche differentiation, and survival of competitively inferior species (Tews *et al*., 2004). The loss of habitat heterogeneity affects highly localized, often flightless species at fine spatial scales, and widely dispersing species at coarser scales (De Palma *et al*., 2017). Plant diversity, especially associated with angiosperm radiation, is often cited as the most important driver of adaptive radiation in beetles (Bernhardt, 2009; Farrell & Sequeira, 2004). Mammal diversity has also contributed to diversity and endemism of dung beetles (Wirta *et al*., 2008), while the ants have driven radiations in both Paussinae (Carabidae) and Staphylinidae beetles (Moore & Robertson, 2014). Historical, phylogenetic and geographic processes also play an important role in driving richness and turnover of beetles (Barraclough *et al*., 1999; Ricklefs, 2006) and it is these processes that produce endemics, para-endemics and rare species (Hahn, 2007).

Despite the close association between plants and arthropods, conserving arthropods pose significant challenges: 1. We don’t fully understand what drive invertebrate diversity; 2. Invertebrate diversity is of such magnitude that we have to use other, less diverse groupings as proxies, called surrogates on which we can base decisions; 3. There’s not enough land to set aside for strict conservation, so we have to find other methods to manage landscapes for invertebrates (see Samways *et al*., 2010).

Drivers and predictors of diversity

Natural areas that are undisturbed have remained relatively stable for long periods of time, allowing assemblages to adapt to local conditions. This enables organisms to fully occupy habitats and niches in which they can obtain food, mates and shelter and generally thrive (Anderson, 1991). Drivers of biodiversity can be divided into two types, a.) those that reduce biodiversity (usually as a result of anthropogenic impacts) (Sala *et al*., 2000) and b.) those that maintain biodiversity (also termed predictors) (Tittensor *et al*., 2010). For this study we examined drivers that maintain biodiversity in the region.

The distribution and abundance of species are determined by resources and conditions, the predictors are either direct measures of these (e.g. temperature) or surrogates of these (elevation) Most trends we observe in community composition can be explained by predictors. Predictors can therefore be the classic set of environmental variables: temperature, elevation, latitude, precipitation, soil, and shade; in addition biotic interactions and resources: keystone species, mutualisms, symbioses, parasitism, competition and even the inherent biology of species can act as predictors in insect communities. Temperature, rainfall and latitude are globally the most significant predictors of biodiversity (Gaston, 2000). Gradients in predictors significantly alter the community from one ‘space’ to another ‘space’, and can include smaller scale variables, such as vegetation cover, rocks, leaf litter and soil (Gough *et al*., 1994; Schoeman & Samways, 2011; Gaiger & Samways, 2014). It is these predictors that often act as ‘drivers’ of diversity, not only of diversity at a point (alpha diversity), but also of the change in diversity over environmental gradients (beta diversity) (Koleff *et al*., 2003).

Olson *et al*., (2001) produced a detailed distribution map of the world's ecoregions. They distinguished 867 distinct units. These ecoregions are intended primarily as units for conservation action as they are considered likely to reflect the distribution of species and communities more accurately. Older maps of global biodiversity have been ineffective planning tools because they divide the Earth into extremely coarse biodiversity units. Within this global context understanding how arthropods respond to the distribution of plant communities within these units is an extremely valuable conservation tool. Such studies provide a framework for comparisons among key biodiversity units and the identification of representative habitats and species assemblages within them. In South Africa Mucina & Rutherford's (2006) habitat classification by vegetation types is commonly used for conservation planning and setting targets (Egoh *et al*., 2011).

Use of surrogates

Constraints on conservation planning due to lack of information on the distribution of species could be reduced by the use of habitat and taxonomic surrogates. Logistically it is not possible to account for all species so we need to know whether the diversity of different taxa is correlated (Vessby *et al*., 2007). Taxa that affect one another show cross taxonomic congruence, and can thus be referred to as surrogates. These surrogates are used to guide conservation planning with the expectation that broader biodiversity will be conserved (Rodrigues & Brooks, 2007; de Morais *et al*., 2018). The use of surrogate taxa in conservation planning is often questioned because the correlation of species richness between pairs of taxa is highly variable (Rodrigues & Brooks, 2007). Su *et al*. (2004) however found a positive correlation in community similarity using Mantel tests between pair wise comparisons of the taxa they studied. In other words sites with similar bird communities also had similar butterfly communities. There is evidence that plants show strong potential as surrogates for arthropod diversity (Foord & Dippenaar-Schoeman, 2016). In the context of large scale conservation planning measures of community similarity may be more appropriate than measures of species richness.

Biosphere reserves

Biosphere Reserves form a world-wide network of environmentally significant sites as their goal is the preservation of representative samples of notable ecosystems, original habitats and remnant populations (Coetzer *et al*., 2014). Biosphere Reserves promote three core functions: conservation, development and logistic support (Elbakidze *et al*., 2013). The biosphere reserve concept is seen as the best model to implement sustainable development with conservation (Coetzer *et al*., 2014; South African Development Community, 2018). Sustainable development is becoming an increasingly important approach in conservation planning because it is unlikely that much more land will be added to the world-wide network of formal protected areas in future. Even though 15% of the earth's surface is protected by reserves (IUCN, 2018), this still falls short of the targeted 17%.

Traditionally conservation meant the preservation of nature *in situ* by limiting human development within the boundaries of a reserve (Sodhi & Ehrlich, 2010). At present though, conservation through the ethical use of resources is also seen as important (Toledo & Burlingame, 2006). In a survey of 213 biosphere reserves globally, increased participation resulted in increased social acceptance of the reserve, which in turn resulted in more effective conservation (Van Cuong *et al*., 2017).

Arthropod conservation in biosphere reserves

South Africa is one of 17 counties in the world recognized as megadiverse by Conservation International (Brooks *et al*., 2006). South Africa has over 13,000 vascular plant species found nowhere else, and a host of endemic animal species (Living National Treasures, 2018). South Africa established its first biosphere reserve in 1998, the Kogelberg Biosphere Reserve. Since then five more have been established, including three in Limpopo Province alone: Waterberg Biosphere Reserve, Kruger to Canyons and Vhembe. The Vhembe Biosphere Reserve, the largest in the country, was designated in 2009. Vhembe is located in the far northernmost reaches of South Africa and includes the Soutpansberg, Blouberg and the northern part of the Kruger National Park. Ongoing efforts are being made to catalogue and map biodiversity in the region with the goal of identifying priority areas for conservation (Desmet *et al*., 2013; Pool-Stanvliet, 2013). The irony of the situation is that those areas identified as regional diversity hotspots are not formally protected. This is important not only nationally, but of international interest, because the area is so large and unique in terms of its biodiversity. We live in the Anthropocene (McGill *et al*., 2015). Anthropomorphic drivers, such as the location of the core, buffer and transition zones, will probably be a greater driver of biodiversity in the future than the large or fine scale natural drivers examined in this thesis.

Studies at small scales suggest relatively high levels of arthropod diversity occur in the Vhembe Region, where biodiversity assessments have yielded extraordinarily high numbers of species for spiders and ants (Foord *et al*., 2002, Foord *et al*., 2008, Munyai & Foord, 2013). The mountains are also a major centre of radiation for tenebrionid beetles such as *Anomalipus* and *Gonopus* (Endrody-Younga, 1988), harbour highly localized bee flies, an endemic dermapteran *Hemimerus*, and butterflies (*Dira swanepoeli*) (Scholtz & Holm, 2008). It is telling that many of the papers on arthropods of the region are descriptions of new species which include spiders (Jocqué, 2008; Haddad, 2009; Azarkina & Foord, 2013), and harvestmen (Schönhofer, 2008). In addition to this arthropod diversity, 44 bat species of have been recorded (Taylor *et al*., 2013) and over 500 tree species (Hahn, 1994).

Aims and Objectives

Our ignorance of arthropod diversity in conservation planning initiatives provides a main motivation for this thesis.

Where are the really diverse natural areas, how do they complement each other, where are the cradles of speciation and museums (endemic taxa are good indicators of these)? Does the current zonation of the Vhembe Biosphere Reserve adequately account for this? We therefore sought to describe the species diversity and distribution of selected groups of arthropods, explain which variables are important in driving diversity, and investigate how effective woody vegetation is as a surrogate for the selected arthropod groups.

Ultimately we examine the effect of scale on the efficacy of surrogates. Initially we examine broad scale processes and test whether vegetation types are good surrogates and then examine how surrogates perform at finer scales. The biological processes they generate vary at scale (Azaele *et al*., 2015). We therefore tested for surrogate efficiency across scale. Does an efficient broad-scale surrogate perform similarly well at finer scales? Ultimately we aim to evaluate the performance of diversity as explained by a variety of classifiable drivers – the natural classification based on vegetation, surrogates, or administrative / human classification as exemplified by the biosphere concept.

This thesis therefore examines variables that drive arthropod diversity at different spatial scales, and how this informs conservation planning of invertebrates within the context of a biosphere reserve in Africa. Chapter 2 describes the response of spider and beetle alpha and beta diversity to broad and fine-scale predictors in the Vhembe Biosphere Reserve. Chapter 3 investigates taxonomic congruence (of species richness and community composition) between woody plants and selected ground dwelling arthropods, and also assesses whether higher taxa are suitable surrogates for species level assemblage patterns and species richness. Chapter 4 assesses the success of the zonation of the VBR in terms of representing and protecting arthropod diversity. Chapter 5 and 6 provide a detailed conspectus of the darkling beetle and ground beetle fauna of the region. We do this to address a fundamental gap in knowledge on these groups as they are very poorly known and poorly represented in biodiversity surveys in Africa. The presence of humans in the biosphere reserve and the sustainable development component makes conservation a complex activity. In Chapter 7 we thus emphasize the importance of adequate zonation and implementation of suitable management strategies for each zone to safeguard biodiversity in the future. The Appendices provide a revision of the tenebrionid genus *Anaxius*, along with the description of new species of *Bantodemus*. New endemic species from these two genera were collected during this study and are valuable for determining conservation priorities in the Vhembe Biosphere Reserve.

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CHAPTER 2

VEGETATION TYPE IS THE BEST PREDICTOR OF EPIGAEIC SPIDER AND BEETLE DIVERSITY IN AN AFRICAN SAVANNA[1]

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Abstract: Spiders and beetles are mega-diverse taxa for which no standardized, large scale, spatial (> 30 000 km^2) diversity studies exist in Africa. Most contemporary studies are limited to a single property or reserve, and broad regional scale comparisons are confounded by differences in sampling protocols and timing. Here, for the first time, we provide a comparative regional assessment of patterns in epigeal spider and beetle diversity in the largest biosphere reserve in South Africa. More specifically we test the ability of a range of large and small scale predictors to explain the variation in the diversity of these two taxa. Epigeal spiders and beetles were sampled across an approximate spatial extent of 30 000 km^2. Replicated sampling units, consisting of pitfall trap grids, were stratified across the dominant vegetation units, aspects and elevational ranges of untransformed sites in the biosphere. The response of α- and β-diversity of the two taxa to broad (rainfall, vegetation type, longitude and latitude) and fine-scale predictors (vegetation structure, bare ground, leaf litter, carbon content of soil, canopy cover, topographic ruggedness) were modelled using Generalized Linear Mixed Effects Models (GLMM) for α diversity, and Canonical Correspondence Analysis (CCA) for β diversity. For both taxa, and both metrics (alpha and beta diversity) vegetation type was the best predictor. Generally alpha diversity increased to the east of the region, decreased to the north, and responded negatively to increases in topographic ruggedness and canopy cover. After accounting for the variation explained by vegetation type, spider and beetle assemblage composition was mainly related to elevation and mean annual temperature. These results show that vegetation type is a major determinant of invertebrate diversity observed and thus the size and isolation of areas conserved in each of these vegetation types would have important implications for the conservation of ground dwelling invertebrates.

Keywords: Araneae, Coleoptera, Vhembe Biosphere Reserve, vegetation type, α-diversity, β-diversity

Introduction

Quantifying alpha and beta diversity and the covariates that drive changes in these are central to the understanding of diversity and its conservation (Vanschoenwinkel *et al*., 2013). Identifying the relative roles of these covariates (Schweiger *et al*., 2005; Mykrä, 2007) and the various scales at which they operate (Cottenie, 2005) provides the empirical underpinnings for conservation biology as a science (Cottenie, 2005; De Meester *et al*., 2005).

Ultimately though, conservation success will be measured by our ability to assess the actual and potential value of sites for arthropods. Arthropoda is an invertebrate Phylum, comprised of four extant classes: Arachnida (spiders and scorpions), Myriapoda (millipedes and centipedes), Crustacea (isopods and amphipods) and Insecta (insects, such as dragonflies, grasshoppers, beetles, butterflies etc.) (Hickman *et al*., 2011). Most of the work that has been done on invertebrate conservation has focussed on members of the Class Insecta, and the term 'Insect Conservation' is often used as an umbrella term to include conservation of other arthropod groups as well (Samways, 2007). Invertebrates have become a major focus for conservationists because they are the most abundant and speciose component of ecosystems. Over 600 families of insects are extant, yet a quarter of all insects are under threat (Samways, 2007).

Schaffers *et al*. (2008) observed that there is an emphasis on the importance of the physical structure of habitat in explaining patterns of invertebrate diversity while Samways (2007) stresses the importance of habitat heterogeneity and quality in maintaining insect diversity in landscapes. Rarely however, is there a focus on the relationship between invertebrate and plant species richness and community composition (Biesmeijer *et al*., 2006).

Vegetation units are considered discrete spatial areas where plant species composition is presumed to be homogenous (Mucina & Rutherford, 2006). This provides the context to quantify conservation concern and set conservation targets. However, beta diversity in tropical ecosystems is so high that such delimitation may not be possible in all cases (Jankowski *et al*., 2009). The relationship between plant communities and insect diversity and assembly seems obvious, but few actual studies explore it in sufficient detail (but see Schaffers *et al*., 2008). Conservation targets based on the percentages and representation of vegetation units could therefore fail to represent the bulk of diversity in a region. Nevertheless, Schaffers *et al*. (2008) found that plant communities were significantly better at predicting arthropod diversity and turnover than habitat structure and heterogeneity. Similar results were obtained for ground-dwelling Carabidae in Scotland, where Blake *et al*. (2003) found that assemblages corresponded to the National Vegetation Classification of British plant communities. Whether this is also the case for tropical regions in the southern hemisphere remains unknown, as most invertebrate assemblage studies are focussed on the relationship between arthropod composition and variables that quantify habitat structure and diversity (Tews *et al*., 2004; Hendrickx *et al*., 2007), but not vegetation units as determined by floristic composition (Olson *et al*., 2001; Mucina & Rutherford, 2006; Schaffers *et al*., 2008).

Invertebrate communities are often too diverse and abundant to sample, which has led to the selection of better known taxa to represent entire invertebrate communities, a concept otherwise known as surrogates (Oliver & Beattie, 1996). Spiders are excellent surrogates for use in surveys for conservation purposes (Sauberer *et al*., 2004; Foord & Dippenaar-Schoeman, 2016), because they are major predators of other invertebrates (Dippenaar-Schoeman *et al*., 2012) that consume an estimated 400–800 million tons of insect prey annually (Nyffeler & Birkhofer, 2017). At last count more than 2200 spider species had been listed for South Africa (Dippenaar-Schoeman, 2014), which makes this a truly mega-diverse taxon.

Ground-dwelling beetles, in particular Tenebrionidae, Carabidae and Scarabaeidae, are very speciose and locally abundant. Carabidae are important predators of arthropods, with a few important seed feeders in the Harpaline and Chlaeniine lineages. Over 960 species of Carabidae are known to occur in South Africa (Picker *et al*., 2004) Tenebrionidae and Scarabaeinae are significant detritivores, with the latter specializing on the dung of large herbivores (Picker *et al*., 2004). In fact beetles, as a whole, can be regarded as an excellent biodiversity surrogate (Gerlach *et al*., 2013). The idea that spiders and beetles can represent overall biodiversity (including floral biodiversity) has rarely been tested (Oliver & Beattie, 1996), but studies have shown that better results are obtained when more than one taxon is used (Sauberer *et al*., 2004).

Large-scale comparisons of regional biodiversity are needed (Bartlett *et al*., 1999) because different species respond to habitats at different spatial scales (Holland *et al*., 2004). Several studies have assessed either spider or beetle diversity relative to vegetation type (Van Rensburg *et al*., 1999; Whitmore *et al*., 2002; Foord *et al*., 2008; Blaum *et al*., 2009) Nevertheless, there are very few standardized and comparable studies in Africa that have assessed spider and beetle diversity patterns at spatial extents greater than a reserve or farm (usually < 10 km^2) (Davis *et al*., 1999; Blake *et al*., 2003; Schaffers *et al*., 2008; Pryke & Samways, 2009).This is especially relevant within the savanna biome of Africa, which is undervalued and yet hosts the continent's most distinctive and threatened species (Parr *et al*., 2014). Therefore, in this study, we (i) quantify spider and beetle diversity across vegetation types in the largest biosphere of South Africa, the Vhembe Biosphere Reserve (VBR), with a spatial extent of 30 000 km^2, (ii) quantify the relative role of fine scale predictors of habitat heterogeneity (topography, ruggedness), broader-scale predictors (elevation, latitude, longitude, temperature) and vegetation type in explaining this variation; and (iii) assess whether these predictors are consistent between the two taxa.

Methods and Materials

The study site is located in the Limpopo Province of South Africa, bordering Botswana, Zimbabwe, and Mozambique, bounded by the Limpopo River (Fig. 1) (Pool-Stanvliet, 2013). The VBR comprises the Blouberg, Soutpansberg, and the northern Lowveld or Limpopo Valley, and the savannah plains south of the mountain range, including the northern sector of Kruger National Park (Fig. 1). It is the largest biosphere reserve in South Africa, with a spatial extent of 30 000 km^2, and also the least disturbed (Pool-Stanvliet, 2013). The savanna biome protected by the VBR is a hyper-diverse ecosystem (Hahn, 2017). The ancient landscapes of this region have remained stable for millions of years, containing relictual taxa that were once more widely distributed (Jocqué, 2008). In spite of being the most faunistically diverse, and harboring almost half of all South African spider species (Dippenaar-Schoeman *et al*., 2015), several areas in the Savanna biome of South Africa remain undersampled (Foord *et al*., 2011a,b), new species continue to be discovered (Jocqué *et al*., 2015), and the spider fauna remains poorly known (Foord *et al*., 2008, Muelelwa *et al*., 2010). Even less is known about beetles in the region, as no study has focussed on them in particular.

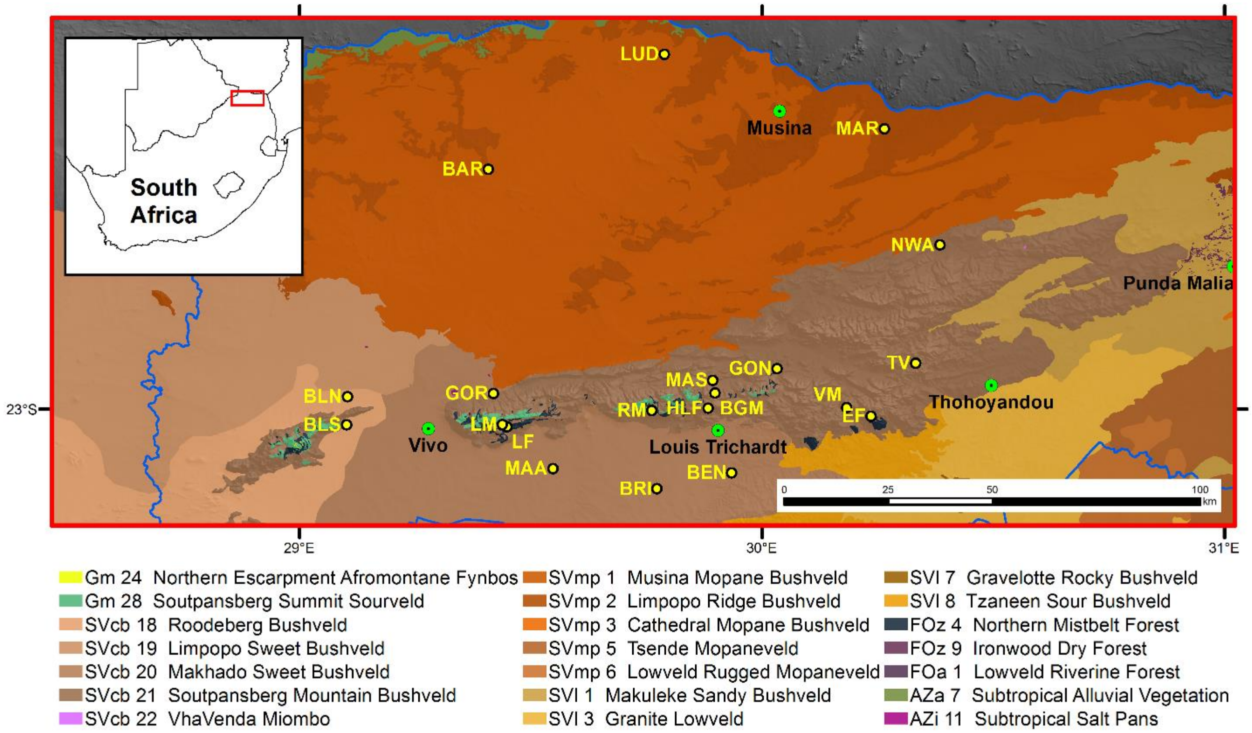

Figure 1. Map showing site localities within the Vhembe Biosphere Reserve (VBR), Limpopo Province, South Africa. Makhado Sweet Bushveld (3 sites), Soutpansberg Summit Sourveld (4 sites), Northern Mistbelt Forest (4 sites), Roodeberg Bushveld (2 sites), Soutpansberg Mountain Bushveld (4 sites), Musina Mopane Bushveld (2 sites), and Limpopo Ridge Bushveld (1 site).

Geology

Geomorphologically the study area is characterised by the Eastern Limpopo Flats representing a relatively flat featureless landscape (Partridge *et al*., 2010). To the south of the Limpopo basin the landscape abruptly rises above the surrounding landscape into two orographic features namely the Blouberg and Soutpansberg (Hahn, 2011). The Blouberg forms an isolated inselberg, its foothills characterised by scrub vegetation while gallery woodlands and thickets traverse the main drainage lines. To the east of the Blouberg, separated by a 40 km stretch of flat plains, lies the Soutpansberg, a 210 km mountain range characterised by a succession of predominantly east–northeast trending homoclinal ridges. The Soutpansberg boasts an incredibly diverse variety of habitats, which can range from Afro-montane forest to semi-desert scrubland along a less than 10 km north south transect (Munyai & Foord, 2015). The Soutpansberg habitat can best be described as forming a continuous mosaic. The south-western section of study area is characterised by the Polokwane Plain, also a flat featureless landscape of predominantly Savannah vegetation (Partridge *et al*., 2010). The south-eastern sites located at Ben Lavin Nature Reserve fall within an undefined geomorphological province lying between Polokwane Plain and the Great Escarpment to the east. This area is characterised by a broken landscape of predominantly bushveld vegetation.

Geologically the Limpopo valley is primarily of Archaean origin, while the mountains are of Proterozoic and Mesozoic. Remnants of the Karoo super-group, was moulded by successive dynasties of ice, sea, lake, swamp, desert and volcanic activity. Most of the soft Karoo rock has been eroded, exposing the ancient sediments of the Soutpansberg and Blouberg (McCarthy & Rubidge, 2005). The plains south of the Soutpansberg are Archaean in origin, mostly made up of metamorphic rock and are geologically comprised of Houtrivier Formation and Bandelierkop Complex.

Climate

Mean annual precipitation varies considerably in the region, peaked at 1250 mm at one study site (although it can reach 2000 mm at Entabeni) and decreases to 300 mm at the site with the lowest precipitation. Mean annual temperatures varies between 17 and 23 °C, is strongly correlated with elevation, while the relationship between precipitation and temperature is negative in the region. Higher elevation sites therefore receive more rainfall than the lower lying regions.

Vegetation and Sampling

Elevation, precipitation and temperature interact to produce distinct vegetation types in the region. These vegetation units occur in longitudinal east-west bands across the Biosphere Reserve (Fig. 1). The Polokwane Plain and Eastern Limpopo Flats harbour geographically large, and continuous plant communities (Fig. 1). We stratified 20 sampling sites across the major vegetation units (Mucina & Rutherford, 2006) and longitudinal extent that the vegetation type covers in the Biosphere Reserve (Fig.1). These were: Makhado Sweet Bushveld (3 sites), Soutpansberg Summit Sourveld (4 sites), Northern Mistbelt Forest (4 sites), Roodeberg Bushveld (2 sites), Soutpansberg Mountain Bushveld (4 sites), Musina Mopane Bushveld (2 sites), and Limpopo Ridge Bushveld (1 site).

All the sites were sampled during November 2012 – January 2013, which falls within the start of the rainy season in the region. Each site consisted of eight sampling units (SU’s) which were spaced more than 300 m apart to ensure independence of samples (Agosti *et al*., 2000). The eight SU’s were all within the same vegetation type. Each SU comprised of five pitfall traps that were regularly spaced in a pentagon with 10 m between each pitfall. Pitfalls were used because it expends the least amount of input with a greater comparable output than any other sampling method (Agosti *et al*., 2000). The pitfalls of each SU were too close to each other to be considered independent and were therefore pooled in the analysis. The unit for data analysis is therefore the SU, for a total of eight SU’s per site × 20 sites = 160 assemblages.

Pitfalls (70 mm diameter, and 120 mm deep) were dug into the ground and quarter filled (100 ml) with propylene glycol. Traps were left open for seven days, after which the contents were collected, washed using a fine net, and stored in 96% ethanol. The 1 m^2 area around each pitfall was imaged and the following variables estimated: percentage leaf litter cover; canopy cover; habitat complexity (scored from 1 (bare ground), 2 (grass cover), 3 (grass cover, and small bushes), 4 (grass cover, large bushes) to 5 (thicket, forest); substrate or soil type (scored as 0: gravel, 1: sand 2: loam, 3: clay, 4: mulch); mean annual temperature; precipitation and elevation variables were extracted from the CliMond Archive (Hutchinson *et al*., 2009; Kriticos *et al*., 2012; Kriticos *et al*., 2014). Topographic complexity was represented by the ruggedness index (Riley *et al*., 1999). The latter as well as slope and aspect were calculated using ArcGIS (ESRI, 2011).

Identification of spider and beetle specimens

Spiders were identified to species or morpho-species level by A.S. Dipennaar-Schoeman. All spider specimens were deposited in the National Collection of Arachnida (NCA) of the Plant Protection Research Institute, Agricultural Research Council, Pretoria. For beetles, we focused on the three dominant families: Carabidae, Tenebrionidae and Scarabaeidae. Tenebrionidae and Carabidae were identified to genus and species level by Ruth Muller (Ditsong National Museum of Natural History) and Mary-Louise Penrith (retired entomologist), Scarabaeidae were determined by Adrian Davis (University of Pretoria). Beetle specimens were deposited in the Ditsong National Museum of Natural History and the University of Venda.

Beetle and spider species richness

Species richness and coverage per site were estimated using iNext (Chao & Jost, 2012; Hsieh *et al*., 2013). Coverage is the total number of individuals in a community that belong to the species represented in the sample; the complement of coverage is the probability that the next individual sampled will be a species that has not been sampled before (Chao & Jost, 2012) (Appendix 1).

Coverage ranges from 0 (no coverage) to 1 (complete coverage). A coverage estimate of 1 means that all species in the sampled area (also known as sample grain (see Samways *et al*., 2010)) has been obtained. A sample coverage of 0 is obtained for samples from which very few specimens have been obtained, and may indicate that a sample cannot be included in multivariate analysis.

All numeric explanatory variables were centred around the mean and standardized. This allows for greater interpretability of coefficients (Schielzeth, 2010). Collinearity between environmental variables was assessed using a corellelogram. If two variables had a significant Pearson's Product Moment Correlation larger than 0.5, the variable that was considered biologically more meaningful was retained (Appendix 2). Mean annual temperature (MAT) co-varied significantly with precipitation, latitude and elevation, and only MAT was retained as a co-variate. Similarly leaf litter cover was significantly related to soil type and canopy cover and we therefore retained leaf litter. The ruggedness index and slope class co-varied and we excluded slope from the analysis (Appendix 2).

A distinction was made between fine and broad scale predictors. The former included leaf litter cover, vegetation complexity and ruggedness and is related to variables that can have a grain of less than 20 m^2 and that can vary non-linearly between sites, whereas broad-scale variables were typically linear, such as longitude, measured at a grain that included all the SU's of a site. Longitude provides some measure of the distance between sites which is particularly relevant here, as distances between sites in different vegetation types were often smaller than between sites within the same vegetation type because of the longitudinal extent of vegetation types in the region (Fig. 1). Vegetation type was included as a categorical variable. The response of richness to these predictors was modelled using Generalized Linear Mixed Effects models (GLMM) with a log-link function and Poisson error distribution, using the function ‘glmer’ in the package nlme (R Core Development Team, 2016). Observed richness values were weighted using coverage. The dredge function in the MuMIn library was used to rank all candidate models using the Bias-corrected Akaike information criterion (AICc). Sites were included as a random factor. Marginal R^2 (R^2_m), measuring variation explained by fixed effects only, and conditional R^2 (R^2_c), measuring variation explained by both fixed and random factors (Nakagawa & Schielzeth, 2013) were calculated for the best model. All model residuals were inspected for the following assumptions: constant mean-variance relationships, normality and independence.

Beetle and spider community structure

The role of environmental variables in structuring ground-dwelling spider and beetle community composition (or change in the identities of species) was determined using multivariate analysis of abundance data. Ordination diagrams with all the measured variables were produced using the CANOCO© software (Lepš & Šmilauer, 2003). Scaling was selected for between species distances, as explained by the measured environmental variables (Fig. 5).

Canonical Correspondence Analysis (CCA) is a direct gradient analysis technique that uses multiple regressions to select linear combinations of environmental variables that account for most of the variation in the species scores on each axis. Therefore, the diagram visually relates the pattern of variation between species and environmental variables (Lepš & Šmilauer, 2003). Species that made up less than 1% of the total abundance were removed. A Monte-Carlo permutation test was conducted to identify predictor variables that explained a significant amount of variation in spider and ground-dwelling beetle community composition and provided an estimate of the significance of the first and second axes in explaining variation assemblage structure (Lepš & Šmilauer, 2003).

Results

A total of 2624 spiders, representing 217 species and 47 families were sampled; Gnaphosidae (39 species), Lycosidae (28 species), Zodariidae (23 species) and Salticidae (22 species) were the most diverse families. These four families represent 57% of the overall abundance. There were 260 beetle species in the three families and altogether 14109 individuals were sampled: 59 carabid, 119 scarabaeid, and 82 tenebrionid species. Scarabaeidae was the most abundant beetle family (9567 individuals), followed by Tenebrionidae (3885 individuals) and Carabidae (657 individuals).

Coverage for beetles was almost twice as high as that of spiders (Fig. 2), with spiders averaging at 0.49 (range = 0 – 0.83, SD = 0.02) and beetles 0.88 (0.22 – 1, SD = 0.13). Beetles were also slightly more species rich at a SU (10.7, SD = 0.5) in comparison to spiders (9.02, SD = 0.4) (Fig. 2, Appendix 1).

Richness (α-diversity) of spider and beetle diversity across vegetation types

Patterns of richness across the vegetation types were mirrored in the two taxa (Fig. 2), peaking in Makhado Sweet Bushveld (MSB), and Roodeberg Bushveld (RB) and decreasing significantly in the higher elevation sites of the Northern Mistbelt Forest (NMF) and Soutpansberg Summit Sourveld (SSS) (Fig. 2). Spider richness was also relatively low in the Limpopo Ridge Bushveld (LRB) and the Soutpansberg Mountain Bushveld (SMB) (Fig. 2). Forests had the lowest richness for spiders and beetles (Fig. 2).

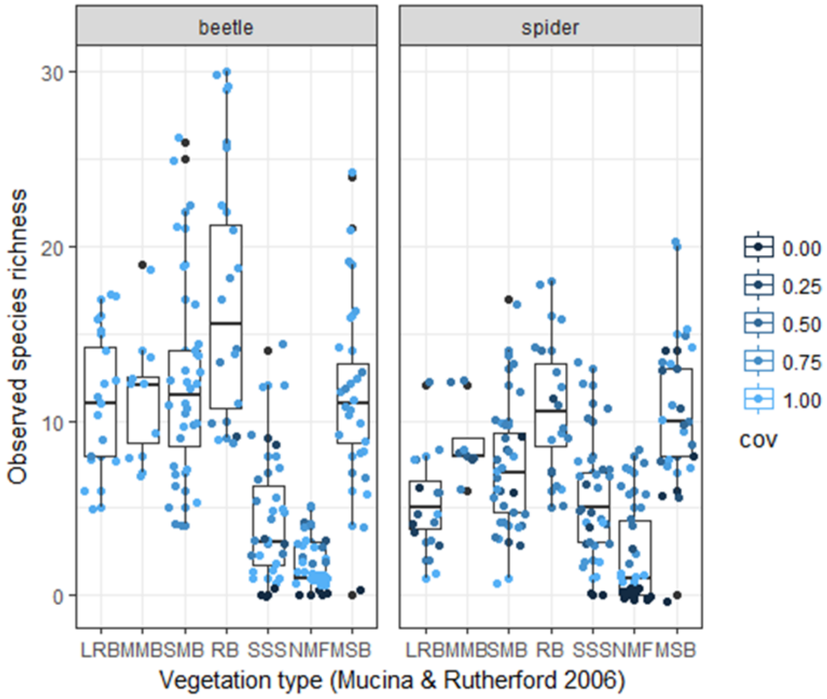

Figure 2. Box and jitterplots of observed spider and beetle richness in each of the vegetation units of the study area. Vegetation types on the x axis are arranged from north to south. LRB = Limpopo Ridge Bushveld, MMB = Musina Mopane Bushveld, RB = Roodeberg Bushveld, SMB = Soutpansberg Mountain Bushveld, SSS = Soutpansberg Summit Sourveld, NMF = Northern Mistbelt Forest, MSB = Makhado Sweet Bushveld. Legend: COV = coverage.

The effect of fine and broad scale predictors on species richness

The weight of co-variates in component models of species richness were the lowest for vegetation complexity and peaked at one for leaf litter cover, the ruggedness index and vegetation type. This was true for both taxa (Table 1 & 2). These three co-variates were also included in the best candidate models. The best model for beetles included vegetation type, leaf litter cover and ruggedness as predictors (Table 1), the latter two variables negatively affected beetle richness (Fig. 3). There was also a weak east-west gradient in beetle diversity, with diversity decreasing towards the east. This contrasts with spiders where spider diversity generally increased to the east.

Table 1. Best models of the relationship between beetle species richness and environmental predictors. Only the best models are shown, judged using Akaike information criterion or AICc values. The best model is judged to be that within an AICc value of 2 or more units lower than any other model. The weighting of environmental variables in all the component models are also shown.

Variables							df	AICc	ΔAICc
	Vegetation complexity	Mean annual temperature	Longitude	Ruggedness index	Leaf litter cover	Vegetation type			
Model 1 (best model)				$P < 0.001$	$p < 0.001$	$p < 0.001$	10	729.3	0
Model 2			n.s.	$P < 0.001$	$p < 0.001$	$p < 0.001$	11	729.8	0.5
Model 3		n.s.		$P < 0.001$	$p < 0.001$	$p < 0.001$	11	731.2	1.9
Weighting	0.26	0.27	0.43	1	1	1			

Best model: Species richness = $e^{2.1 (\pm 0.1) - 1.01 (\pm 0.21) \text{ NMF} - 0.5 (\pm 0.13) \text{ RB} + 0.34 (\pm 0.12) \text{ SMB} - 0.64 (\pm 0.14) \text{ SSS} - 0.18 (\pm 0.04) \text{ Leaf litter cover} - 0.26 (\pm 0.06) \text{ Ruggedness index}}$, $R^2_m = 0.83$ $R^2_c = 0.8402887$

Table 2. Best models for the response of spider species richness to environmental predictors. Only the best models are shown; judged using Akaike information criterion (AICc) values. The best model is judged to be that within an AICc value of 2 or more units lower than any other model. Weighting of environmental variables in all the component models are also shown.

Variables							df	AICc	Δ AIC_c
	Vegetation complexity	Mean annual temperature	Longitude	Ruggedness index	Leaf litter cover	Vegetation type			
Model 1			ns	ns	ns	$p < 0.05$	11	504.5	0
Model 2 (best model)					$p < 0.05$	$p < 0.05$	9	504.9	0.5
Model 3				ns	$p < 0.05$	$p < 0.05$	10	504.2	0.7
Model 4			ns		$P < 0.05$	$P < 0.05$	10	505.4	0.9
Model 5			ns	$P < 0.05$		$P < 0.05$	10	505.9	1.4
Model 6				$P < 0.05$	$P < 0.05$		4	506.1	1.6
Model 7		ns			$P < 0.05$	$P < 0.05$	10	507.3	1.8
Weighting	0.25	0.29	0.47	0.61	0.76	0.84			

Best model: Species richness = $e^{2.1 (\pm 0.1) - 1.01 (\pm 0.21) \text{ NMF} - 0.5 (\pm 0.13) \text{ RB} + 0.34 (\pm 0.12) \text{ SMB} - 0.64 (\pm 0.14) \text{ SSS} - 0.18 (\pm 0.04) \text{ Leaf litter cover} - 0.26 (\pm 0.06) \text{ Ruggedness index}}$, $R^2_m = 0.48$ $R^2_c = 0.63$

Temperature was found not to be a significant variable affecting species richness. Fixed factors explained 21% of the variation in beetle species richness ($R^2m = 0.21$, $R^2c = 0.67$). There were considerably more candidate models for spider richness (Δ AICc < 2, Table 2). Apart from vegetation type, only leaf litter cover was included in the best model for spiders (Table 2) which negatively affected species richness (Fig. 3). Once again vegetation type had the largest weighting overall (Table 2) and together with leaf litter explained 48% in the variation of species richness ($R^2_m = 0.48$, $R^2_c = 0.63$).

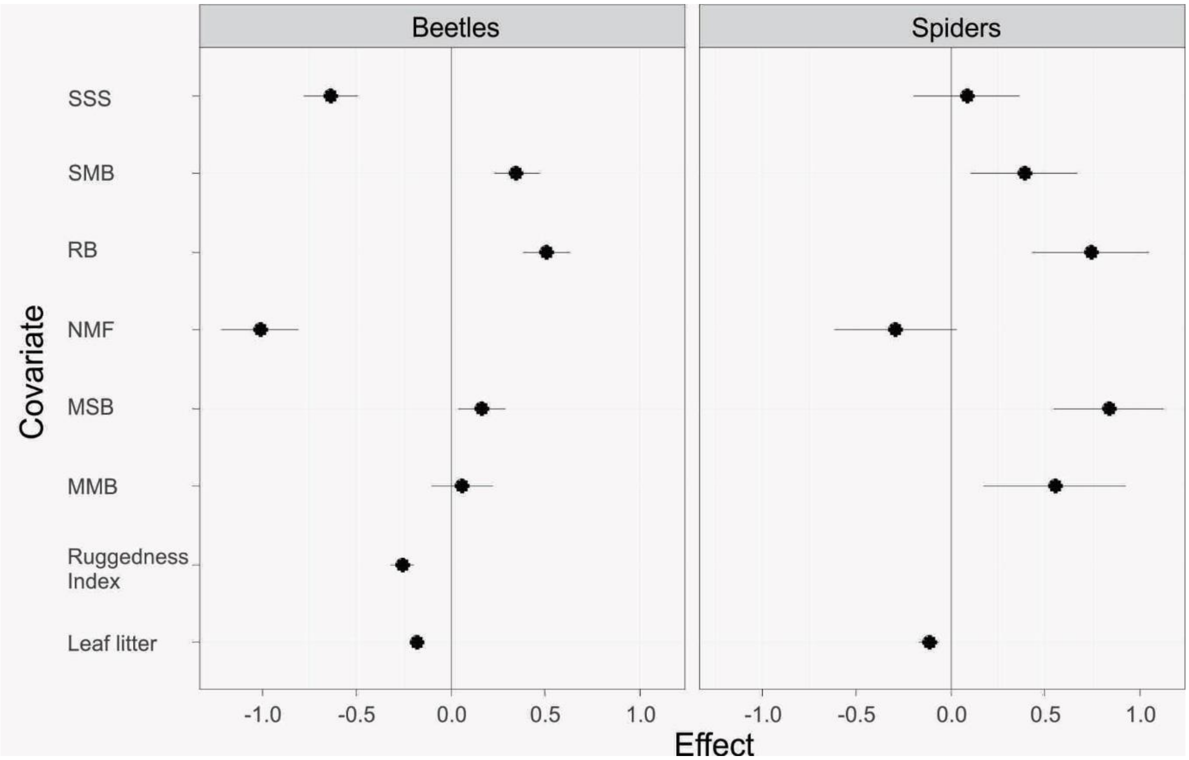

Figure 3. Effect sizes of covariates that were included in the best model on species richness for spiders and beetles. Error bars not overlapping zero are significant. Sites were included as random factors. SSS: Soutpansberg Summit Sourveld, SMB: Soutpansberg Mountain Bushveld, RB: Roodeberg Bushveld, NMF: Northern Mistebelt Forest, MSB: Makhado Sweet Bushveld, MMB: Musina Mopane Bushveld.

The effect of fine and broad scale variables on community composition (β-diversity)

The effect of vegetation types on beetle and spider species assemblages indicates that vegetation types drive variation in communities for these taxa. Forward selection on Monte Carlo permutation tests show that vegetation units had a generally greater effect on the structuring of beetle and spider community composition (Tables 4 and 5) followed by large scale variables. Makhado Sweet Bushveld, Roodeberg Bushveld, Musina Mopane Busveld were also important drivers for both beetle and spider community composition (Tables 3 and 4). Soutpansberg Mountain Bushveld emerged as an important variable for spiders (Table 4), but not for beetles (Table 3). Unlike beetles, some micro-habitat variables such as leaf litter cover and soil type were significant in structuring spider communities.

Broad scale variables had a significant effect on change in spider community assembly (Table 4). Separate vegetation units (Northern Mistbelt Forest, Soutpansberg Sourveld, Limpopo Ridge Bushveld and Musina Mopane Bushveld) and broad scale environmental variables (longitude, mean annual temperature) had p-values equal to 0.002. Fine scale variables that played a role in community assembly are leaf litter cover and soil type ($p = 0.002$). Spider species strongly associated with high temperatures were *Ibala lepidaria* and *Capheris decorata*, while species strongly associated with ruggedness were *Segregara paucispinulosus* and *Cydrela spinifrons*; *Stenaelurillus natalensis* had a strong positive relationship with both ruggedness and temperature (Fig. 4).

Despite an observed decrease in spider richness with increased canopy cover and ruggedness in the best models, *Segregara paucispinulosus* was strongly associated with these variables, and may be regarded as a specialist. Termite specialist spiders (*Ammoxenus psammodromus* and

Ammoxenus amphalodes) illustrate the importance of termites in driving community composition in the savanna biome of Africa (Dippenaar-Schoeman *et al*., 1996a; Dippenaar-Schoeman *et al*., 1996b). Temporal variation of these spiders was observed in a study conducted in the Cederberg, indicating that genera like *Ammoxenus* are dependent on fluctuations of termite abundances (Foord & Dippenaar-Schoeman, 2016).

Table 3 Environmental variables that explained a significant amount of variation in beetle assemblage composition using forward selection CCA (conditional effects). LRB = Limpopo Ridge Bushveld, MMB = Musina Mopane Bushveld, MSB = Makhado Sweet Bushveld, NMF = Northern Mistbelt Forest, RB = Roodeberg Bushveld, SMB = Soutpansberg Mountain Bushveld, SSS = Soutpansberg Summit Sourveld, lat = latitude, long = longitude, T = temperature, P = precipitation, RI = ruggedness index, El = elevation, LL = leaf litter, SC = slope, AS = aspect, VC = vegetation complexity, OC = soil type, SH = canopy cover.

Variable	Variance explained	P-value	F
NMF	0.8	0.002	32.6
T	0.35	0.002	15.92
MSB	0.27	0.002	13.75
MMB	0.17	0.002	9.18
lat	0.1	0.002	5.4
long	0.09	0.002	5.33
LRB	0.08	0.002	4.87
P	0.07	0.002	3.82
SSS	0.04	0.002	2.86
SH	0.04	0.01	2.4
AS	0.03	0.052	2.06
RI	0.04	0.02	2.44
LL	0.03	0.038	1.94
RB	0.03	0.07	1.69
VC	0.02	0.12	1.51
OC	0.02	0.234	1.22
El	0.02	0.468	0.96
SC	0.01	0.782	0.64

Beetles Eigenvalues: 1st axis = 0.837, 2nd axis = 0.596

Vegetation units are the main drivers of variability in ground-dwelling beetle communities. Monte Carlo permutation tests show that vegetation units had a generally greater effect on the structuring of beetle community composition (Table 3) than fine-scale environmental variables did. Assemblages in the Northern Mistbelt and Soutpansberg Summit Sourveld housed communities that were very distinct from the other sites, although here temperature plays a role in structuring community assemblages across various environmental gradients. Makhado Sweet Bushveld, Roodeberg Bushveld and Musina Mopane Bushveld were also important drivers of beetle community composition (Table 3).

Table 4 Environmental variables that explained a significant amount of variation in spider assemblage composition using forward selection CCA (conditional effects). LRB = Limpopo Ridge Bushveld, MMB = Musina Mopane Bushveld, MSB = Makhado Sweet Bushveld, NMF = Northern Mistbelt Forest, RB = Roodeberg Bushveld, SMB = Soutpansberg Mountain Bushveld, SSS = Soutpansberg Summit Sourveld, lat = latitude, long = longitude, T = temperature, P = precipitation, RI = ruggedness index, El = elevation, LL = leaf litter, SC = slope, AS = aspect, VC = vegetation complexity, OC = soil type, SH = canopy cover.

Variable	Variance explained	P-value	F
NMF	0.6	0.002	3.5
lat	0.4	0.002	2.37
SSS	0.36	0.002	2.18
long	0.27	0.002	1.6
LRB	0.26	0.002	1.59
MMB	0.3	0.002	1.78
T	0.27	0.002	1.67
P	0.26	0.002	1.6
LL	0.24	0.002	1.45
El	0.23	0.062	1.44
OC	0.23	0.002	1.39
RB	0.21	0.02	1.32
RI	0.21	0.046	1.29
MSB	0.19	0.078	1.18
AS	0.19	0.092	1.14
SC	0.18	0.162	1.14
SH	0.15	0.596	0.95
VC	0.13	0.946	0.81

Spider Eigenvalues: 1st axis = 0.627, 2nd axis = 0.480

Species strongly associated with increased temperature were *Allogymnopleurus thalasinus* and *Onthophagus sagilatus*; *Onthophagus* sp. Y was strongly associated with longitude. Species strongly associated with soil type were *Anachalcos convexus* and *Scarabaeus schultzi*, a Soutpansberg endemic; *Wahlbergiana alternans*, endemic to the Afromontane forests of the Soutpansberg was strongly associated with ruggedness. Temperature and longitude acting together had a strong effect on *Gymnopleurus humeralis*, *Onthophagus* sp. C and *Zophosis* sp. C (Fig. 4) (See Appendix 3 for species and species codes used in Fig. 4).

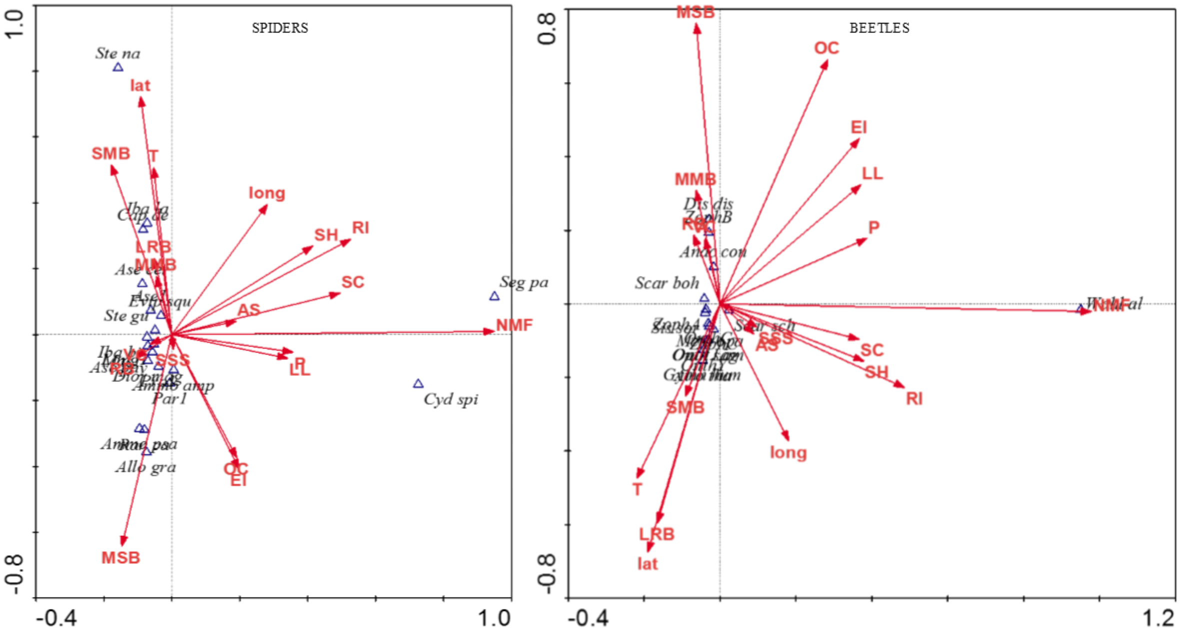

Figure 4. Canonical correspondence analysis illustrating the effect of environmental variables on spider and beetle community composition of the most abundant species. Scaling is focused on inter-species correlations. LRB = Limpopo Ridge Bushveld, MMB = Musina Mopane Bushveld, MSB = Makhado Sweet Bushveld, NMF = Northern Mistbelt Forest, RB = Roodeberg Bushveld, SMB = Soutpansberg Mountain Bushveld, SSS = Soutpansberg Summit Sourveld, lat = latitude, long = longitude, T = temperature, P = precipitation, RI = ruggedness index, El = elevation, LL = leaf litter, SC = slope, AS = aspect, VC = vegetation complexity, OC = soil type, SH = canopy cover. See Appendix 3 to see species name corresponding to code.

Discussion

Spider and beetle species richness was best predicted by vegetation type, and was negatively affected by increases in ruggedness and canopy cover. Vegetation types on the foothills and pediplain had more species than those on the Soutpansberg Mountain, and species richness was less than expected in the forests and more than expected in the Mopane Shrubland of the Limpopo Valley. At the scale of this study much of the variation in community composition in both taxa was explained by vegetation type followed by larger scale predictors such as longitude and temperature, while the only significant fine scale variables were soil type and leaf litter.

Very few studies have evaluated diversity patterns of ground dwelling invertebrates at spatial extents as large as that of the VBR. Because of this there is little consensus on the relative roles of fine scale habitat heterogeneity, topography and large scale vegetation or habitat type on structuring invertebrate species richness and community composition. Understanding these drivers and correlates of invertebrate diversity has important implications for how biodiversity is mapped, managed and conserved. We need to understand the extent to which these co-variates drive species before including them in biodiversity plans. This requires that we have some knowledge of how species are distributed within (fine-scale) and between (large scale) vegetation units. Large scale selection of conservation units has been found to be remarkably effective in conserving regional biodiversity (Rouget, 2003; Schaffers *et al*., 2008; Ramos *et al*., 2018). However, species may be patchily distributed, and preserving only part of a vegetation unit may miss an important component of the unit's species. This is why it is important to supplement course scale conservation strategies with fine scale data on patterns of invertebrate diversity (Lombard *et al*., 2003; Barton *et al*., 2011).

Both Blake *et al*. (2003) and Schaffers *et al.* (2008) reported that vegetation type emerged as the best predictor variable for arthropod community composition in northern Hemisphere countries. Carvalho *et al*. (2011) found that broad scale environmental gradients drove Mediterranean spider species richness. Van Rensberg *et al*. (1999) (dung beetles) and Botes *et al*. (2007) (Tenebrionidae and Carabidae) found that habitat type or vegetation units were strongly predictive of beetle community assembly. Botes *et al*. (2007) also found a strong east-west gradient in richness among Tenebrionidae, observing that the decline in richness towards the east reflected movement away from the southwest African centre of tenebrionid diversity. This trend in tenebrionid richness in particular is reflected southwards from the south of Angola, through to the Caprivi Strip in Botswana to the northern boundaries of the VBR along the Limpopo River (Koch, 1962). Rouget (2003) also found that selecting broad scale vegetation types in the Cape Floristic Region was relatively effective in representing plant species diversity. Our results for the VBR are especially remarkable considering that physical distance between sites within the same vegetation type were much larger than between sites of different vegetation types, i.e. nearest neighbour sites were often in different vegetation types. This may be because floral assemblages ultimately determine spatial structure which increases diversity by localizing the impact of organisms on their environment (Amarasekare, 2003), as well as the historical context in which communities get assembled. Vegetation units or types are important drivers of species richness and community composition because they integrate all other environmental variables (Schaffers *et al*., 2008), such as climate (rainfall, temperature, evaporation), soil type, and terrain, such that they form a relatively homogenous bioregional unit. Rouget (2003) and Foord *et al*. (2003) found however that a much finer scale of classification of vegetation types was better at representing unique assemblages and rare species, including endemics. Carvalho *et al*. (2011), Van Rensberg *et al*. (1999) and Botes *et* *al*. (2007) did not explore the invertebrate assemblages they sampled in terms of narrow endemism, high compositional turnover, or climatic and disturbance history which can result in relictual populations (but see Foord & Dippenaar-Schoeman, 2016). Detailed analysis of the faunal assemblages of the region (see Chapter 5 and 6) suggest that the survival of certain species is dependent on fine scale habitat features, e.g. the endemic carabid beetle *Wahlbergia alternans* occurs mostly under moist rocks in the Afromontane forests. MacLeod *et al*. (2004) have also shown that fine scale refuges and shelters are essential for the maintenance of carabid assemblages. Similarly, Barton *et al*. (2010) found that two different species of co-occurring eucalyptus supported different assemblages of litter-dwelling beetles.

The low diversity we observed at higher elevations is strongly associated with ruggedness, and emerged as a covariate of elevation during the data analysis. A decrease in species richness with elevation has been recorded for several studies (Theurillat *et al*., 2003; Munyai & Foord, 2015; Classen *et al*. 2015). This decrease is hypothesized to be driven by decrease in temperature which lowers the activity of ectotherms at higher elevations, reduction in possible habitat (e.g. mountain tops), and a decrease in resource abundance associated with reduced habitat size (Classen *et al*., 2015). Although richness often decreases with elevation, there is also a definite increase in complementarity with elevation, so that sites on the mountain are distinct, harbouring a considerable number of endemics (Munyai & Foord, 2015. Muluvhahothe *et al*., in review)

Although species poor, a distinct community was associated with leaf litter cover which is linked to canopy cover. We may have observed a decrease in richness with leaf litter content because pitfall traps catch invertebrates that tend to be more active. Some of the litter dwelling invertebrates might not be active enough to fall in the pitfalls and we might have better sampled them using leaf litter sampling. This assertion is further supported by the observation that there were few very few collembolans and Staphylinidae in samples for this study. These are normally abundant faunas associated with leaf litter (Geralch *et al*., 2013; Janion-Scheepers *et al*., 2016). A study by Maudsley *et al*. (2002) found high numbers of Carabidae in leaf litter in hedgerows in England. Speciose carabid taxa associated with leaf litter and recorded from the region (Harpalinae, Chleiniinae, Pterostichinae and Orthogoniinae) were very poorly represented in our samples. Another limitation of this study is that we did not measure soil moisture. Maudsley *et al*. (2002) found that soil moisture was a major fine scale determinant in community assembly in hedgerows, and we may have found similar results for this study.

In contrast to our main findings, various authors have found that spiders are driven mainly by finer scale processes (Clough, 2005; Horváth *et al*., 2015). Those studies were, however, carried out in highly modified landscapes where responses may be different and communities may have been substantially altered. The relative importance of environmental variables in structuring these altered communities remains largely unexplored (Sarthou *et al*., 2014). Soininen (2016) showed that dispersal ability is limited for spiders over large areas. (Although Aisen *et al*. (2017) considers that spiders are good dispersers.) This may be explained by highly localized availability of resources (Wise, 2006; Saxer *et al*., 2009) with the resultant observation of distinct communities. Spider community assembly may be more affected by fine scale variables such as shade, soil composition and moisture, leaf litter, etc. where resources are limited, particularly in landscape mosaics of semi-natural and modified habitats. Other factors that may covary, that are temporally ephemeral (such as termite colonies in the veld) may also shape the spider faunas of the savannah biome of Africa (Foord & Dippenaar-Schoeman, 2016).

In our study more diversity was explained for beetles than spiders and this was in the case of both richness and beta diversity. Much more variation was explained for beetles by fixed factors than for spiders, indicating that for spiders, site specific effects have a greater impact on richness. Bonn *et al*. (2004) found that ground beetle species assemblages varied more than for spiders according to different flood regimes in a study on European riparian habitat. The fact that coverage was better for beetles is a direct result of the fact that we caught considerably more beetles than spiders. Pétillon *et al*. (2008) found similar results for carabid and spider communities in salt-marsh ecosystems in France. Robertson *et al.* (2011) however found 72 beetle species and 128 spider species, but these were from plots invaded by *Opuntia stricta* which was shown to have had a negative impact on beetle species richness.

The Savanna biome of Africa is very species rich, and still forms a largely contiguous system from east Africa all the way to the central bushveld of South Africa (Parr *et al*., 2014). It may not remain so for long however. Various threats are posed to the savanna including mining, overgrazing and erosion, fragmentation, global warming (Bond & Parr, 2010). Agriculture remains the biggest threat however. From an original extent of 13.5 million km^2, 22% had been lost by 2000, and since then another 50% has been transformed to new cropland and villages (ESA, 2010; Riggio *et al*., 2013).

We need further research on the minimum viable habitat area for invertebrate communities to persist in these ecosystems (to avoid ecological relaxation (Samways, 2005)), as it is highly likely that existing reserves and game management areas will become increasingly isolated as the surrounding savanna is transformed for agricultural land use (Newmark, 2008). Landscape modification outside (and often inside) reserves restricts the movement of wildlife – which is likely to mirror the situation with invertebrates. Habitat modification outside reserves is likely to have an impact on specialists restricted to small vegetation units such as grassland and forest fragments which rely on stepping stone habitats occurring outside reserves. In fact, in Malawi, protected areas are visible from Google Earth because the surrounding areas have been so overgrazed (Juffe-Bignoli *et al*., 2004). A study in Malaysia found that approximately 40 km^2 was needed to conserve the ant community intact (Brühl *et al*., 2003). We need to understand these processes for invertebrates, because it won't be possible to use charismatic carnivores and megaherbivores as flagship species for conservation always (Walpole & Leader-Williams, 2002), for the simple fact that they are becoming locally extinct in sites that still continue to provide significant ecosystem services.

We aimed to test the ability of a range of large and small scale predictors to explain variation in the diversity of beetles and spiders. We found that the most significant predictors were broad scale vegetation units, which explained more variation in beetle than spider species richness. The vegetation units were also the most important predictors of beetle and spider community composition. The size, isolation of areas and quality of habitat conserved for each vegetation type therefore have important implications for ground dwelling invertebrates. Area for conservation per vegetation unit need to be quite substantial in size to conserve the full range of habitat conditions and limit extinction debt in highly modified landscapes. This also means that smaller habitat fragments need to be conserved outside protected areas, as well as smaller vegetation units that may act as stepping stepping-stone habitats.

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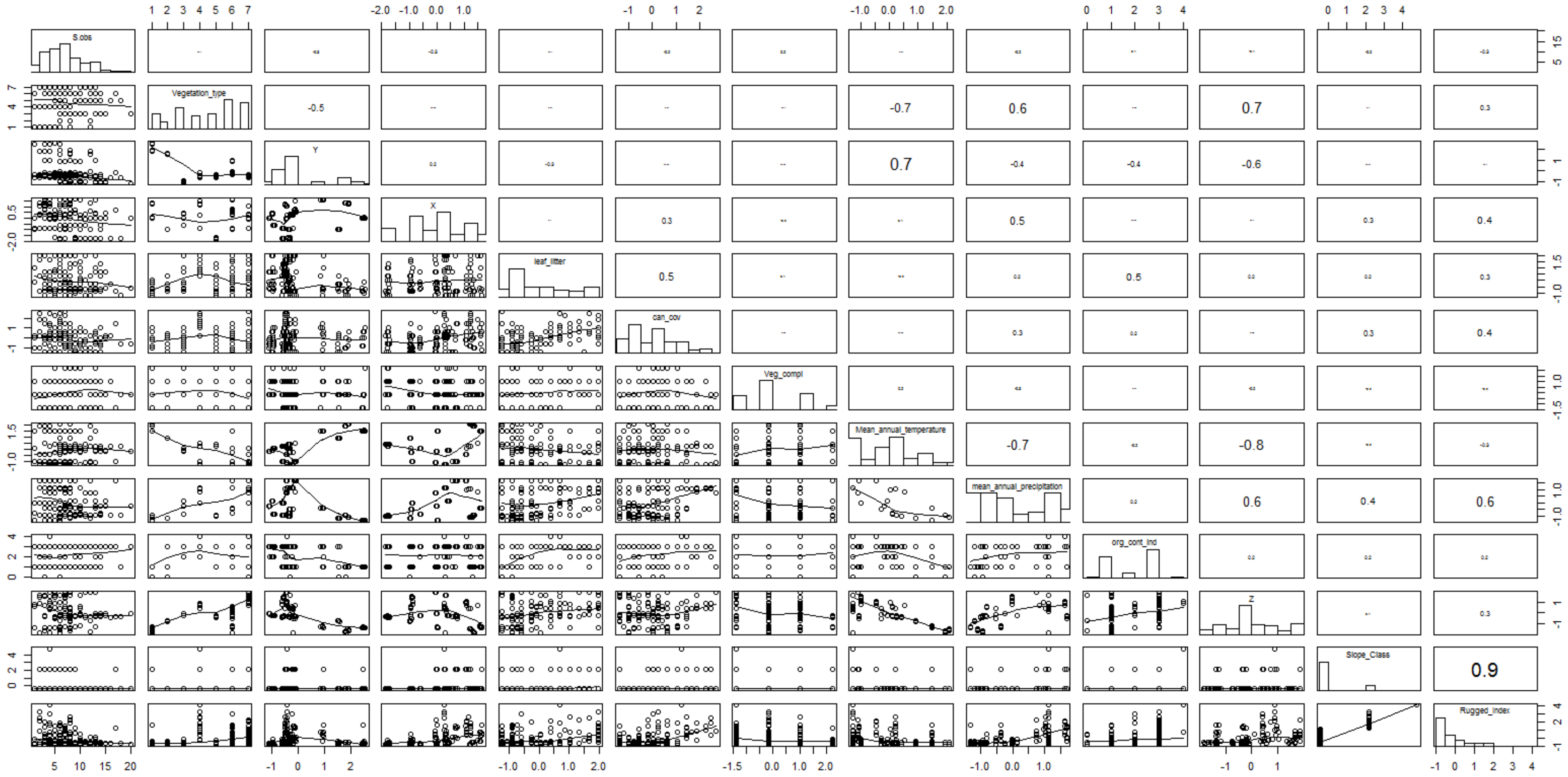
Appendices

Appendix 1. The abundance (n), observed species (S.obs), estimated species (S.hat) and sample coverage ($\hat{S}$) for sites in the study area. Makhado Sweet Bushveld (BEN, BRI &MAR), Soutpansberg Summit Sourveld (GON, GOR, MAR & NWA), Northern Mistbelt Forest (LF, HLF, EF & TV), Roodeberg Bushveld (BLN, BLS), Soutpansberg Mountain Bushveld (RM, BGM, LM & VM), Musina Mopane Bushveld (MAA, LUD), and Limpopo Ridge Bushveld (BAR).

	Beetles				Spiders			
Site	n	S.obs	$\hat{S}$	$\hat{C}$	n	S.obs.	S.hat	C.hat
BEN	316	30	51.06	0.9589	163	47	98.76	0.8471
MAA	393	37	48.97	0.9695	145	42	66.03	0.8492
BRI	1291	55	107.04	0.9806	763	51	79.53	0.9738
LF	15	8	13.83	0.6847	5	4	7.6	0.4857
HLF	74	4	6.96	0.9595	26	10	27.31	0.7723
EF	73	7	9.96	0.9589	114	27	37.47	0.8872
TV	43	7	7.98	0.9556	4	4	8.5	0
RM	127	19	26.94	0.9375	153	46	84.81	0.8373
BGM	81	16	60.44	0.8765	84	25	29	0.8957
LM	113	26	85.96	0.9028	55	23	50.65	0.7656
VM	89	21	70.44	0.8879	48	20	28.16	0.7969
BAR	785	30	33.6	0.9924	107	41	65.27	0.8053
MAR	867	29	38.99	0.988	90	26	27.98	0.9355
LUD	4088	34	40.75	0.9974	48	19	28.91	0.816
BLN	667	63	86.11	0.973	120	38	81.73	0.8257
BLS	742	61	77.64	0.9731	237	56	81.93	0.8949
GOR	1316	57	74.99	0.9863	100	33	48.91	0.8514
GON	500	50	81.44	0.9581	118	40	68.33	0.8315
MAS	897	60	76.94	0.9766	124	36	79.74	0.8313
NWA	1545	45	84.97	0.9695	119	32	79.76	0.8576
ALL	14109	260	331.11	0.9948	2624	217	294.37	0.9745

Appendix 2. Collinearity between environmental variables was assessed using a corellelogram. If two variables had a significant Pearson's Product Moment Correlation > 0.5, the variable that was considered biologically more meaningful were retained.



Appendix 3. Spider species and respective codes used in the CCA diagram in Fig. 4; only species that made up more than 1% total abundance were included in the analysis.

Araneae Species	**abbreviation**	**SUM**	**% total abundance**
Ibala bilinearis	Iba bi	29	1.12
Pardosa sp. 1	Par1	29	1.12
Cydrela spinifrons	Cyd spi	30	1.16
Capheris decorate	Cap de	31	1.20
Ammoxenus amphalodes	Ammo ampha	32	1.24
Mastidiores sp. 1	Mas1	32	1.24
Proevippa sp. 1	Pro1	33	1.27
Stenaelurillus natalensis	Ste na	38	1.47
Langonella sp. 1	Lang1	39	1.51
Allocosa gracilitarsis	Allo grac	43	1.66
Ibala lapidaria	Iba la	47	1.82
Ranops caprivi	Ran ca	59	2.28
Segregara paucispinulosus	Seg pa	59	2.28
Asemesthes paynteri	Ase pay	78	3.02
Asemesthes ceresicola	Ase cer	83	3.21
Diores magicus	Dior mag	83	3.21
Asemesthes sp. 1	Ase1	87	3.37
Stenaelurillus guttiger	Ste gu	105	4.06
Evippomma squamulatum	Evip squa	107	4.14
Ammoxenus psammodromus	Ammo psam	618	23.95

Appendix 4. Beetle species and respective codes used in the CCA diagram in Fig. 4; only species that made up more than 1% total abundance were included in the analysis.

Coleoptera species	**abbreviation**	**sum**	**% total abundance**
Wahlbergiana alternans	Wahl al	150	1.06
Onthophagus sp. Y	OnthY	198	1.41
Distretus discoideus	Dis dis	215	1.53
Onthophagus lameliger	Onth Lam	243	1.73
Sisyphus sordidus	Sis sor	252	1.79
Onthophagus sp. C	OnthC	278	1.98
Zophosis sp. A	ZophA	371	2.64
Allogymnopleurus thalassinus	Allo tha	400	2.85
Metacatharsius opacus	Meta opa	426	3.03
Scarabaeus schultzi	Scar sch	684	4.87
Scarabaeus bohemani	Scar boh	715	5.09
Anachalcos convexus	Anac con	726	5.17
Zophosis sp. C	ZophC	733	5.22
Onthophagus sagillatus	Onth sag	1345	9.59
Zophosis sp. B	ZophB	1763	12.57
Gymnopleurus humeralis	Gymn hum	2741	19.54

CHAPTER 3

REGIONAL INVERTEBRATE CROSS- AND WITHIN-TAXON SURROGACY ARE SCALE AND TAXON DEPENDENT[2]

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Abstract

Coarse scale environmental predictors and vegetation types can be used to explain patterns of diversity. However, finer scale information on plant and animal diversity, when available, might provide an even better surrogate for diversity than these broad scale predictors. This study measured within- and cross-taxon congruence, in diversity of epigeal invertebrates (spiders, beetles and millipedes) and woody vegetation sampled at small spatial grains (0.25 ha) across a large extent (30 000 km^2) within the Vhembe Biosphere Reserve (VBR) in South Africa. Beetle, spider, millipede and woody plant diversity was recorded at 160 point localities in 20 sites stratified across the dominant vegetation types of the VBR. Surrogacy relationships were explored using linear regression (species richness) and mantel tests (composition), while complementarity was analyzed using the species accumulation index (SAI). Very little (< 10%) of the variation in invertebrate species richness was explained by woody vegetation richness only performing marginally better for beetle richness. These relationships between woody and invertebrate species richness were even more inconsistent for dominant invertebrate families with Scarabaeidae, Gnaphosidae and Lycosidae having positive relationships, while none or very little existed for Tenebrionidae, Carabidae and Salticidae. Woody vegetation assemblages showed a positive, but weak congruence with beetle assemblages, for all families examined: Carabidae, Tenebrionidae and Scarabaeidae. The strongest congruence was however found for the Tenebrionidae assemblages and woody vegetation. Woody vegetation assemblage showed poor congruence for spider communities in general, with the exception of Lycosidae. Although cross taxonomic congruence was observed between woody vegetation and invertebrate taxa, the relations based on SAI were stronger than expected for Coleoptera, positive but weak for spiders, and weak for millipedes which had several localized endemics. Tests of higher taxonomic categories as surrogates were shown to have much greater potential than cross taxon surrogacy. Genera in particular are excellent surrogates for species. Tribal or generic level determinations can be a cost efficient approach for regional conservation planning exercises which aim to represent smaller scale variations in invertebrate diversity.

Keywords: surrogacy, woody vegetation, epigaeic invertebrates, savanna biome, Vhembe Biosphere Reserve, Limpopo Province

Introduction

Animal taxa respond strongly to variation in vegetation structure and floristic composition, suggesting that changes in vegetation could be a readily observable surrogate for changes in animal assemblages (Barton *et al*., 2014). Haddad *et al*. (2001) ascribed a positive effect of plant richness and composition on insect diversity to the greater availability of alternate plant resources or greater vegetation structure. Sauberer *et al*. (2004) recommended using vascular plants as an essential first step in selecting surrogates as these showed the highest correlations with overall invertebrate species richness, while Kati *et al*. (2004) concluded that woody plants acted as the best surrogate for biodiversity.

The use of habitats as surrogates for biodiversity is dependent on the ability of habitat classifications to portray homogenous communities (Hermoso *et al*., 2013; Dixon-Bridges *et al*., 2014). Congruence in the responses of different taxa across an environmental gradient often points to similar mechanisms driving diversity, while low correspondence might suggest that the relative importance of drivers vary between affected taxa and spatial scales (Hulshof *et al*., 2013). Unfortunately, not all taxa are affected by the same processes, and the use of a variety of taxa is generally recommended when used as surrogates for biodiversity (Rodrigues & Brooks, 2007; Leal *et al*. 2010). Many studies in Africa have explored the umbrella potential of the "big five" animals (William *et al*., 2000; Moore *et al*., 2003; Dalerum *et al*., 2008) and birds (Bonn *et al*., 2002).

Based on reviews (Thuiller *et al*., 2006; see Table 1 in Rodrigues & Brooks, 2007), very few studies have explored the efficiency of hotspots (areas that are diverse) and complementarity for plant and animal assemblages in sub-Saharan Africa (but see Lovell *et al*., 2007 and Foord *et al*., 2013). Lewandowski *et al*., (2010) found that a surrogate was more likely to be effective with a complimentary approach than with a hotspot approach – which is the approach of most published studies. In speaking of a complimentary approach, surrogacy value can be measured by evaluating how well a set of sites selected to maximize the representation of one taxon performs in representing another (Brooks & Rodrigues, 2007), in other words, surrogates that can be used to select a combination of sites that together maximize total species richness (Lewandowski *et al*., 2010).

Woody vegetation is an important component of the savanna biome vegetation and is relatively easy to identify compared to grass (Eckhardt *et al*., 2000). Because plants are sedentary they are easier to sample and it is probably quicker to achieve inventory completion. For instance there is a detailed checklist of all the plants of South Africa, with information on endemism, red-list status, and locality (Germisheuizen & Meyer, 2003). No such list exists for insects in general (see Mecenero, 2016) although a list is being developed for spiders (Dippenaar-Schoeman *et al*., 2015). Plant species' distributions are also much better known while large gaps remain for invertebrates. Despite the usefulness of woody plants as surrogates for biodiversity (Kati *et al*., 2004), their use has serious limitations (Chiarucci *et al*., 2005). Woody vegetation does not always represent invertebrate diversity in general, and may in some cases be a poor surrogate for certain groups (Chiarucci *et al*., 2005; Foord *et al*., 2013). For conservation science and policy to be truly representative of global biodiversity a representative cross-section of invertebrates should ideally be included (Clausnitzer *et al*., 2009; Leal *et al*., 2010). This may be because surrogacy may only be effective at certain spatial scales and the resources that make up the habitat of a species may only cover a subset of a vegetation type or may be dispersed over several vegetation types (Vanreusel & Van Dyck, 2007). Woody vegetation may also not mirror groups whose distribution across the landscape shows highly localized endemicity and is the products of strong historical signatures (Bonn *et al*., 2002). This can produce conflicting and varied results since the difference between study regions might be large and unquantified (Grantham *et al*., 2010), undermining the commonly held view that vegetation is a cost effective and readily observable surrogate for change in animal assemblages (Barton *et al*., 2014).

Several authors have found that patterns of compositional heterogeneity of species is maintained at higher taxonomic levels such as genus and family (Báldi, 2003; Cardoso *et al*., 2004; Heino & Soininen, 2007; Lovell *et al*., 2007; Terlizzi *et al*., 2009). Terlizzi *et al*. (2009) found that differences in heterogeneity in the identity of species were maintained for genera and for families, but not at coarser levels of taxonomic resolution (order or class) for mollusks in marine ecosystems. Cardoso *et al*. (2004) & Foord *et al*. (2013) found that taxonomic surrogacy was only maintained at the genus level for spiders.

Vegetation type was the best predictor of epigeal invertebrate (spiders and beetle) alpha and beta diversity across a large geographic area (Chapter 2). To what extent this predictive capability can be extended to finer scale data of vegetation composition is unknown, Barton *et al*. (2010) have shown that variation in vegetation composition at very small scales can be a very good surrogate of beetle diversity.

Spiders are major predators of other invertebrates (Dippenaar-Schoeman *et al*., 2015; Foord & Dippennaar-Schoeman, 2016), have a relatively stable taxonomy, are easy to sample, are ecologically well known, include widespread and specialized species, and may have diversity patterns that correlate with other taxa (Gerlach *et al*., 2013). The taxonomic and functional diversity of Coleoptera allows for the inclusion of multiple trophic levels and the group as a whole can be regarded as a biodiversity surrogate (Gerlach *et al*., 2013). Scarabaeidae are highly specialized detritivores that are sensitive to landscape changes (Van Rensburg *et al*., 1999), while Carabidae are keystone predators (Gerlach *et al*., 2013). The value of Tenebrionidae as a surrogate taxon has not been assessed for South Africa, but they are speciose (Koch, 1962) with an estimated 7000 species occurring in southern Africa. They are habitat-dependent specialists, detritivores and mostly flightless and therefore have limited dispersal abilities. Millipedes are herbivores, with a preference for dead and decaying plant material and show high levels of local endemicity (Hamer, 1998). Millipedes are potentially useful surrogates, yet many taxonomic issues remain unresolved (Gerlach *et al*., 2013).

This study aims to assess the degree of cross taxon congruence between woody vegetation communities and that of spiders, beetles and millipedes at varying taxonomic levels; we also assess within taxon congruence for these invertebrate groups. Based on the ability of vegetation to predict invertebrate diversity at larger scales we predict that its performance is not affected by scale and that woody vegetation would be an efficient surrogate of invertebrate species diversity. We further predict that within taxon congruence, in the form of higher taxonomic categories (such as genus and tribe), would also allow for the use of higher taxa (genus and family) as surrogates of diversity.

Methods and Materials

Sampling

The study site is located in the northernmost region of South Africa, the Vhembe Biosphere Reserve (VBR), bordering Botswana, Zimbabwe, and Mozambique, bounded by the Limpopo River (Fig. 1) (Pool-Stanvliet, 2013). The VBR comprises the Blouberg, Soutpansberg, the Limpopo Valley, and the savanna plains south of the mountain range, including the northern sector of Kruger National Park (Fig. 1). The Vhembe Biosphere Reserve (VBR) is the largest biosphere reserve in South Africa, with a spatial extent of 30 000 km^2, and also the least disturbed (Pool-Stanvliet, 2013). The region’s strong environmental gradients in rainfall and vegetation structure (Hahn, 2007; Hahn, 2011) provides a template to test the efficacy of biodiversity surrogates. The savanna biome protected by the Vhembe Biosphere is a hyper-diverse ecosystem, comparable to the tropical forests in biodiversity (Parr *et al*., 2014). Studies at small spatial scales suggest that high levels of invertebrate diversity occur in the Vhembe Region (Endrody-Younga, 1988; Foord *et al*., 2002; Foord *et al*., 2008; Schönhofer, 2008; Haddad, 2009; Azarkina & Foord, 2013; Munyai & Foord, 2015). In addition to this diversity, 44 species of bat have been recorded (Taylor *et al*., 2013) and over 500 tree species (Hahn, 2017). Hahn (2019) recorded 2443 taxa for the Soutpansberg Mountain belonging to 922 genera, 18 families and 64 orders in an area of 6700 km^2. The mountain's higher taxonomic diversity compares favorably with that of the world renowned Cape Floristic Region that is 90760 km^2 in extent, has more species (9383) almost the same amount of genera (997) and less families (178) (Manning & Goldblatt, 2012).

The region occurs in the greater Limpopo River Basin that includes the Makgabeng, Waterberg Range, the Bushveld Igneous Complex and the Zimbabwe Craton (McCarthy & Rubidge, 2005). Geologically the Limpopo Valley is primarily of Archaean origin, the mountains Proterozoic and Mesozoic. The Karroo super-group, of high mineral value, was moulded by successive dynasties of ice, sea, lake, swamp, desert and volcanic activity (Johnson *et al*., 1996). Most of the soft Karroo rock has been eroded, exposing the ancient sediments of the Soutpansberg and Blouberg (McCarthy & Rubidge, 2005).

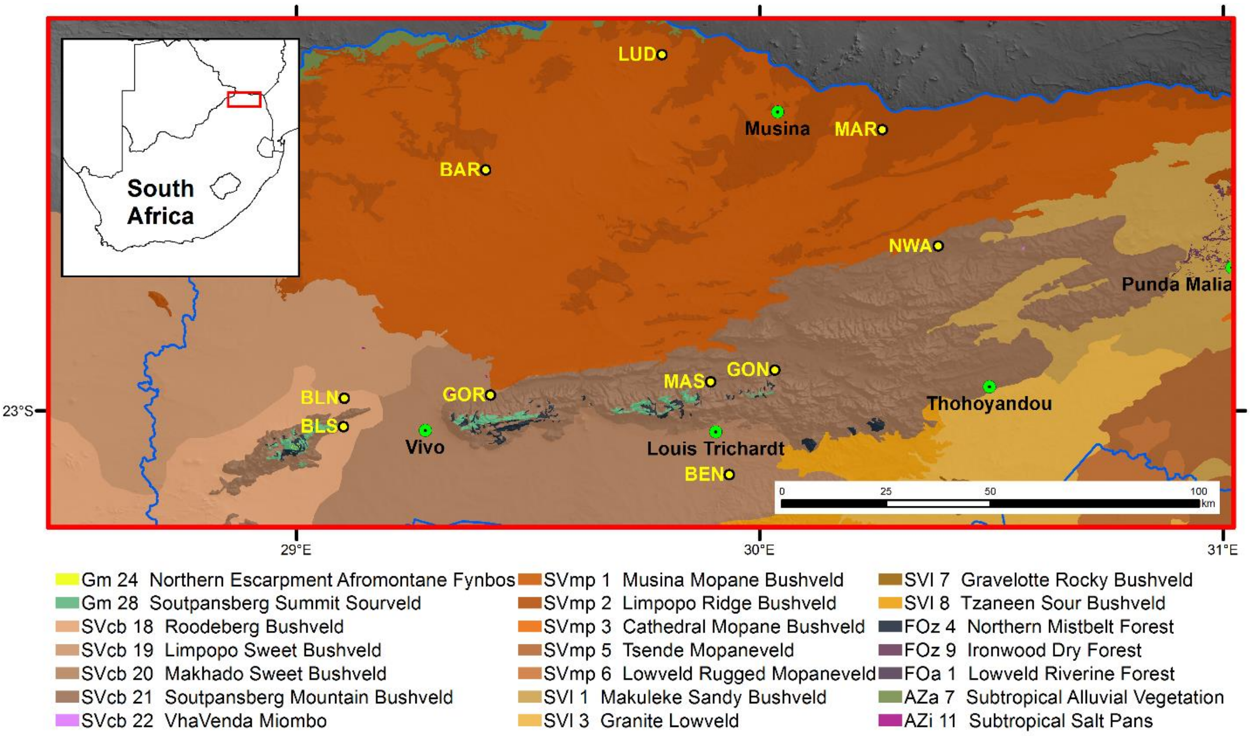

Fig. 1. Map of sites in vegetation units in the Vhembe Biosphere Reserve.

The vegetation types found in the region, and across the Soutpansberg in particular, occurs in roughly longitudinal west to east bands (Mucina & Rutherford, 2006). The southern and northern lowveld plains harbour geographically large, continuous communities (Mucina & Rutherford, 2006). Here we use Mucina & Rutherford (2006) to classify these major vegetation units. Sampling was stratified across the dominant vegetation types of the region; a botanic expert available for ten of the twenty sites selected in the Vhembe Biosphere Reserve (Chapter 2). There were thus only ten sites for which woody vegetation data was available for analysis.

We sampled invertebrates during November 2012 – January 2013. (Fig. 1). Within each site, we selected eight sampling points, hereafter referred to as sampling units (SU’s). These SU’s were spaced between 300 - 2000 m from each other to ensure independence of samples. Each SU comprised five pitfalls, placed in a circle with a diameter of 10 m. Pitfalls were used because it expends the least amount of input with a greater comparable output than any other sampling method (Agosti *et al*., 2000). We wanted to capture as much variation in the immediate habitat as possible and were careful to place our pitfalls in such a way as to consider microscale-heterogeneity. The pitfalls of each SU were too close to each other to be considered true replicates. The unit for data analysis is therefore the Sampling Unit (SU), for a total of 8 SU × 10 sites = 80 SU's. Pitfalls (7 cm diameter, and 12 cm deep) were dug into the ground and quarter filled with propylene glycol. Traps were left out for seven days, then washed using a fine net, and stored in 96% ethanol.

The woody vegetation at the SUs was identified to species level by the third author within a 50 x 50 m quadrat. Only presence was recorded (Appendix 3). Trees have a relative long lifespan and their species assemblage at our sites is thus a reflection of edaphic factors and long term climatic conditions of a specific habitat. In addition, tree species are relatively easy to identify *in situ*. A total of 150 tree species were recorded; the most common genera were *Senegalia, Combretum* and *Gymnosporia* (see Appendix 3 for the tree-list).

Spiders were identified by A.S. Dippenaar-Schoeman and specimens were deposited in the National Collection of Arachnida (NCA) of the Plant Protection Research Institute, Agricultural Research Council, Pretoria. Beetles were identified by Ruth Muller and Adrian Davis. Beetles were deposited in the Ditsong National Museum of Natural History (DNMNH) and the Univen Zoology Collection. Millipedes were identified by the second author and will be deposited in DNMNH.

Data analysis

We used species accumulation curves to estimate sampling completeness for spiders, beetles and millipedes.

Relationships between beetle, spider, millipede richness and that of woody vegetation richness were explored using linear regression with the bivariate function in PAST (Hammer & Harper, 2006). The richness of the most speciose families (dependant variables) – Coleoptera: Carabidae, Tenebrionidae and Scarabaeidae; Araneae: Gnaphosidae, Lycosidae, Salticidae and Zodariidae; and Diplopoda were regressed against that of tree species richness. We also performed linear regression exploring the within taxon relationships between tribes and genera for and families (Araneae and Diplopoda).

Multivariate congruence by first calculating the Pearson's correlation coefficient between two ranked similarity (Bray-Curtis) matrices of the taxa involved, resulting in an observed R-value which ranges from -1 (complete negative correlation) to 1 (complete positive correlation). A Mantel test then allows for the calculation of a p-value based on the null distributions generated by randomly permutating site labels and recalculating correlations (Hammer & Harper, 2006). This analysis also included tests for cross-taxon (trees) congruence of the most speciose families in Coleoptera (Carabidae, Tenebrionidae and Scarabaeidae) and Araneae (Gnaphosidae, Lycosidae, Salticidae and Zodariidae).

Complementarity was assessed using the Surrogacy Accumulation Index (SAI) (Rodrigues & Brooks, 2007). First surrogate efficiency was visually assessed by comparing species accumulation curves to that of random (randomly selected sites) and optimal (using the target taxon to select sites). The closer the surrogacy curve is to the optimal curve, the higher is the surrogacy value. Where the optimal and surrogacy curve coincide, the Surrogacy Accumulation Index (SAI) would be one, indicating perfect surrogacy. An SAI between one and zero is when the surrogate curve occurs mainly above the random curves (positive surrogacy value), is zero when the surrogate and random curves coincide on average (zero surrogacy), and is negative when the surrogate curve is mainly below the random selection (negative surrogacy value)

(Rodrigues & Brooks, 2007). As several randomizations are possible, random permutations allow for the identification of 95 % confidence intervals.

Results

Sample rarefaction

Species accumulation curves did not reach an asymptote which suggests that not all the species were sampled (Fig. 2). This was especially true for beetles and millipedes.

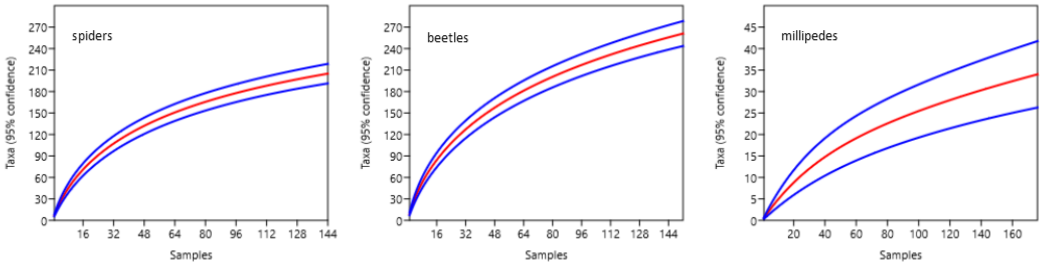

Fig. 2. Species accumulation curves for spiders, beetles and millipedes.

Species Richness

Although positive and significant, tree species richness explained only six percent of the variation in beetle richness (R^2 = 0.06, p = 0.03) (Fig. 3) and this relationship was not significant for either spiders (R^2 = 0.001, p = 0.73) (Fig. 3) or millipedes (R^2 = 0.01, p = 0.35) (Fig. 3).

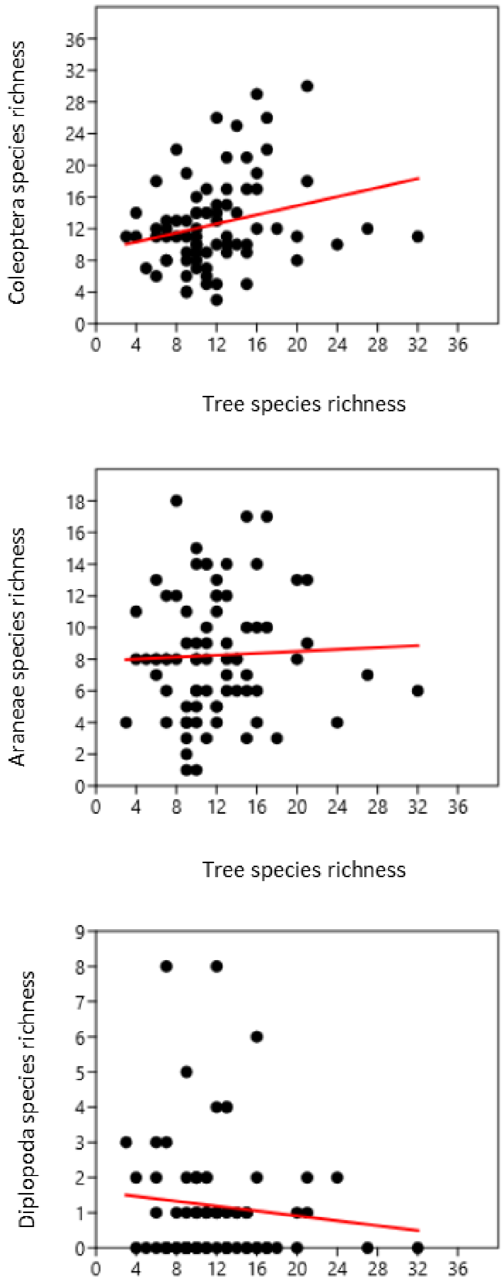

Fig. 3. Cross-taxon relationship between three taxa, a) Coleoptera (Carabidae, Scarabaeidae and Tenebrionidae), b) Araneae, and c) Diplopoda and tree species richness using linear regression of species richness per sampling plotted against tree species richness at the point localities.

There was an overall weakly positive yet statistically significant relationship between species richness of some invertebrate families and tree species richness ($R^2 = 0.04$, $p = 0.02$). Scarabaeidae (dung beetle) richness was positively related to tree species richness but no such response was evident for Tenebrionidae or Carabidae (Table 1, Appendix 1). Weak evidence exists for a positive relationship for Lycosidae and Gnaphosidae and none for Salticidae and Zodariidae (Table 1, Appendix 1). There was no relationship between millipede species richness and woody vegetation richness (Table 1, Fig. 3)

The use of higher taxonomic categories as surrogates for species diversity show much greater promise. Beetles (tribes and genera), spiders and millipede (families and genera) richness explained large and significant amounts of variation for within-taxon species richness (Table 1, Fig. 4).

Table 1. Linear regression testing of cross taxon surrogacy (woody vegetation) and within taxon surrogacy (family, tribe and genus) in the Vhembe Biosphere Reserve

	woody vegetation			family			tribe			genus		
	slope	R^2	p	slope	R^2	p	slope	R^2	p	slope	R^2	p
Coleoptera							0.55	0.81	0.00*	0.61	0.91	0.00*
Carabidae	0.04	0.02	0.17									
Scarabaeidae	0.17	0.04	0.05*									
Tenebrionidae	0.05	0.02	0.18									
Araneae				0.46	0.71	0.00*				0.84	0.93	0.00*
Gnaphosidae	0.07	0.07	0.01*									
Lycosidae	0.05	0.04	0.06									
Salticidae	0.001	0	0.96									
Zodariidae	0.03	0.03	0.09									
Diplopoda				0.72	0.91	0.00*				0.72	0.91	0.00*

Assemblage composition

Mantel tests showed that of the beetles, Scarabaeidae and Tenebrionidae composition were weakly positive, yet statistically significant, congruent with woody vegetation (Table 2). Of the spiders the Lycosidae and Gnaphosidae assemblages showed significant congruence with woody vegetation assemblage (Table 2) while no relationship existed for millipedes (Table 2).

There was strong evidence for within taxon congruence in terms of composition for all the taxa considered (Table 2).

Table 2. Results of the Mantel Test (tree—x taxa) testing cross taxon and within taxon congruence between community composition of woody vegetation and invertebrate (spiders and beetles) community composition across sample units (SU's),using Bray-Curtis dissimilarity matrices. The significance of R was calculated relative to the null distribution based on 9999 permutations. * indicates a significant p value.

	woody vegetation		family		tribe		genus	
	R	p	R	p	R	p	R	p
Coleoptera	0.08	0.13			0.85	0.0001*	0.89	0.0001*
Carabidae	0.06	0.06						
Scarabaeidae	0.36	0.0001*						
Tenebrionidae	0.17	0.009*						
Araneae	0.07	0.14	0.71	0.0001*			0.85	0.0001*
Gnaphosidae	0.03	0.28						
Lycosidae	0.09	0.01*						
Salticidae	0.002	0.49						
Zodariidae	0.06	0.11						
Diplopoda	0.05	0.14	0.96	0.0001*			0.96	0.0001*

Complimentarity

Woody vegetation was a poor surrogate for spiders and millipedes with low and negative SAI scores respectively (Table 3, Appendix 2). Woody vegetation was a good surrogate for beetles however with a positive SAI score (0.4). Spiders and beetles are weak surrogates of each other (SAI = 0.21 and 0.24 respectively), and very weak surrogates for millipedes (negative SAI scores) (Table 3, Appendix 2).

For complementarity, both spiders and beetles genera showed almost perfect surrogacy (SAI = 0.83 and 0.68respectively), however millipede genera were poor surrogates (SAI = 0.15) while spider families(SAI = 0.57) and beetle tribes (SAI = 0.67) were strong surrogates (Table 3, Appendix 2).

Table 3. Assessment of cross taxon and taxonomic surrogacy using Species Accumulation Index (SAI) of Surrogate Efficiency.

	Coleoptera	Araneae	Diplopoda
woody vegetation	0.39	0.14	-0.29
Coleoptera		0.21	-0.14
Araneae	0.24		-0.01
Family		0.57	
Subfamily	0.44		
Tribe	0.67		
Genus	0.68	0.83	0.15

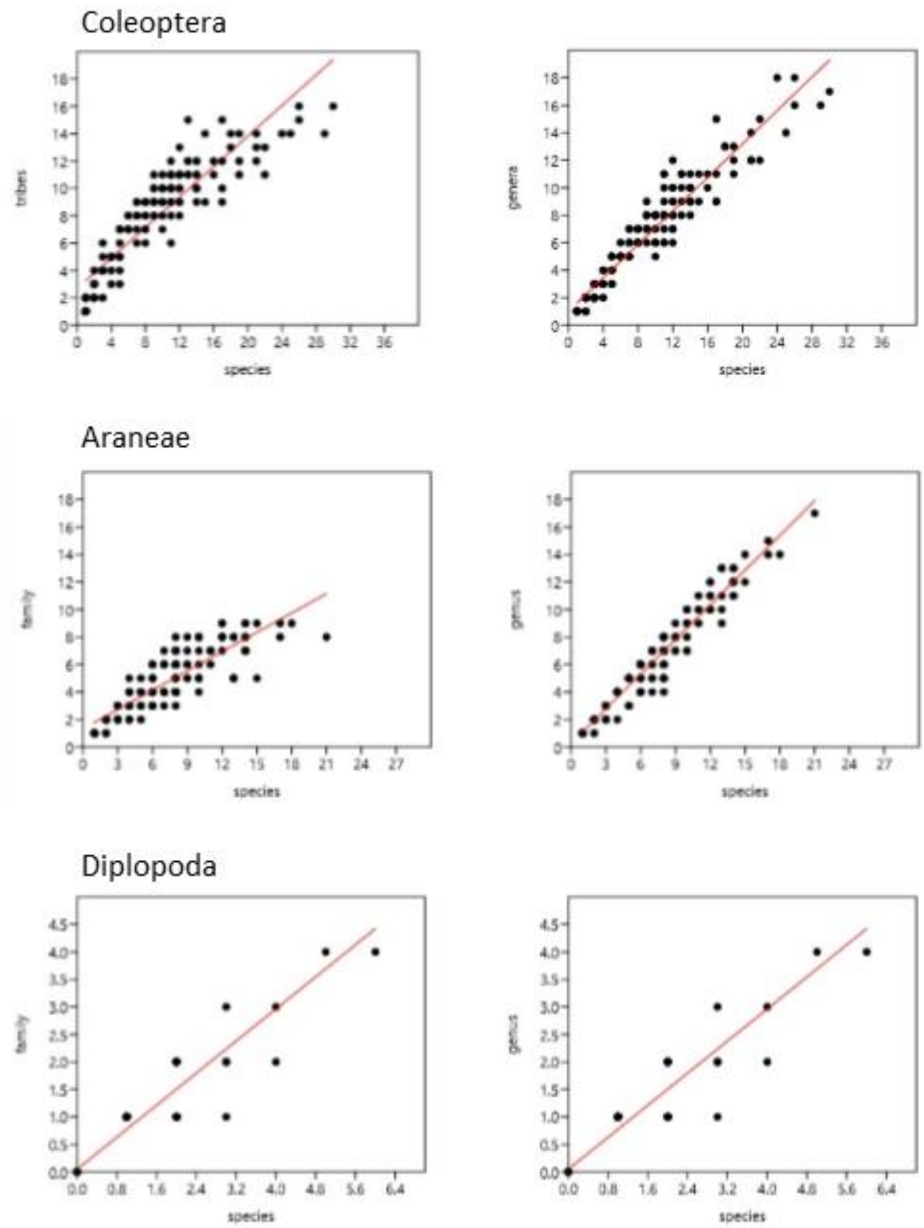

Fig. 4. Linear regression of higher taxonomic surrogates for the three taxa investigated. Tribes = the number of tribes, family = number of families, genera = number of genera and Species = number of species.

Discussion

Results from this study suggest that surrogate performance is both scale and taxon dependent. The ability of vegetation (woody vegetation diversity) to act as a surrogate for invertebrate diversity broke down at these finer scales and seems to be scale-dependent. There were exceptions, and these were only found for composition and for certain lower taxonomic levels, such as families (Scarabeidae, Tenebrionidae and Lycosidae). In contrast higher taxa was a much more effective surrogate, particularly at the genus level determinations. However, all the surrogate measures for millipede diversity performed weakly.

Cross taxon congruence between woody vegetation and invertebrate diversity

Various authors have found that plant species richness is an adequate surrogate for invertebrates (Saetersdal *et al*., 2002, Maccherini *et al*., 2009; Fraser *et al*., 2010; Santi *et al*., 2010; Castagneyrol & Jactel, 2012). Koch *et al*. (2013) found that measured correlation between plants and butterflies, that community assembly was a better measure of cross-taxon congruence than species richness. Exceptions are to be found in wetland ecosystems where plant diversity was found to display poor congruence with aquatic beetle diversity (Kirkman *et al*., 2012) and may also deteriorate with disturbance (Rooney & Bayley 2012).

Scarabaeidae in particular is associated with large herbivore dung, and a positive relationship with woody plant species richness would probably not have been expected. Davis *et al*. (2008) found that African dung beetle distribution was strongly correlated with major ecoregions. It has also been found that a more diverse floral assemblage supports a higher diversity of mammals (Tews *et al*., 2004), which is a major driver of dung beetle diversity (Davis & Scholtz, 2001). This suggests that there is an indirect relationship between tree diversity and dung beetle diversity.

Although a very weak surrogate for invertebrate diversity hotspots in general, there is support for woody vegetation as a hotspot surrogate for Tenebrionidae in particular. This could be explained by the strong association of ground dwelling Tenebrionidae with plant debris (Wharton & Robert, 1982). Tenebrionidae is most diverse and abundant in the deserts and semi-deserts of South Africa (Koch, 1962). Because nearly all are flightless, tenebrionid communities have a very strong biogeographic signature, and species and tribes common in one ecoregion may be completely replaced by other taxa in neighbouring ecoregions (Kaminski & Ras, 2012; Kaminski & Iwan, 2013).

Lycosidae, the spider taxon for which woody vegetation was a relatively good surrogate, typically associated with cooler, moister and more vegetated areas of the VBR (Foord *et al*. 2008) being considerably more abundant and diverse in forest and thicket areas. Gnaphosidae tends to occur in more arid areas, with less tree cover.

Within taxon congruence

Tests of higher taxonomic categories as surrogates have shown much greater potential than cross taxon surrogacy. Genera in particular are excellent surrogates for species. Generic richness in beetles (Rosser & Eggleton 2012), Hymenoptera (Vieira *et al*. 2012), and spiders (Cardoso *et al*. 2004; Lin *et al*. 2012) have been shown to be suitable surrogates of species richness and that relatively higher taxonomic hierarchies such as tribes (beetles) and families (spiders) can be effective surrogates for species richness. In the case of groups like beetles it might even be preferable, since a wide range of tribes from different families would have greater surrogacy potential than species from one beetle family as is often-times the case in many studies (Koch *et al*., 2000; Spector, 2006; Tshikae *et al*., 2008). Identification to the level of tribe poses less of a taxonomic challenge than identification to genus or species, and still provides data of great taxonomic resolution (40 beetle tribes in this study). For rapid biological assessments of beetles, the use of tribes may be preferable to the use of genera. However, not all groups reflect species diversity at higher taxonomic levels, e.g. ants in both Australia (Andersen, 1995) and tropical Africa (Rosser & Eggerton, 2012), where small groups of genera contributes to a large number of species.

Other processes beside vegetation type, structure and composition can affect the spatial variation of animal taxa. The retention of large herbivores in savannah is a significant contributor to the maintenance of insect diversity (Rahagalala *et al*., 2009). Geology and soil type are also determinants and have in fact been used as environmental surrogates (Wessels *et al*., 1999). Even termite mounds may affect invertebrate communities (Joseph *et al*., 2014), by increasing functional diversity in the landscape.

Rodrigues & Brooks (2007) recommend that practical conservation planning based on data for well-known taxonomic groups is effective – but must proceed with caution because of the limitations of using surrogates (Van Rensburg *et al*., 2002). Using higher taxonomic levels such as genera, tribes and families as surrogates for invertebrate species diversity has proven to be more effective than cross-taxon surrogates (Gerlach *et al*., 2013). This study did however show that woody plants, even though they are poor surrogates for hotspots of invertebrate richness, can still be used as surrogates for invertebrate assembly and complementarity, but only for select groups. As cross-taxon congruence was very low, we recommend the use of a variety of taxa (or several families) to represent functional types in an ecosystem and use generic or tribal level identification to save time and money (Lovell *et al*., 2007; Rodrigues & Brooks, 2007).

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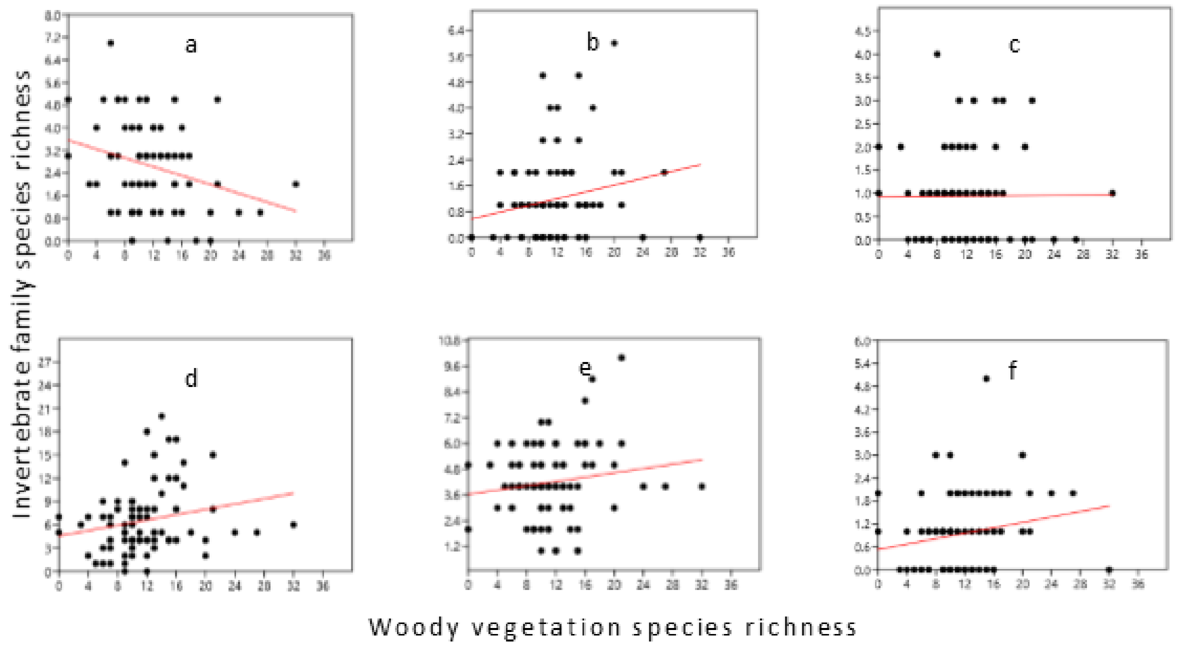
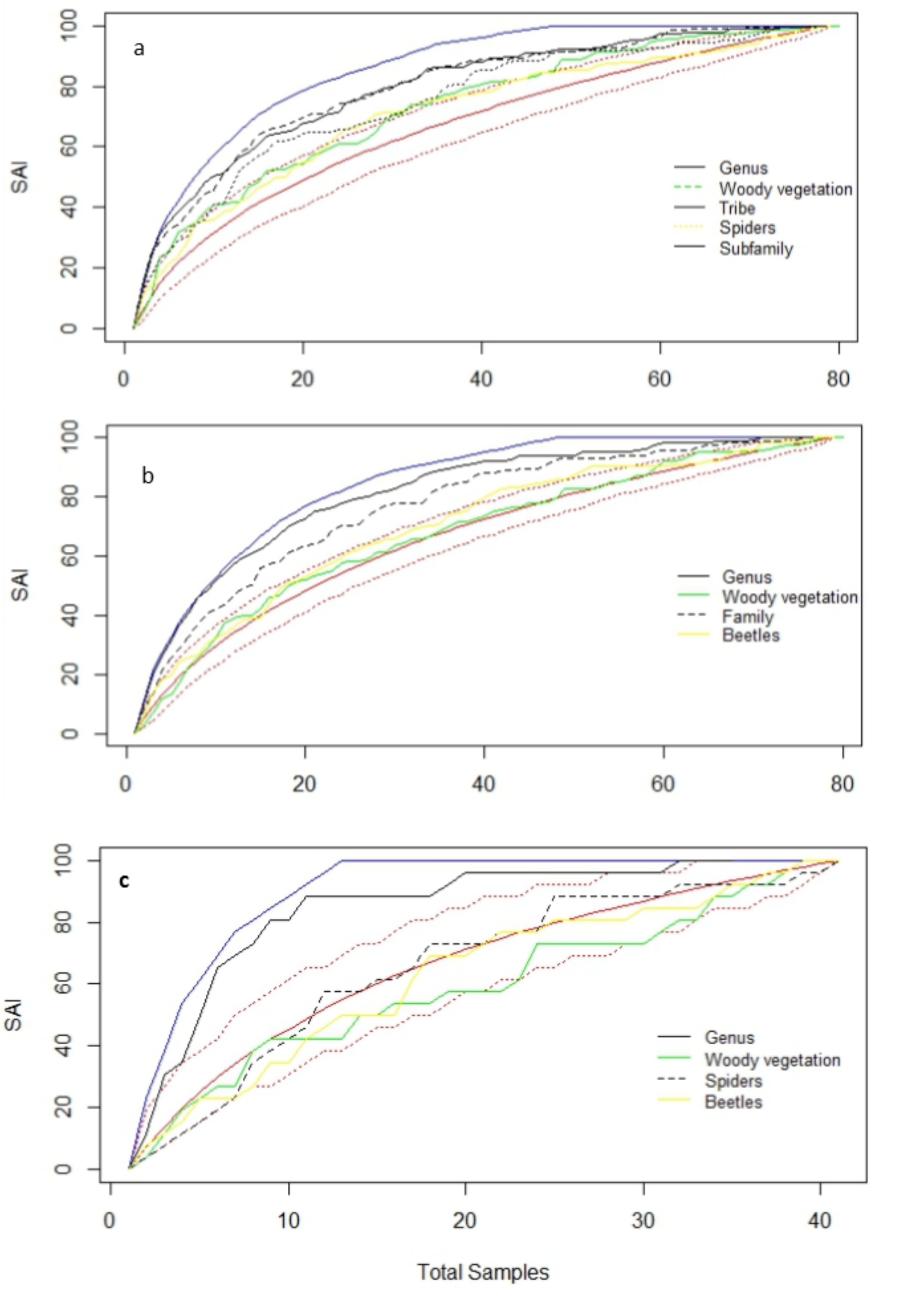
Appendices



Appendix 1. Assessment of cross taxon correlation using linear regression of species richness per family per SU plotted against tree species richness at the same point locality. a) Carabidae, b) Scarabaeidae, c) Tenebrionidae, d) Gnaphosidae, e) Lycosidae, f) Salticidae



Appendix 2 Assessment of cross and within-taxon surrogacy using the Species Accumulation Index (SAI) of surrogate efficiency. The red lines represent the mean and 95% SAI confidence intervals when sites are randomly selected. a) Coleoptera, b) Araneae, c) Diplopoda.

Appendix 3. List of tree species, with abundance counts at each site showing count of abundance per site (with a maximum of 8 sampling points per site).

Tree or woody shrub	BAR	BEN	BLN	BLS	GON	GOR	LUD	MAR	MAS	NWA
Acalypha glabrata			1		1					
Adansonia digitata					2	1	3	1		2
Albizia anthelmintica				1						
Albizia brevifolia					1					1
Androstachys johnsonii					1					1
Artabotrys brachypetalus					2				1	1
Balanites maughamii		1							1	
Berchemia zeyheri		1			1					
Boscia albitrunca				2	1	1	1	2	1	2
Boscia filipes					1					
Boscia foetida								1	1	
Brachylaena huillensis									2	
Brachylaena transvaalensis									1	
Bridelia mollis				1	3				1	1
Burkea africana					1	2			2	
Cadaba termitaria				1						
Canthium armatum		2	2	2	1	1			2	
Capparis tomentosa				1						
Carissa edulis		1								
Cassia abbreviata									1	
Clerodendrum glabrum		2			1				1	
Coddia rudis		2			1				3	
Colophospermum mopane	8						8	8		2
Combretum apiculatum	6		3	4		5	6	2	2	3
Combretum erythrophyllum		1								
Combretum hereroense		5		2	1				1	
Combretum imberbe		1	1				1			1
Combretum molle		1				2		1	2	
Combretum mossambicense			3	1						1
Combretum padoides	2									
Combretum vendae									2	
Combretum zeyheri					2	2			3	
Commiphora africana			5				1	1		
Commiphora angolensis			1							
Commiphora edulis							1			
Commiphora glandulosa			1				4	3	1	4
Commiphora marlothii										1
Commiphora mollis	2		7	2	2	1	4	3	2	3
Commiphora pyracanthoides			1		1	1		3		
Commiphora schimperi									1	
Commiphora tenuipetiolata								2		5
Commiphora viminea						1				

Cordia monoica					1	1	1			
Croton gratissimus					1					
Croton pseudopulchellus					1					1
Dalbergia nitidula						1				
Dichrostachys cinerea		1			1		1			
Diospyros lycioides		1								
Diospyros villosa		3								
Dombeya rotundifolia		2		1					2	
Dovyalis zeyheri		1								
Ehretia rigida		5		2	3				1	
Elaeodendron transvaalensis		1								
Elephantorrhiza burkei					1				1	
Empogona kirkii						2				
Englerophytum magalismontanum									1	
Euclea crispa		1								
Euclea divinorum		1		1						
Euclea natalensis					2				3	
Euclea schimperi		1		6						
Flueggea virosa			1		1					
Gardenia resiniflua								1		3
Gardenia volkensii			1							
Grewia bicolor	4	2	3	8	1	1	6	8	2	8
Grewia flava	2		4	3						
Grewia flavescens	1	6	8	6	4	1	5	2	1	3
Grewia hexamita					4					5
Grewia monticola					1	1			2	1
Grewia retinervis						3				
Grewia subspathulata	3	1	5	1	1	1	4	2		1
Grewia tenax							1			
Grewia villosa			1		3		2			1
Gymnosporia buxifolia		2								
Gymnosporia glaucophylla		1								
Gymnosporia pubescens								1		
Gymnosporia senegalensis		2								
Gyrocarpus americanus					1					
Heteropyxis natalensis									1	
Hexalobus monopetalu				1	2	2			2	
Hyperacanthus amoenus									2	
Indigofera subcorymbosa									1	
Kirkia acuminata					4	1		2		2
Kirkia wilmsii									1	
Lannea schweinfurthii					1		5			1
Lycium cinereum						1				
Maerua parvifolia				1	1		1			
Maesa lanceolata										1
Markhamia zanzibarica			1							
Obetia tenax					1					
Ochna inermis				1	1	1	2	1		3

Ochna pulchra						3			2	
Olea africana									1	
Olea enervis									1	
Orbivestus cinerascens			1							
Ormocarpum trichocarpum		4		1					1	
Ozoroa paniculosa		1	2	0					2	
Pappea capensis		2		1	1				6	
Pavetta eylesii					2					
Peltophorum africanum		3	1	2	1	1			2	
Philenoptera violaceae			1	1	2			1		
Phyllanthus reticulatus			1							
Pseudolachnostylis maprouneifolia					1	2			1	
Psiadia punctulata					2				3	3
Psydrax livida					1	1			1	
Ptaeroxylon obliquum					1					
Pterocarpus rotundifolius									3	
Pyrostria hystrix				1						
Rhigozum zambesiacum	2						1			
Rhoicissus sp.									1	
Schotia brachypetala				4	1			1		
Sclerocarya birrea		2	7			1	3	2	2	1
Scolopia zeyheri		1								
Searsia leptodictya				2	1				1	
Searsia magalismontana subsp. *coddii*									1	
Searsia pentheri		2								
Senegalia ataxacantha									1	
Senegalia burkei						1				
Senegalia caffra		4							1	
Senegalia erubescens							2			1
Senegalia nigrescens	2		6	5	1		2	1		5
Senegalia schweinfurthii					2					
Senegalia senegal	1							2		2
Senegalia welwitschii					1					
Senna petersiana					1					
Sesamothamnus lugardii										1
Spirostachys africana			1	2						
Sterculia rogersii					1			4		1
Strychnos madagascariensis				3	3	3			2	1
Strychnos pungens						1				
Tarchonanthus parvicapitulatus									2	
Teclea pilosa		2								
Terminalia prunioides	2		3		3	1	6	6		4
Terminalia sericea			2	1	2	3			2	
Tinnea rhodesiana							1			2
Toddaliopsis bremekampii					1				1	
Vachellia gerrardii		5		3						
Vachellia karroo		1			1					
Vachellia nebrownii								1		

Vachellia nilotica		2	1							
Vachellia permixta		5								
Vachellia rehmanniana		2							1	
Vachellia robusta				1				1		
Vachellia tortilis	3	2	3	4	2		3	3	1	2
Vangueria dryadum					4				1	
Vangueria infausta		1			1				1	
Vangueria lasiantha						1				
Vangueria parvifolium						2				
Vitex pooara					1					
Vitex rehmannii									4	
Ximenia americana	3			3	1		2	4	1	1
Ximenia caffra			1		1					
Ziziphus mucronata		6	1	8	3				1	
Ziziphus rivularis		1								

CHAPTER 4

VHEMBE BIOSPHERE RESERVE ZONATION: LARGER CORE AND BUFFER ZONES ARE NOT NECESSARILY BETTER WHEN CONSERVING INVERTEBRATE DIVERSITY [3]

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Abstract

Biosphere reserves are a special class of protected area that seek to conserve biodiversity while still promoting sustainable development. This model of conservation is particularly attractive for developing countries which encompass most of the world's key biodiversity areas and where large segments of the populace still rely directly on natural resources. Biosphere reserves implement this model of conservation and sustainable development through unique zonation of strictly protected areas (core zones), semi-protected areas (buffer zones) and human modified landscapes (transition areas). We sampled selected ground dwelling invertebrate taxa in core, buffer and transition areas of the Vhembe Biosphere Reserve using pitfall traps, and assessed the performance of existing and proposed zonation representing the focus taxa. Our approach is novel as previous work has failed to address how biosphere reserves can perform in terms of conserving invertebrate diversity. The existing zonation, although considerably smaller than the proposed zonation, did significantly better than expected in conserving invertebrate species (conserving 47% of species). The proposed zonation conserved more species but was less effective than the current zonation. Invertebrate conservation in the VBR would benefit from targeted efforts that focus on rare and endangered species in transition areas that would complement the existing network of core and buffer zones

Keywords: Vhembe Biosphere Reserve, savanna, South Africa, Coleoptera, Araneae, Diplopoda

Introduction

As humans continue to dominate and destroy biodiversity worldwide, biosphere reserves may be the last places where significant biodiversity co-exists with human presence (Batisse, 1997). Traditional national parks do not usually include human settlements within their boundaries as they are managed as strict reserves that aim to protect biodiversity by excluding human impact (Bruner *et al*., 2001). Biosphere reserves on the other hand aim to minimize human impacts by implementing a range of activities that may benefit both humans and the natural world (Bridgewater, 2002). In some cases a holistic view of humankind's relationship with nature is envisaged, where the 'ecosystem' replaces the 'ego-system' (Scharmer & Kaufer, 2013). The philosophy behind this is that humankind becomes neither the master of its destiny nor the planet's, but an integral part of the ecosystem in which *Homo sapiens* evolved. In this way humanity can restore its relationship with the natural world.

Biosphere reserves remain an important model for conservation in developing countries, because they are often the only sites that attempt to reconcile biological conservation with sustainable development (Ishwaran *et al*., 2008). It is perhaps for this reason that developing countries have established biosphere reserves at a faster rate in recent years than developed countries (Coetzer *et al*., 2014). In their review on the effectiveness of biosphere reserves worldwide, Coetzer *et al*. (2014) identified the integration of sustainable use of resources and preservation of biodiversity as a significant challenge in the implementation of the Man and the Biosphere (MAB) model. This is because biosphere reserves are not managed by UNESCO but remain under the legislation of the countries in which they are found. Thus, a 'Biosphere Reserve' may remain only a bureaucratic label, with little resemblance to the model envisioned by UNESCO and MAB (Coetzer *et al*., 2014). And yet, Stoll-Kleeman & Welp (2008) and Schultz *et al*. (2011), suggest that the effectiveness of conservation and sustainable development is influenced by scientists and local inhabitants, particularly in Africa where the need for socio-economic development and poverty alleviation is often prioritized over nature conservation.

Although biosphere reserves contain strict parks and nature reserves, biosphere reserves world-wide correspond as a whole to category V (protected landscape / seascape) and VI (Managed resource protected area) of the IUCN protected areas categories, and are similar on a number of levels to the way in which British national parks are managed (British National Parks, 2017). Biosphere reserves consist of three zones that are managed differently. Core areas comprise strictly protected reserves; buffer zones surround the core areas and provide an extra 'layer' of conservation; transition zones are areas of sustainable ecological practices and include human habitation. There are at present 669 biosphere reserves in 120 countries, including 20 transboundary sites (UNESCO, 2017). Africa, with 75 sites, is the continent with the fewest biosphere reserves.

South Africa has eight biosphere reserves. In order of date of establishment they are Kogelberg (1998), Cape West Coast (2000), Kruger to Canyons (2001), Waterberg (2001), Cape Winelands (2007), Vhembe (2009), Magaliesberg (2015) and Gouritz Cluster (2015) (Pool-Stanvliet, 2013; Environmental Affairs, 2015). The distribution of biosphere reserves in South Africa is uneven, with four situated in the Cape Floristic Region, and three in the Savanna of the Limpopo Province. The remaining one is in Gauteng and part of North-West Province. Detailed assessments of the effectiveness of these reserves have been done for the Cape Winelands (Pool-Stanvliet & Giliomee, 2013), Waterberg (Baber & Abram, 2013) and Kruger to Canyons (Coetzer *et al*., 2010; Thomson & Uys, 2013). Although the National Protected Areas Expansion Strategy (Government of South Africa, 2010) and Limpopo Conservation Plan (SEF, 2016) identify critical biodiversity areas and focus regions in need of protection, this paper is the first assessment of invertebrate diversity across most of the Vhembe Biosphere Reserve.

The Vhembe Biosphere Reserve (VBR) was inscribed in 2009 (Pool-Stanvliet, 2013). It is situated in the northernmost region of Limpopo Province of South Africa. At 3 037 590 ha, the VBR covers a diverse array of biomes and habitats, including mist-belt forest, mountainous flora, arid bushveld and moist savanna (Mucina & Rutherford, 2006). The VBR also contains important rivers and catchment areas, including the Limpopo and Levuvhu Rivers (Modiba *et al.*, 2017). There are nine core zones in the reserve, including Kruger National Park and Mapungubwe National Park and Nwanedi Game Reserve. An important site, because it is the only nature reserve in Makhado Sweet Bushveld, is Ben Lavin Nature Reserve. Three of the buffer zone sites managed as fully protected areas are the Venetia-Limpopo Nature Reserve (private), and the Cycad Reserve and Makuya Game Reserve (provincial). A Strategic Environmental Management Plan was completed in 2016 that proposes revised core and buffer areas based on a more detailed analysis of biodiversity information (SEF, 2016).

It is impossible to review the effectiveness of biosphere reserves without inventorying biodiversity within core, buffer and transition zones. Checklists, inventories and regional monographs of the local fauna and flora provide data that is particularly relevant. Bird, vertebrate diversity and vegetation in particular are often utilized to prioritize areas (Myers *et al.*, 2000; Brooks *et al.*, 2006). By contrast invertebrates are poorly known and rarely used in designating management strategies and protected areas (Samways *et al.*, 2010). Yet invertebrates comprise the bulk of biodiversity and are useful surrogates of biodiversity in general (Gerlach *et al.*, 2013), with the proviso that a combination of invertebrate taxa are used (Lovell *et al.*, 2007).

There are currently 631 spider species recorded from the VBR. This represents 29% of all known species in South Africa (Dippenaar-Schoeman *et al*. 2010). Together with ants and beetles spiders dominate epigeal assemblages in the region (Munyai & Foord 2012) and unlike ants their taxonomy is better developed (World Spider Catalogue, 2018). More than 50% of ant species in ecological surveys are identified as morpho-species (Bishop *et al*., 2015) while this is often less than 20% for spiders. Apart from Scarabeidae, and although they can rival ants in terms of biomass caught in pitfalls, beetles have been largely neglected in ecological studies. In terms of phylogenetic disparity, millipedes compliment spiders and beetles and although also underrepresented in ecological studies South Africa, there is taxonomic expertise for the group (Hamer, 1998).

One of the major problems faced by protected areas worldwide, including core areas, is the increasing isolation of these protected areas, with resultant edge effects and disruption of movements between remnant wild landscapes. Outside the borders of the Kruger National Park, large human communities exist right up to the border of the Park (Coetzer *et al*., 2010). Buffer zones are also not recognized as protected areas as they do not fit into the IUCN categories, and therefore have no legal status. Their effectiveness is completely dependent on buy in from local organizations, land owners and resident communities. Buffer zones may include privately managed reserves.

The worldwide network of protected areas recognized in the Protected Planet Report (2014, 2016) includes biosphere reserves, including the 75 biosphere reserves in Africa. Of these, the VBR, the largest, faces significant threats to its biodiversity and natural resources from mining, poaching, over harvesting of natural resources, increasing population expansion and rural area developments and consequently the increasing isolation of core and buffer zones.

In this paper we assess the effectiveness of core, buffer and transition zones in conserving two dominant epigeal invertebrate taxa, beetles (Carabidae, Tenebrionidae and Scarabaeidae) and spiders (Araneae) and a third cryptic taxon, millipedes. More specifically we wanted to assess the relative effectiveness of these zones in terms of hotspots (species richness), complementarity and composition. and ask the following questions, (1) How effective is the current zonation in conserving invertebrate diversiy? (2) Does the effectiveness of zonations improve by increasing the size of core and buffer zones?

Methods and Materials

We sampled sites within the core, buffer and transition zones of the Vhembe Biosphere Reserve (Fig. 1). Sampling was conducted at three sites within the existing core areas, four sites within buffer zones, and 13 sites within the transition areas. In each site, eight sampling units were selected. Sampling units were a minimum of 300 m apart to avoid pseudoreplication (Samways *et al*., 2010). At each sampling unit we dug pitfalls in a pentagon, with each pitfall spaced at least 1m from the next. The pitfalls were filled with propylene glycol. We left pitfalls out for seven days during the summer season, sampling only once. There were a total of 800 pitfalls divided by 160 SU’s.

After seven days, pitfalls were collected, and all contents were poured into honey jars, which were then labeled by site, sampling unit and pitfall. In the lab, the contents of the honey jars were washed using a micro net and clean water, and further stored in 96% ethanol, and relabeled. We then sorted the contents of pitfall samples into their respective higher taxa, after which, each pitfall trap’s invertebrate content was sorted.

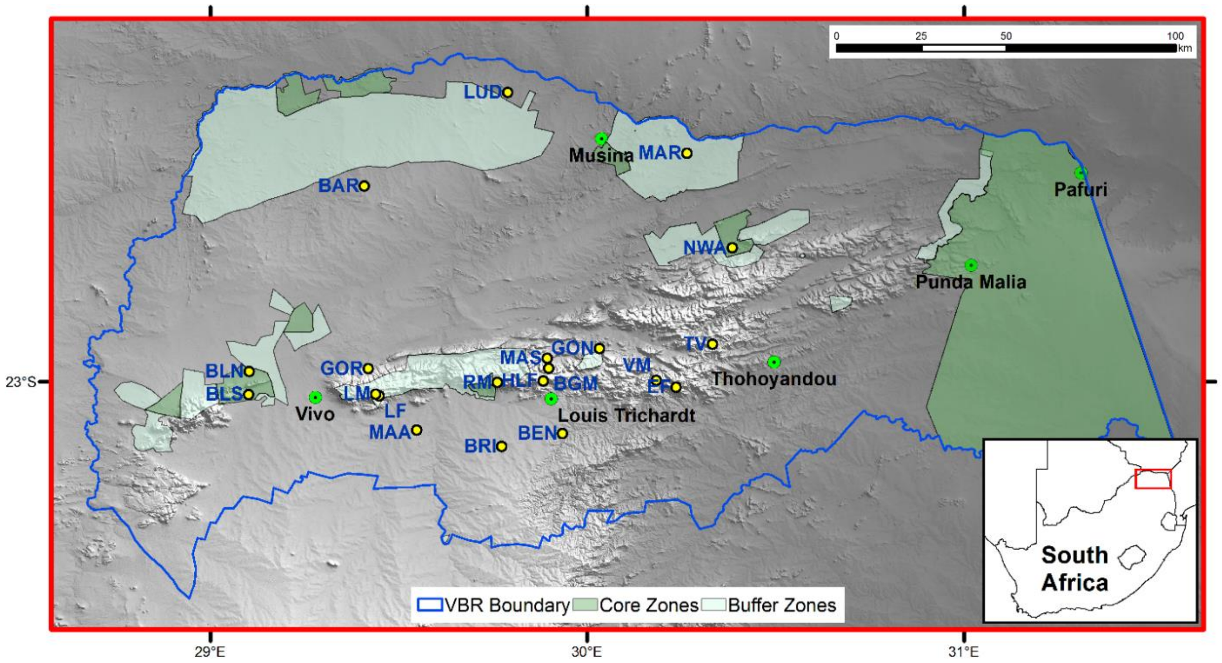

Fig. 1. Map of the Vhembe Biosphere Reserve showing distribution of existing core and buffer zones and transition areas; current core areas in dark green and buffer zones in lighter green, and outline of the reserve in blue. The remainder of the area outlines in blue is transition area.

The protocol for sorting entailed sorting morphospecies into groups on a large glass petri-dish using a stereo microscope. A representative individual of each morphospecies was pinned using black enamel insect pins, and labelled. The information on the label included habitat, site, sampling unit, pitfall number, date and number of individuals of morphospecies for that pitfall number. This process was repeated for each pitfall until completion. Once all representatives were pinned, final sorting of the pinned specimens into their morphospecies took place. This method enables one to immediately rectify mistakes in the data.

Species level determinations of Tenebrionidae and Carabidae were done by Ms R Muller from Ditsong Museum of Natural History. Scarabaeinae were identified by Dr A Davis from the University of Pretoria. Araneae were identified by Prof A.S. Dippenaar-Schoeman of the Agricultural Research Council. Spiders are housed in the Arachnida collection of the Agricultural Research Institute, Pretoria. Tenebrionidae and Carabidae were split between the

Coleoptera collection of the Ditsong Museum of Natural History, Pretoria and the University of Venda Natural History Collection, Thohoyandou. Millipedes were identified by Prof M. Hamer, South African National Biodiversity Institute and will be deposited in the Ditsong National Museum of Natural History.

Comparison of species richness in the different zones

Diversity in the three zones was first compared in a Kruskal-Wallis test of species richness with an unbalanced design. We analyzed data separately for beetles, spiders and millipedes. Sample means were calculated for SU's per zone. Mann-Whitney pairwise post-hoc tests were performed to identify contrasts that were responsible for overall significant differences. We did this analysis only for the existing zonation.

Assessment of performance of the zones to conserve invertebrate species

The performance of the existing and proposed zonation was evaluated by comparing them to null models. Here the number of species that would be conserved if core, buffer and transition zones were randomly selected was calculated by permuting labels across sites and recalculating the number of species conserved in the core or the core and buffer zones. This was repeated 999 times to generate a null distribution against which the actual number of species conserved in the existing or proposed core and buffer areas were compared. This provides some measure of the degree to which the current (Fig. 1) and proposed (Appendix A) zonation perform relative to randomly allocating zonations.

Comparison of community composition in the different zones

To assess whether the current zonation of the biosphere reserve is representative of the selected invertebrate community assemblages we also calculated what percentage of invertebrate taxa are conserved by core, buffer and transition zones.

Results

Mean beetle, spider and millipede richness peaked in the core areas (Fig. 2). Highly significantly differences existed for beetles ($p < 0.001$) and spiders ($p < 0.001$), but not for millipedes ($p = 0.97$). Transition zones were more species rich than buffer zones, with buffer zone sites having the lowest mean species richness for beetles, spiders and millipedes (Fig. 2). However, none of the posthoc comparisons were significant. They indicate that for spiders and beetles, the core zones alone do not contribute significantly towards species richness, as the transition zone roughly conserves the same number of spiders and beetles as core and buffer zones together. For both beetles and spiders buffer zones are not as diverse as the core conservation areas.

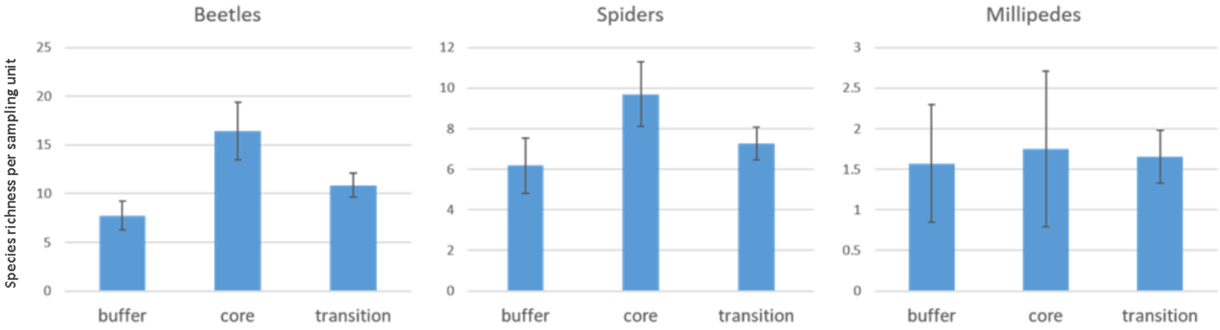

Fig. 2. Histogram comparing richness of taxa conserved within core, buffer and transition zones for beetles, spiders and millipedes. Standard error is plotted on the bars.

From the results for the permutation it is clear that in terms of the current zonation, core areas conserve significantly more species than if sites were to be selected randomly for beetles ($p = 0.003$) (Fig. 3, Table 1), while the evidence for spiders is weaker ($p = 0.09$) (Fig. 3, Table 1) while an evaluation of core and buffer zones together suggest that they don't perform better than random, with beetles achieving the best representation (Fig. 4, Table 1). Zonation performs poorly in representing millipede species (p = 0.95) (Fig.3 & 4, Table 1), and almost significantly weaker than random in certain cases.

Although the proposed zonation will increase the number of species conserved by the current zonation it does not perform better than the random expectation (Table 1).

Table 1. Comparison of species richness conserved in existing and proposed zonation of the Vhembe Biosphere Reserve. P-values report the proportion of permutations (random allocation of zonation to the 20 sites) that conserved a larger number of species than the zonation (current and proposed)

		Current zonation		Proposed zonation	
		No. of species conserved	p	Species conserved	p
All taxa (498)	Core	232 (47%)	0.01*	404 (81%)	0.75
	Core and Buffer	312 (63%)	0.27	449 (90%)	0.58
Beetles (260)	Core	129 (50%)	0.003**	210 (81%)	0.36
	Core and Buffer	170 (65%)	0.15	231 (88%)	0.69
Spiders (205)	Core	93 (45%)	0.08	166 (80%)	0.52
	Core and Buffer	129 (62%)	0.39	189 (92%)	0.4
Millipedes (33)	Core	10 (30%)	0.8	21 (63%)	0.95
	Core and Buffer	26 (79%)	0.99	29 (87%)	0.49

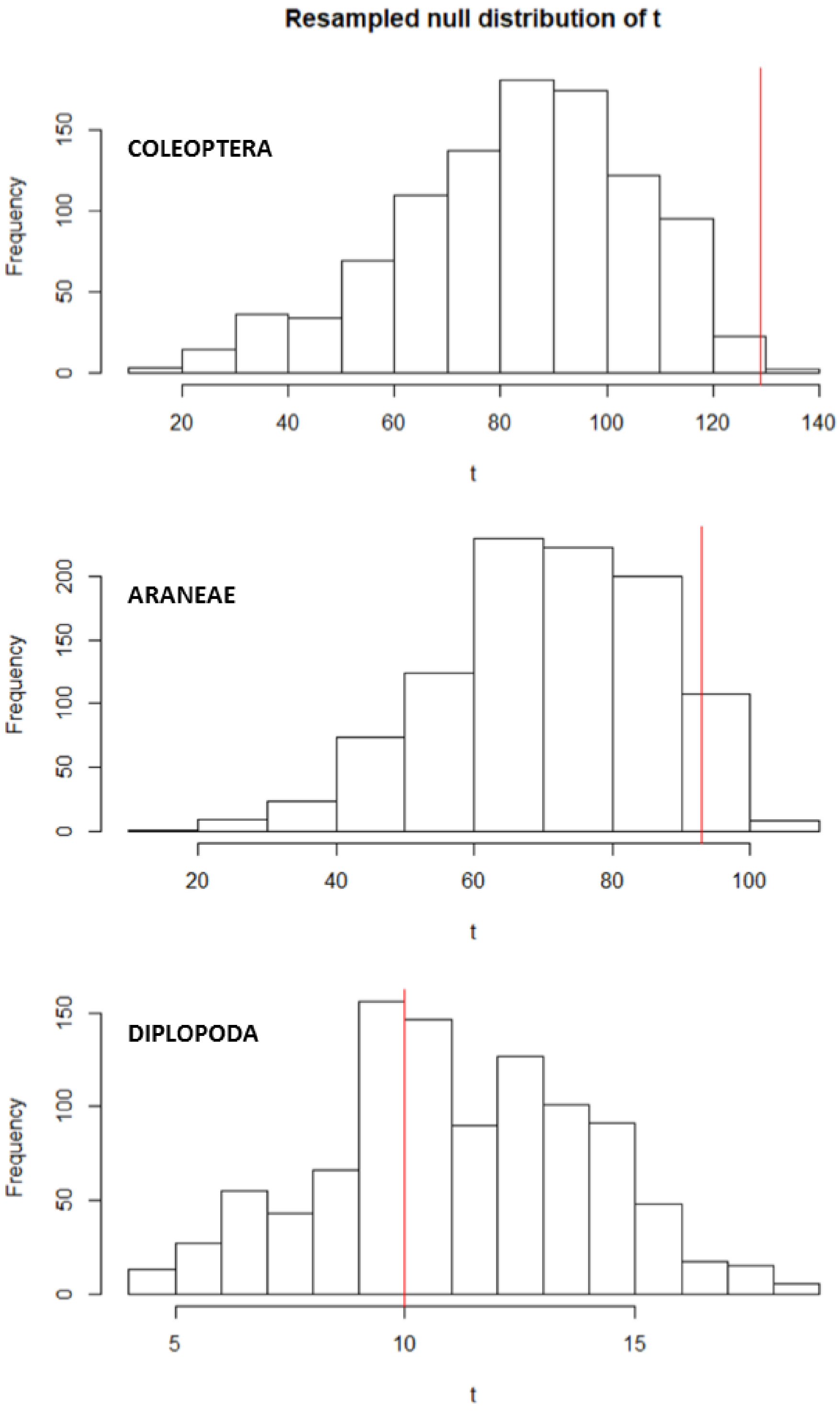

Fig. 3 Histogram of number of species conserved by permuted (999 permutations) and actual (red line) number of species conserved in the existing core zones of the Vhembe Biosphere Reserve. Coleoptera (p = 0.003), Araneae (p = 0.09), Diplopoda (p = 0.8).

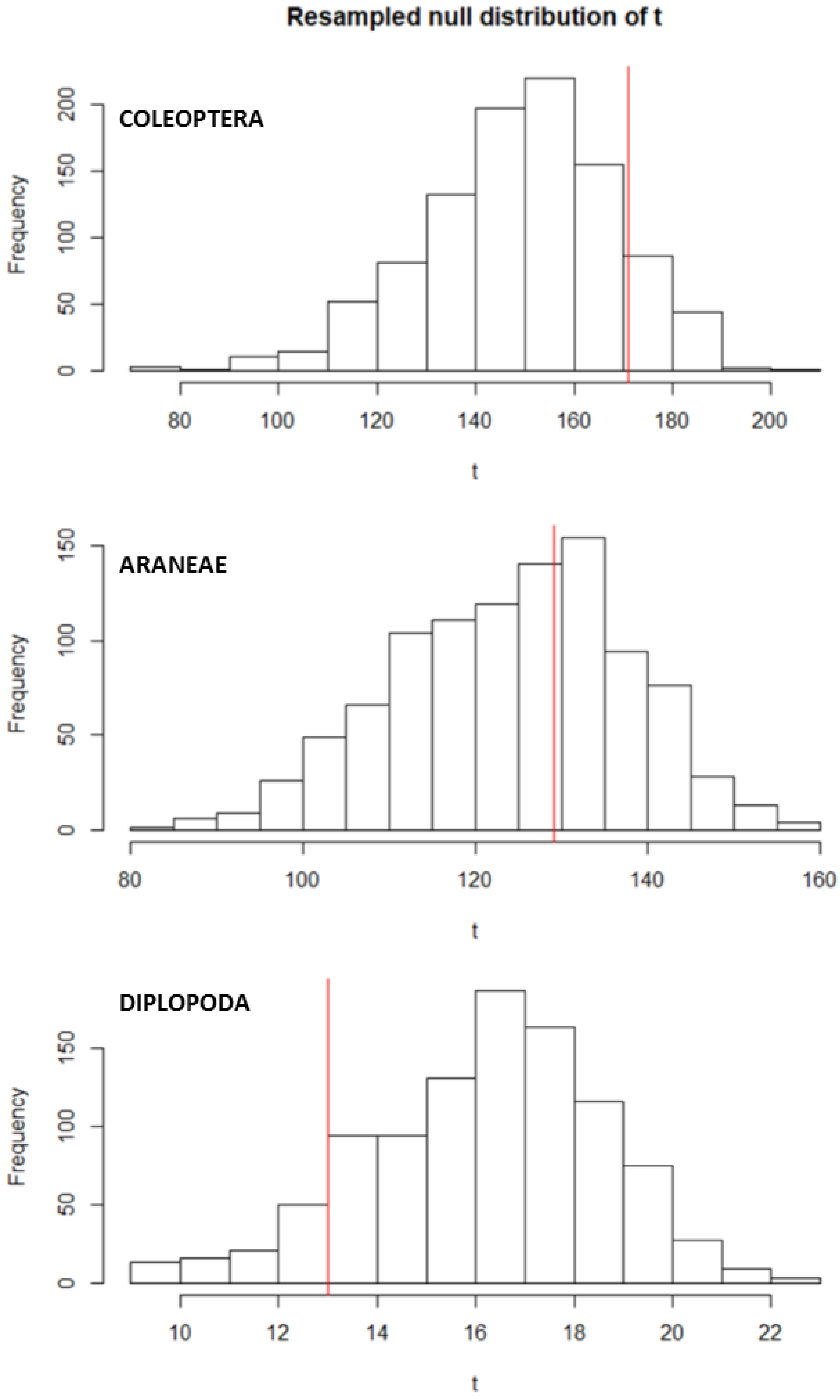

Fig. 4 Histogram of number of species conserved by permuted (999 permutations) and actual (red line) number of species conserved in the existing core and buffer zones of the Vhembe Biosphere Reserve. Coleoptera (p = 0.13), Araneae (p = 0.42), Diplopoda (p = 0.95).

Discussion

The existing core areas were very effective in representing diversity for the megadiverse taxa (beetles and spiders) and this is true for both richness and complementarity. This was however not true for the cryptic millipede taxon. Although the proposed zonation would include more species within core and buffer areas it was not as effective as the existing zonation, not performing better than chance for both Araneae and Diplopoda.

In the current zonation, topographically complex sites such as the western Soutpansberg and Blouberg were included in the core and buffer zones as they have low human population density and unproductive quartzitic derived soils. Topographically complex sites such as these are characterized by more environmental diversity largely associated with increased biodiversity (Engelbrecht *et al*. 2016). These two mountains can also be considered to represent old, climatically buffered, infertile landscapes (OCBIL) within the VBR (Hopper, 2009). Similar to the Cape Floristic Region these two mountains are characterised by high levels of diversity and endemism. The narrow distribution ranges and limited dispersal capabilities of taxa coupled with strong environmental gradients and relative climatic stability on these mountains could account for the high richness patterns we observed in the core areas. Davis *et al*. (1999) and Botes *et al*. (2007) found that diversity of carabids, tenebrionids and scarabs at higher altitudes were determined by a suite of drivers, all of which can be conserved by maintaining landscape heterogeneity while invertebrate diversity also typically declines with human management intensity (Marini *et al*. 2009).

Core areas were particularly weak in conserving millipedes, and the proposed zonation almost performed weaker than randomly allocating areas. Moir *et al*. (2009) found that millipede endemism was positively associated with differences in elevation. Ott & Van Aarde (2014) found that topographic variables on regenerating dunes in Natal alone determined the diversity of forest specialist millipedes. Murphy *et al*. (2008) found however that conditions in the ground layer, such as the presence of humus, pH, rotting wood and fruit, significantly affected millipede diversity and suggests that for millipedes, micro-habitat conditions are of primary importance in structuring communities. It is also important to note that these endemic millipede species could be relictual species and their distribution could largely be a function of history and therefore chance. The combination of very fine scale determinants and historical contingency and relatively depauperate community compared to spiders and beetles could explain why millipedes do not conform to the results for the other two taxa.

The millipede community in this study is comprised almost entirely of endemics, while the beetle and spider communities are a combination of endemics (Vhembe Biosphere Reserve, Limpopo) and generalists. In this context it is significant that for beetles at least, the core areas alone include most of the endemics. As an example, the core areas contributed to the greatest species richness of Anthiinae and Chlaeniinae (Carabidae), and *Scarabaeus* and *Onthophagus* (Scarabaeidae). Core and buffer zones also contributed all new species of the following genera found in the study: *Anaxius*, *Zoutpansbergia*, *Micrantareus* (Tenebrionidae), *Scarabaeus* (Scarabaeidae) and *Sacranemus* gen. nov. (Curculionidae). However some rare and endemic species including *Scarabaeus schultzi*, *Microstizopus transvaalensis* and *Wahlbergiana alternans* are not protected by core or buffer zones, although fortunately part of this assemblage was sampled on properties that are managed as protected areas. Beetle endemism seems to be driven by topography. Species of the darkling beetle genus *Anaxius* (Kaminsky & Schoeman, 2018) for instance are limited to elevations higher than 900 m.a.s.l. across the bushveld of southern Africa, with endemic species limited to particular ranges. The majority of rare and endemic species of spiders are also mainly found in the Soutpansberg and Blouberg and their surrounding foothills.

The proposed zonation is an expansion of the existing one, so the area added does not necessarily complement the existing zonation. Using the South African avifauna as a case study, Evans *et al*. (2006) found that total and threatened species richness exhibit modest increases with the proportion of protected land. Similarly, we found for this study that newly proposed core zones did not necessarily complement the existing core area assemblages. The proposed zonation has far more core and buffer zones than the existing, but they tend to be situated more closely to each other (Strategic Environmental Focus, 2016). The existing zonation has fewer core and buffer zones (three core areas in the existing as compared to 14 in the proposed), yet does exceptionally well in conserving species within this limited area.

There are no studies that measure the effectiveness of core and buffer zones in protecting invertebrate biodiversity within biosphere reserves in Africa. There are also very little data on how beetles do in protected vs. non-protected areas, and nothing on millipedes, although an impressive body of work exists on the persistence of African butterfly assemblages in forest fragments of west-central Africa and east Africa (Bobo *et al*., 2006; Bossart *et al*., 2006; Larsen, 2008; Sundufu & Dumbuya, 2008; Bosart & Opuni-Frimpong, 2009; Larsen *et al*., 2009; Sáfián *et al*., 2011), as well as spider faunal assemblages within southern Africa (Dippenaar-Schoeman *et al*., 2015). This study attempts to show that core and buffer zones must adequately represent key regional biodiversity areas (Juffe-Bignoli *et al*., 2014). This is important because faunal assemblages are declining within the borders of protected areas (Newmark, 2008; Barrett *et al*., 2009; Hutton, 2010). These declines are associated with disruption of migratory patterns due to increasing isolation (Douglas-Hamilton *et al*., 2005; Newmark, 2008), and edge effects associated with ongoing habitat degradation outside the borders of African protected areas (Woodroffe & Ginsberg, 1998; Clerici *et al*., 2007; Wegmann *et al*., 2014). The implementation of buffer zones as semi-protected areas around the existing network of protected areas might be an effective strategy at limiting these declines, as well as maintaining a network of suitable habitat outside protected areas (Newmann, 1997; Green *et al*., 2013). But they can only be effective if they protect significant remnants of natural habitat. For instance, forest fragments in western Africa are in a far from pristine state, yet are still effective at conserving butterflies (Larsen, 2008). In the Vhembe Biosphere Reserve there seems to be a similar overall persistence of a remarkable invertebrate fauna – possibly maintained by key biodiversity areas. We know of 63 families, 652 species (25% of all known spiders in SA), and 277 genera of spiders in the Vhembe Biosphere reserve (Dippenaar - Schoeman, 2010).

Local scale processes however play a highly significant role in maintaining invertebrate diversity in core areas. Studies on beetle fauna in southern Africa have largely found that the management of large herbivore populations, as well as the protection of sufficient habitat inside protected areas must form part of the conservation strategy for the protection of ground dwelling beetles in the region (Van Rensburg *et al*., 1999). Van Rensburg *et al*. (1999) found significant heterogeneity in dung beetle assemblages between reserves in KwaZulu-Natal. Some drivers decrease invertebrate diversity, and these must be ameliorated through appropriate management practices. Robertson *et al*. (2011) showed that plant invasions inside Kruger National Park had a significant negative effect on beetle community assemblages, though these had no effect on spiders. McGeoch *et al*. (2006) showed that high densities of elephants in KwaZulu-Natal had an adverse effect on the dung beetle fauna.

No studies in Africa have assessed how ground dwelling invertebrates persist within vs outside formally protected areas (although see Van Rensburg *et al*., 1999). Studies in west central and east African butterflies in forest fragments showed that butterflies have shown remarkable persistence in the landscape of large contiguous forest, modified habitat and remnants of forest of different sizes (Rogo & Odulaja, 2001; Larsen *et al*., 2009). In most cases significant remnants are protected in small reserves (Larsen *et al*., 2009), or sacred sites (Bossart *et al*., 2006), and conserve a significant proportion of regional butterfly assemblage. Up to the present, no butterfly species extinctions have been reported from West Africa (Larsen, 2008) – this despite continued fragmentation of rainforest in the region. There may however still be an extinction debt; yet Sáfián *et al*., (2011) showed that butterfly communities recover very quickly in secondary growth forests.

Although the proposed zonation marks a distinct improvement over the existing zonation as it includes private reserves within the core zones, a more real-world assessment of what areas can actually be conserved within the logistic framework of the VBR needs to be made. The proposed zonation is difficult to apply in reality, as some of the proposed core and buffer zones occur in densely populated areas, private land used for agriculture and communal properties which would be impossible to manage as protected areas – especially in the Pafuri area (Strategic Environmental Focus, 2016). As an example, it makes sense to include Makuya Nature Reserve as a core area in the proposed zonation. The surrounding habitat is however seriously degraded due to overgrazing, invasive aliens and soil erosion. Yet a study by Foord *et al*. (2018) conducted in Vyeboom and Ndengeza, two tribal areas in Limpopo Province, suggest that even overgrazed and degraded areas conserve a remarkable amount of animal diversity. It is very challenging to manage properties as core or buffer zones that do not already have an existing system of protection or conservation in place; such areas may face the same challenges as sites outside formally protected areas (DeFries *et al*., 2007).

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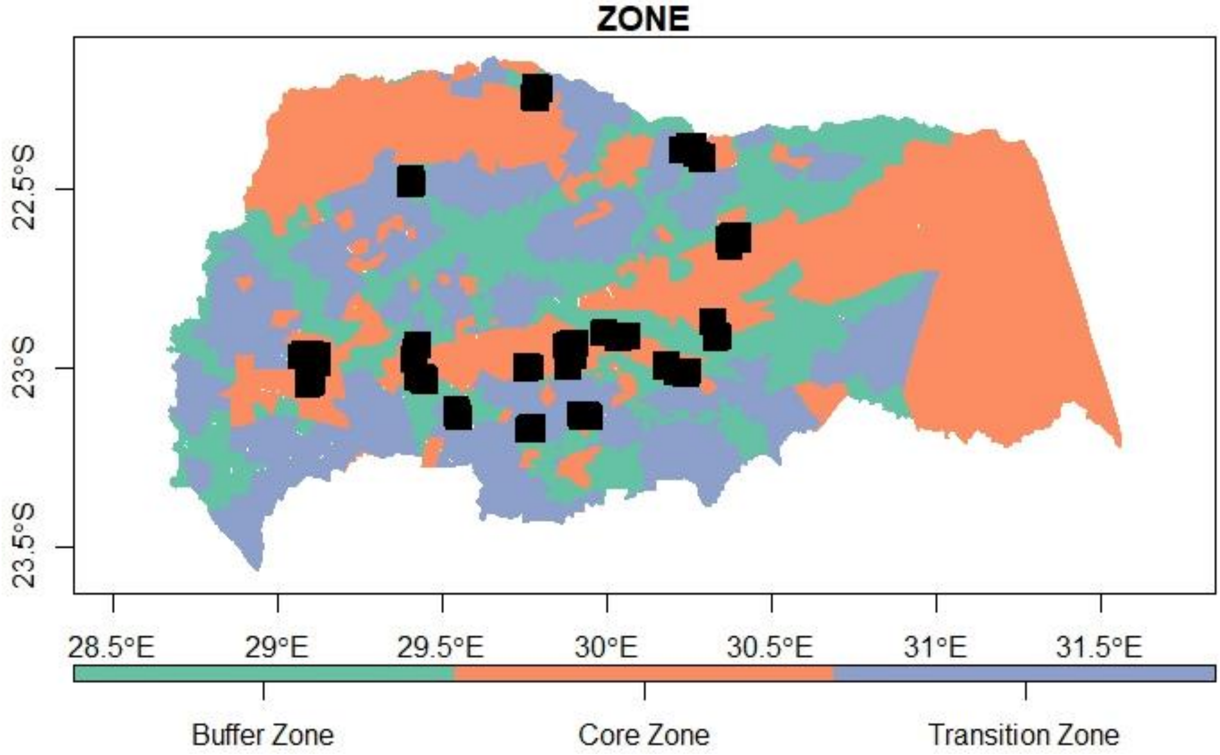
Appendix



Appendix A. Map of the Vhembe Biosphere Reserve showing distribution of proposed core and buffer zones and transition areas. Black markers represent the sampled sites.

CHAPTER 5

ANNOTATED CHECKLIST OF THE DARKLING BEETLES OF THE VHEMBE BIOSPHERE RESERVE, SOUTH AFRICA (COLEOPTERA: TENEBRIONIDAE)[4]

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Abstract

A checklist of genera and species of the Tenebrionidae of the Vhembe Biosphere Reserve is provided, as well as a short history of darkling beetle research in southern Africa. We briefly summarize the biology of tribes and genera of Tenebrionidae, and argue for their inclusion as a focal taxon in conservation planning. A total of 84 species are covered, which includes three new species endemic to the Vhembe Biosphere Reserve.

Keywords

Darkling beetles, biological notes, Savanna Biome, Limpopo Province, Soutpansberg

Introduction

Coleoptera, the most speciose order of animal on earth (Erwin, 1982; Erwin, 1988; Engel & Kristensen, 2013), still poses a considerable taxonomic challenge to ecologists who wish to use them for assemblage studies (Gerlach *et al*., 2013; Janion Scheepers *et al*., 2016), and to conservationists who may wish to assess threat status of species. .Although good guides are available to aid in the identification of a wide range of beetles in southern Africa (Stals & de Moor, 2008; Davis *et al*., 2008; Koch, 1956; Iwan, 2002), some of the literature remains intractable for non-specialists, although these groups yield genuinely useful results on drivers and correlates of diversity when effort is made to include them in conservation planning (Botes *et al*., 2007, Robertson *et al*., 2011) and provide significant ecosystem services to humankind (Nichols *et al*., 2008).

Of the ground-living beetles, Carabidae Latreille 1802 (ground beetles), Tenebrionidae Latreille 1802 (darkling beetles) and Scarabaeidae Latreille 1802 (dung beetles) are among the most abundant and diverse (Vohland *et al*., 2005) and dominate beetle assemblages caught in pitfall traps. The Staphylinidae Lameere 1900 are also an extremely diverse component of epigaeic faunal communities (Janion-Scheepers *et al*., 2016). Other families of super-abundant beetle families include Curculionidae, Chrysomelidae and Cerambycidae (Kergoat *et al*., 2014) – though these families are predominantly arboreal (Scholtz & Holm, 1985). Of these the darkling beetles (Tenebrionidae) rank as the 7th most speciose (Kergoat *et al*., 2014). They are important detritivores and granivores, and constitute a significant food source for reptiles and small mammals, especially in arid and semi-arid environments (Polis *et al*., 1998).

Beetles, with the exception of Scarabaeidae (Van Rensburg *et al*., 1999; Davis *et al*., 1999; Davis, 2002; Van Schalkwyk *et al*., 2017), pose a considerable taxonomic challenge in Africa. Other epigaeic taxa such as ants and spiders are not only well reviewed, but are covered in easily accessible books, revisions and field guides facilitating identification (Dippenaar-Schoeman & Jocqué, 1997; Hölldobler & Wilson, 1990). Beetles as a whole, are almost too diverse to be completely sampled at most sites (Janion-Scheepers *et al*., 2016), yet Carabidae, Tenebrionidae and Scarabaeidae may adequately represent ground dwelling arthropod diversity in its entirety. Many beetle families remain very poorly known, with few taxonomists available in Africa to describe new species, revise groups and offer assistance in determination of specimens. Yet beetles show possibly higher levels of diversity in the southern hemisphere than in the northern hemisphere, and latitudinal gradients in diversity do not quite follow trends observed north of the equator (Platnick, 1991). The Cape Floristic Region is abundant in tenebrionid tribes that have few or no representatives in the sub-tropical savannah (Endrody-Younga, 1978; Kamiński, 2015; Kamiński, 2016; Botes *et al*., 2007), inadvertently giving the impression that this family is species poor in the rest of South Africa (Gerlach *et al*., 2013).

The Tenebrionidae are remarkably diverse in the arid and semi-arid western regions of southern Africa (Koch, 1962a) including the Northern Cape, Namibia, and southern Angola; some groups, such as *Caenocrypticus*, are restricted to this region (Endrody-Younga, 1996). Nevertheless, arid associated taxa (Koch, 1962a) are encountered in the northern bushveld, especially the Limpopo Valley north of the Soutpansberg. At least 40 tribes are known to occur in sub-Saharan Africa (Heyns, 1959).

The history of darkling beetle taxonomy in southern Africa started fortuitously with Louis Albert Péringuey (Plate 1A), who wrote monographs on the Carabidae, Meloidae Gyllenhal, 1810 and Scarabaeidae of South Africa (Péringuey, 1896, 1902, 1909). Péringuey was in the process of preparing a monograph on the Tenebrionidae of South Africa when he died in 1924. This work was never published posthumously, although the lithographed illustrations prepared by A. Raffray were reproduced in Koch's (1955) monograph on the Tentyriinae. Dr Charles Koch (Plate 1B) worked as Head of the Coleoptera Department at the then Transvaal Museum from 1953-1970. He published prolifically on the Tenebrionidae of southern Africa, describing many new tribes and genera (Koch, 1950). He also established the Namibian Desert Research Institute at Gobabeb (Müller pers. comm.). Dr Mary-Louise Penrith worked at this station and the Namibian Museum, publishing important revisions of the tenebrionid tribes Zophosini (Penrith, 1979b-1983) and Adesmiini (Penrith, 1979a) before retiring from Entomology to pursue an academic career in Veterinary Science.

After Dr Charles Koch's death, Dr Sebastian Endrody-Younga (Plate 1C), was appointed head curator in his place. He was a world renowned coleopterist, a superb field biologist and gifted scientific illustrator. Mathews Mathebathe (Plate 1D) was born 1934 and started working at the Transvaal Museum with Dr. Charles Koch as a very young man and worked there until his retirement in 2002. He was a very gifted preparator. Examples of their meticulous curation are recorded in the Transvaal Museum Annual Reports. Endrody-Younga wrote: "Curation in 1992/1993: South American Expedition material: more than 50 000 specimens mounted, and more than 25000 specimens of South African material mounted, and labelled more than 40000 specimens over this two year period". Dr Endrody-Younga passed away in 1999, and with no specialist taxonomist replacing him, the taxonomy of a host of coleopterous families, including Tenebrionidae, based in South Africa has stagnated; although European-based taxonomists have continued to make important contributions to our knowledge of the South African fauna (Ferrer, 1991; Iwan, 1999, 2000; 2002; Iwan & Ferrer, 2000; Iwan & Kamiński, 2014; Kamiński, 2011, 2015b; Iwan & Schimroschyk, 2007, 2009; Iwan *et al.*, 2010; Schawaller, 2007, 2013; Schawaller & Bremer, 2013).

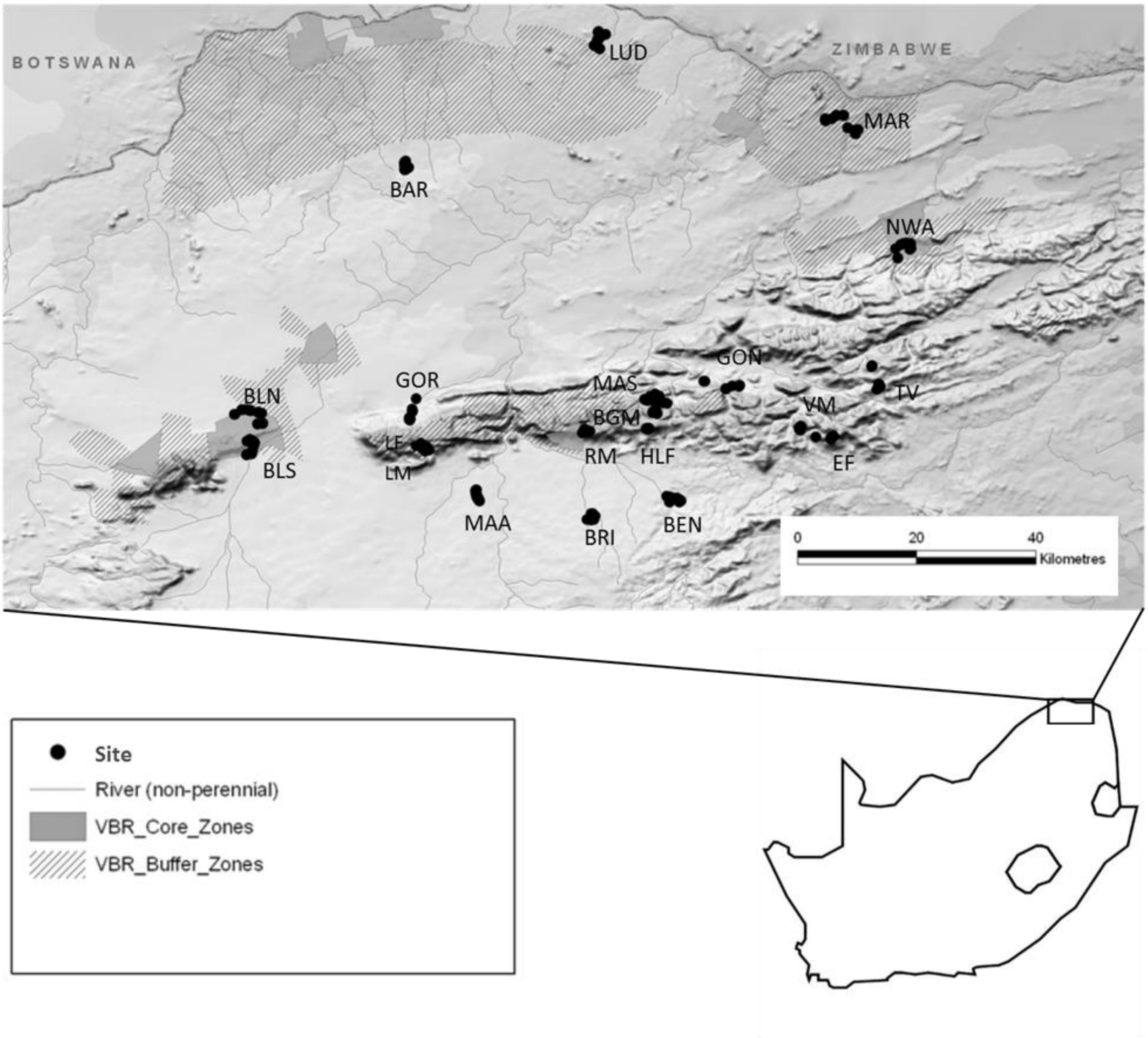


Fig. 1. Map of the Vhembe Biosphere in South Africa with locality of site names used in text and the gazetteer.

The checklist covers the darkling beetle fauna of the Vhembe Biosphere Reserve which is known to have rich plant (Hahn, 1994) and spider (Foord *et al.*, 2002) diversity, but with significant gaps in our knowledge of other hyper-diverse taxa in the region.

Methods and Materials

The Vhembe Biosphere Reserve (VBR), situated in Limpopo Province, South Africa, was established in 2009, and is by far the largest in the country with a size of 3 070 000 ha. Vhembe is located in the far northernmost reaches of South Africa and includes the Soutpansberg, Blouberg, the Limpopo Valley and the Pafuri region. It covers the entire Vhembe District of Limpopo Province, Blouberg Local Municipality and the northern part of the Kruger National Park (Pool-Stanvliet, 2013).

Twenty sites in the VBR were sampled using pitfall traps (maps were drawn using vector layers from DIVA-GIS) (Fig. 1). The sites covered different habitat types (Fig. 2-3) identified using Mucina & Rutherford's (2006) vegetation classification (Table 1). Within each site, we selected eight a-priori sampling points, hereafter referred to as sampling units (SU's). These SU's were spaced between 300 - 2000 m from each other.

Each SU comprised five pitfalls, placed in a circle, with a diameter of 10 m. Pitfall traps (7 cm diameter, `12 cm deep) were dug into the ground and a quarter filled with propylene glycol. Propylene glycol is non-toxic, and does not repel or attract animals through smell (Agosti *et al*., 2000). It also acts partly as a preservative until specimens can be processed and stored in alcohol.. Pitfalling expends the least amount of input with a greater comparable output than any other sampling method (Agosti *et al*., 2000). Left out for seven days, as was done here, it is possible to attain inventory completion for each point. Moreover, we wished to capture as much variation in the immediate habitat as possible and were careful to place our pitfalls in such a way as to consider microscale-heterogeneity.

After collection, the contents of each trap were washed using a fine net, and stored in 96% ethanol. Thereafter, the specimens from each trap were sorted into pill vials with acquisition numbers placed in each. This was an initial step before sorting each taxonomic group into morphospecies.

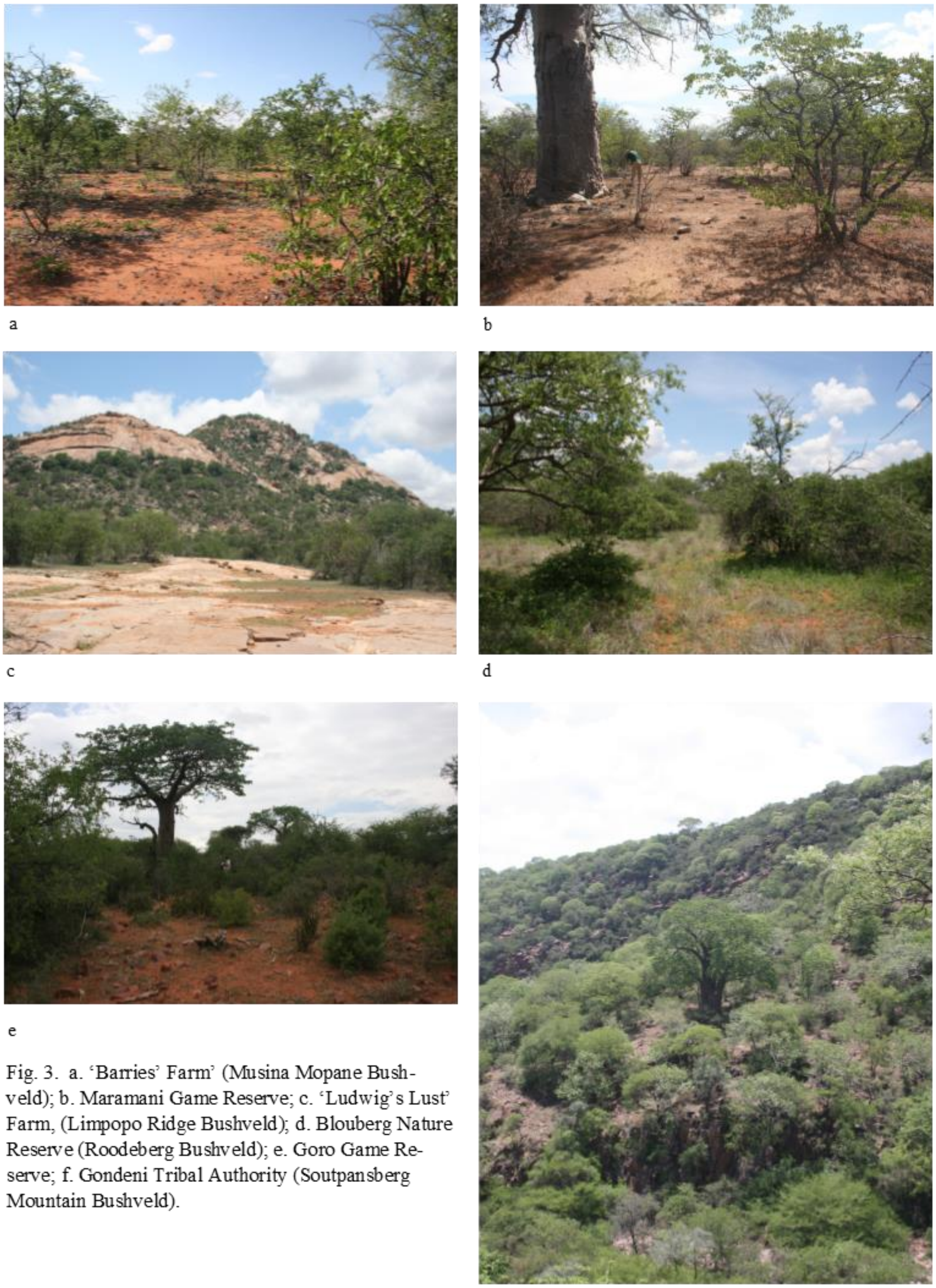
Beetles were sorted initially to families and subfamilies using Scholtz & Holm (1985). The most diverse beetles found in the pitfall samples were Tenebrionidae (31%), Scarabaeidae (45) and Carabidae (23%). Darkling beetles were sorted to morphospecies and where possible identified to the tribe level using Koch (1955) and Endrody-Younga (1988). Tenebrionidae identifications were then confirmed to genus and species level by Ruth Müller (Ditsong

National Museum of Natural History), and Mary Louise Penrith (retired entomologist). Vouchers of each species are housed in the Coleoptera Collection of the Ditsong Museum of Natural History and in the UNIVEN Natural History Collection.

In this paper we present 6 plates, depicting 24 species of Tenebrionidae found in the VBR (Plates 2-7). The photos were taken with a Kodak digital camera at the Soutpansberger Newspaper offices (Louis Trichardt, Limpopo) by Isabel Venter, who also photo-shopped the images to remove shadows and increase clarity and contrast.

This checklist of the darkling beetles of the VBR is the first published record of a major ground-dwelling beetle family for the region. It is also the first checklist of a major beetle family for any of the biosphere reserves in South Africa. Only those species that were recorded from the VBR are covered, and a brief overview is provided of the South African fauna at the level of the genera and tribes. In so doing we have collated the widely scattered biological information available, with the goal of increasing the usefulness of the checklist. Authorities with dates, synonymns, general distribution records and Vhembe Biosphere localities (Gazetteer and Fig. 1) are given for each species and morphospecies. Synonyms were obtained from primary references, as well as electronic resources: Catalogue of Life (Roskov *et al*., 2016). Infraspecific taxa are not distinguished in the checklist presented here. We include suspected species (designated with cf.) and morphospecies (identified to genus and tribe) in the checklist, highlighting future taxonomic research needs.

Fig. 2. a. Mara Research Station, b. Ben Lavin Nature Reserve, (Makhado Sweet Bushveld); c. Lajuma Mountain Retreat d. Vuvha Tribal Authority (Soutpansberg Summit Sourveld); e. Lajuma Mountain Retreat, f. Hanglip Forest, (Northern Mistbelt Forest).



a

b

c

d

e

f

Fig. 3. a. ‘Barries’ Farm’ (Musina Mopane Bushveld); b. Maramani Game Reserve; c. ‘Ludwig’s Lust’ Farm, (Limpopo Ridge Bushveld); d. Blouberg Nature Reserve (Roodeberg Bushveld); e. Goro Game Reserve; f. Gondeni Tribal Authority (Soutpansberg Mountain Bushveld).

Results

TENEBRIONIDAE Latreille, 1802

Tenebrionidae ranks as one of the most speciose beetle families, with at least 20 000 species described world-wide. They range widely in size, and adults feed mostly on decaying vegetation, and are nocturnal in habit (Kergoat *et al*., 2014). A few species seem to be active during the day as well (pers. obs.)

Southern African species are generaly moderate to strongly convex, occasionally flattened (*Stips*, *Eurychora*) beetles. The hind body is usually much larger than the fore-body (head and pronotum). The head is in many cases hypognathous (especially Sepidiini), or prognathous (Koch, 1955). Antennae are 11-segmented, inserted beneath the lateral expansion of the genae, the base of which is covered by a shelf-like canthus (Watt, 1992). They are dark brown to black, sometimes variable in colour – hence ‘darkling beetles’ (Kergoat *et al*., 2014). Legs are slender or often with well-developed processes on the fore-tibia, or mid-femora; the tarsal formula is 5-5-4 (Koch, 1955; Scholtz & Holm 1985); procoxal cavities closed externally (Kergoat *et al*., 2014). The first three abdominal segments are not loosely articulated, but fused together (Watt, 1991; Kergoat *et al*., 2014).

Watt (1974) produced a key to subfamilies of both adults and larvae. Of the seven subfamilies known to occur in South Africa (Scoltz & Holm, 1985), four subfamilies were sampled in the VBR: Diaperinae, Pimilinae, Stenochinae and Tenebrioninae .

The higher classification of the family has been reviewed by Watt (1974), Bouchard *et al*. (2005) and Kergoat *et al*. (2014).

DIAPERINAE

Diaperini

***Stomylus* Fahraeus, 1870**

Schawaller (2006) provides a summary of the African species.

Stomylus bicolor Fåhraeus, 1870
Schawaller 2006
Accession no: CSS-5/LF1a
Distribution: Sub-Saharan Africa
VBR locality: LF

PIMELIINAE Latreille, 1802

Many of the southern African Pimellinae were reviewed earlier by Koch (1955) as part of his delineation of the subfamily "Tentyriinae", according to which the abdomen has an intersegmental membrane between the distal segments, a still useful morphological feature in separating members of the subfamily from others (Watt, 1974) . The largest tribe is Sepidiini Eschscholtz, 1829, the tok-tokkies, which can be distinguished from other tribes on the bases of the presence of a trochantin on the meso-coxae. Koch (1955) provides a key to the tribes.

Adesmiini Lacordaire, 1859

The Adesmiini are pear-shaped beetles with slender, spindly mid- and hind-legs, often longer than the anterior legs, and distinctive elytral sculpturation. They are sun-loving, flightless, fast running beetles that occupy the savannah, grassland and desert biome. Their centre of diversity is Namibia and Botswana. Adesmiini were treated by Koch (1951), and Penrith (1979a, 1986) who provides keys to the genera and species. Lamb & Bond (2013) review the Namibian genus *Onymacris*. A total of three species are recorded.

Cephaladesmia Gebien, 1920

Cephaladesmia arachnoides Gerstaecker (?)
Accession no: Teneb55/LUD7e
Distribution: South Africa (N. Limpopo)
VBR locality: LUD
Note: Author date not found

Renatiella Koch, 1944

Medium sized beetles; elytra are ovate to rounded, and generally convex; the integument is black; legs are short and moderately slender (Penrith, 1979a). The pronotal surface is densely reticulate, the elytra have raised longitudinal and transverse ridges with tubercles on these raised elements and between them. The result is a reticulate-granulate sculpture (Koch 1951).

Renatiella reticulata (Gerstaeker, 1854) Plate 3D
  Macropoda reticulata Gerstaeker, 1854
Koch 1948, Penrith 1979a
Accesion no: TN19/BAR4c
Distribution: South Africa (Limpopo), southern Zimbabwe, northern Botswana, Malawi
VBR localities: MAR, BAR, BLN, GON, LUD, NWA
Note: Koch (1948) recognized 13 subspecies.

Stenocara Solier, 1835

Small to medium size beetles; elytra are ovate to rounded, moderate to strongly convex; the integument is black, appendages are often reddish; elytral sculpturation is longitudinally arranged or costate, slightly more elongate than *Renatiella* (Penrith, 1979).

Stenocara aenescens Haag, 1875
  Stenocara nervosa Haag, 1879
  Stenocara sericeiceps Péringuey, 1885
  Stenocara undulicostis Gebien, 1920

Koch 1951, Penrith 1979a
Accession no: Teneb29/LUD4c
Distribution: South Africa, Botswana, Namibia
VBR locality: LUD

Asidini Fleming, 1821

Most genera of Asidini are endemic to southern Africa and Madagascar (Koch, 1962b). The head is partly hidden from above, the pronotum has prominent lobes located antero-laterally, while the elytra are strongly convex with ridges and tubercles present, sometimes with a pair of sharply elevated costae. Koch (1962b) revised the sub-Saharan genera, of which seven occur: *Amachla*, *Machla*, *Asidomorpha*, *Machlomorpha*, *Machleida*, *Afrasida*, and *Cryptasida*. They are found predominantly in montane habitat and afromontane forest in undergrowth and may be hard to collect (Koch 1955).

***Amachla* Koch, 1962**

Medium sized beetles; the lateral margin of the pronotum is normal, and heart-shaped in dorsal view. The pronotum also has raised processes that are congruent with the elevated costae of the elytra; the prosternum has deep antennal grooves beneath the lateral pronotal margin; and the elytral costae are tuburculate (Koch, 1955). Antennae appear ten segmented, as the eleventh segment is fused broadly with the tenth segment (Koch, 1962b).

Amachla schmidti Wilke, 1924
Accession no: Teneb51/TN15/BEN5d
Distribution: South Africa
VBR localities: BEN, BLS, MAS

Amachla sulcicollis (Fåhraeus,1870)
Koch 1962b
    Pseudomachla sulcicollis Fåhraeus, 1870
Accession no: Teneb22/MAR2c
Distribution: South Africa
VBR localities: MAR, BLS, MAA

Amachla echinoderma Fairmaire, 1899
Koch 1962b
Accession no: CSS-06
VBR localities: VM, LM

Amachla sp. A Plate 4B
Accesion no: Teneb46/BLS7c
VBR locality: BLS

Machlomorpha Péringuey, 1899

The body of these beetles is small to medium in size, with the lateral margins of the pronotum carinate, never heart-shaped, and without a distinct antennal groove on the prosternum. The scutellum has a deep longitudinal groove; the elytra have sharply elevated costae, without tubercles occurring on the costae. A pseudopleural crest is situated between the posterior margins (or costa) of the elytra and the abdominal sternites (Koch, 1962b).

Machlomorpha cf. *evanida* Wilke, 1924
Accession no: TN11/BEN1b
Distribution: South Africa
VBR localities: BEN, LM, VM

Machlomorpha cf. *mossambica* Péringuey, 1899 Plate 4A
Accession no: Teneb45/VM8b
Distribution: South Africa
VBR localities: EF, VM

Epitragini

Himatismus Erichson, 1843

Himatismus sp. A
Accession no: 14S4-A3

VBR localities: BRI, LM, LUD

Adelostomini Solier, 1834

Koch (1955) and Scholtz & Holm (1985) refer to this tribe as Eurychorini Solier, 1837. These are specialized tenebrionids with approximately 20 endemic South African genera (Koch, 1955). The vertex of the head is slightly concave in dorsal view, with a narrow neck, the pronotum has broad lateral flanges. The elytra are also very broad. Several genera have stridulatory organs on the inner surface of the middle femora (Schawaller, 2007). They often bear soil particles and other debris held by long hairs on the dorsal surface, which may be indicative of myrmecophyly (Schawaller, 2007). Haag-Rutenberg (1872) and Koch (1952) provide keys to the different genera and Schulze (1962) provides a key of the larvae. Brown (1958) summarizes information on the distribution of the genera in South Africa. Other genera occurring in the Vhembe region (not sampled for this study) include *Geophanus*, *Prunaspila* and *Phytolostoma*.

***Eurychora* Thunberg, 1789**

The antennae are thick and strong. Antennal segment three is as large as four and five together or larger (Haag-Rutenberg, 1872); the antenna are much longer than the breadth of the head (Koch, 1952). The prothorax has broad lateral flanges, attached to the rounded elytra via a narrow constriction, the lateral margins of the elytra are smooth or lightly granulate (Koch, 1952).

Eurychora barbarta Olivier, 1795 Plate 3C
Haag-Rutenberg 1872
Accession no: Teneb37/MAR6a
Disribution: South Africa, Botswana, Namibia
VBR localities: MAR, BRI

Eurychora sp. A
Accession no. UVICT_EuA
VBR locality: RM, GON

Pogonobasis Solier, 1837

These beetles are smaller than *Eurychora*. Overall the body is more compressed, the pronotum has lateral flanges, and the elytral surface is punctate and covered in rufous setae (Haag-Rutenberg, 1872). The genus *Pogonobasis* Solier, 1837 has been extensively studied by Haag-Rutenberg (1875) and Koch (1952a), but needs revision (Ferrer, 2006).

Pogonobasis ovatus Fåhraeus, 1870
Haag-Rutenberg 1872; Koch 1955
Accession no: Teneb38/GOR8c
Distribution: South Africa (Limpopo)
VBR localities: GOR, LM, LF

Serrichora Koch, 1952

These beetles occur predominantly in the western parts of southern Africa (Brown, 1958). They are similar in general appearance to the other Eurychorines, but much smaller in size, with the pronotum and hind body with finely serated margins, and each elytron with a very sharp margin (Koch, 1952).

Serrichora fahraei (Haag 1872)
Koch 1952, Robertson *et al*. 2011
Accession no: Teneb34/LM4b
Distribution: South Africa (Limpopo, KwaZulu-Natal), Mozambique
VBR localities: GON, LM, RM

Sepidiini Eschscholtz, 1829

Koch (1955) and Scholtz & Holm (1985) refer to this tribe as Molurini Solier, 1834. The presence of a membrane between the distal sternal segments, of a trochantin on the mesocoxae, and a very broad scutellum above the elytra serve to differentiate the Sepidiini , or tok-tokkies, from other Tenebrionidae. They are flightless beetles, usually strongly convex and globular; the elytra are extremely variable in shape, and loosely attached to the pronotum.

Sepidiini generally show a smooth, punctate, or costate type of elytral sculturation in which raised longitudinal costal elements dominate the sculpture patterns – these may be smooth, denticulate or irregular (Koch, 1955). Their common name derives from the habit of rapidly tapping the ground with the abdomen to attract a mate. About 1000 species and many genera occur over the African continent. The Sepidiini are a mostly sub-Saharan group, but with representatives in the Sahara and the Middle-East. Koch (1955) provides a key to subtribes.

***Amiantus* Fåhraeus, 1870**

These beetles have a punctate pronotum and costate elytra: costae are smooth and densely punctate in intervals, or denticulate with tubercles in the intervals between the costae. Legs are densely setose (Koch, 1955).

Amiantus cf. *gibbosus* Fåhraeus, 1870
Hesse 1935, Koch 1955
Accession no: Mspp14/BRI7e
Distribution: South Africa (Limpopo)
VBR localities: BLN, BRI

Amiantus pusillus Péringuey, 1904 Plate 5A
Accession no: Mspp15/BLS3d
Distribution: South Africa (Limpopo)
VBR localities: BLS, BRI

***Dichtha* Haag-Rutenberg, 1871**

The head is nearly concealed from above by the densely punctate pronotum. The surface of the elytra are smooth without dorsal costae, but with sharp lateral costae which gives the hind body a box-like shape; the legs are densely fulvous with light-coloured setae (Koch, 1955).

Dichtha cubica Guérin-Méneville, 1845 Plate 5B
Bertkau 1875, Koch 1955
Accession no: Mspp18/NWA1c

Distribution: South Africa (Limpopo)
VBR localities: BEN, BGM, BRI, GON, GOR, MAS, NWA

Distretus **Haag-Rutenberg in Harold, 1871**

Similar to *Dichtha*, except that the lateral costae expand distally in dorsal aspect (Koch, 1955). The pronotum is coarsely punctate, with a matte elytral surface.

Distretus discoideus (Guérin, 1845) Plate 5C
Koch 1955
Accession no: TN8/BAR1d
Distribution: South Africa (Limpopo)
VBR localities: BAR, BEN, BLN, BLS, BRI, GON, GOR, MAA

Euphrynus **Fairmaire, 1897**

Euphrynus carinatus Fåhraeus, 1870
Accession no: Teneb48/BLN3d
Distribution: South Africa (Limpopo)
VBR locality: BLN

Phanerotomea **Koch, 1958**

= *Phanerotoma* Solier, 1843 syn. by Koch (1958)

These beetles are dark brown to black in colour. The anal sternite of the abdomen is marginate; males have a densely haired patch on the underside of the anterior femora; the tibiae have scattered, dark bristles; the apex of the posterior tibia is often dilated; the elytra smooth, without costae and globular. *Phanerotomea* contains some of the largest darkling beetles in the world (Koch, 1955). Besides of the species listed below eight different morphospecies were collected and are available with the following accession nos: sp. A. UVICT_PhaA VBR locality: RM; sp. B UVICT_PhaB VBR localities: BLN, BRI, MAS, NWA; sp. C UVICT_PhaC VBR localities: LM, BGM, VM; sp. D UVICT_PhaD VBR localities: LM, VM; sp. E UVICT_PhaE VBR localities: BGM, LM, RM, VM; sp. F

UVICT_PhaF VBR localities: BRI, GON, LM, MAS; sp. G UVICT_PhaG VBR localities: LM. VM; sp. I UVICT_PhaI VBR localities: GON, GOR, LM.

Phanerotomea rowleianum Westwood (?) Plate 6B
Accession no: Mspp10/BRI7e
Distribution: Namibia, Botswana, South Africa
VBR locality: BRI
Note: author date not found

Phanerotomea scrobicollis (Fåhraeus, 1870) Plate 6C
Ocnodes scrobicollis Fåhraeus, 1870
Ferrer 2006
Accession no: Mspp2/MAS1d
Distribution: Namibia, Botswana, South Africa
VBR localities: BGM, BLN, BLS, BRI, GON, GOR, LUD, MAS, NWA

Psammodes **Kirby, 1819**

= *Hypomelus* Solier, 1844
= *Ocnodes* Fåhraeus, 1870
= *Piazomera* Solier, 1843
= *Psammodius* Berthold in Latreille, 1827
= *Psammodophys* Péringuey, 1899

Very similar in general appearance to *Phanerotomea*. The anal sternite of the abdomen is immarginate (without an edge). In males the underside of the femora is without distinctive characters (Koch, 1955). Posterior tibiae are not dilated apically.

Psammodes cf. *janitor* Koch (?)
Accession no: Mspp19/BRI2c
Distribution: South Africa
VBR localities: BRI, MAA
Note: author date not found

Psammodes cf. *ventricosus* Fåhraeus, 1870 Plate 6D

Hesse 1935; Koch 1955
Accession no: Mspp11/13/MAS3d/e
Distribution: South Africa
VBR locality: MAS

Psammodes vialis (Burcell, 1822) Plate 6A
Koch 1955
Accession no: Mspp1/BLN1b
Distribution: Namibia, South Africa
VBR localities: BLN, GON, GOR

Psammophanes **Lesne, 1922**

= *Psammolophus* Koch, 1953
= *Psammophrynopsis* Koch, 1953
= *Psammophrynus* Koch, 1953
= *Psammostretus* Koch, 1953
= *Psammotyriopsis* Koch, 1953

Psammophanes sp. A Plate 5D
Accession no: UVICT_Ps4
VBR localities: RM, LM

Somaticus **Hope, 1859**

= *Trachynotus* Haag, 1871 syn. by Koch (1955)

This is a very large genus, which is treated in great detail by Koch (1955). The pronotum is hexagonal in shape, with a sharp anterior margin ventrally; the head is clearly visible from above; the shape of the body ranges from slender to moderately globular. The dorsal costae are well pronounced.

Somaticus cf. *metropolis* Koch, 1955
Koch 1955
Accession code: Teneb64.2/RM2e
Distribution: South Africa

VBR locality: RM

Somaticus angulatus Fåhraeus, 1870
Koch 1955
Accession no: UVICT_SOM1
Distribution: South Africa
VBR locality: MAS

Somaticus varicollis Koch, 1955 Plate 7A
Koch 1955
Accession no: Teneb64/RM2a
Distribution: South Africa (incl. KwaZulu-Natal, Free State, Mpumalanga, Limpopo), southern Zimbabwe
VBR locality: RM

Somaticus aeneus (Solier, 1843)
Koch 1955
Accession no: UVICT_SOM2
Distribution: Namibia, Botswana, South Africa
VBR locality: TV

***Ossiporis* Pascoe, 1866**

These are unusual Sepidiini , with an overall lightly coloured body; eyes are strongly raised above the level of the vertex; antenna inserted close to the anterior region of the vertex giving the head a curculionid-like appearance, although the antennae are clearly not elbowed; the elytra with one pair of lateral costae (Koch, 1955).

Ossiporis fragilis (Fåhraeus, 1870)
Koch 1955
Accession no: CSS-07
Distribution: South Africa, Zimbabwe
VBR locality: BLS

Zophosini Solier, 1834

***Zophosis* Latreille, 1807**

Anacardiosis Endrödy-Younga, 1986
Calcarosis Penrith, 1977
Caroliphosis Penrith, 1981
Gahanosis Penrith, 1983
Namaphosis Penrith, 1981
Predactylosis Penrith, 1977
Propemicrosis Penrith, 1981
Protocalosis Penrith, 1977
Protodactylus Koch, 1952
Septentriophosis Penrith, 1982
Zophodactylus Koch, 1962

Coffee-bean beetles are often seen running very rapidly over bare ground (Picker *et al.*, 2004). When caught they are usually covered with a fine yellow dust which rubs off when handled. The tribe is monogeneric: but there are many sub-genera and species and they are often the most abundant beetles in pitfalls (Penrith, 1977). The elytra may display small pits, raised costae, or be completely smooth. Their centre of diversity is the arid western part of southern Africa, including Angola (Koch, 1956). Penrith (1977, 1979b-1983) revised the genus.

Zophosis (Zophosis) mellyi Deyrolle, 1867
    Zophosis difficilis Deyrolle, 1867
    Zophosis obsoleta Deyrolle, 1867
Penrith 1981
Accession no: UVICT_ZophA
Distribution: South Africa, Botswana, Namibia
VBR localities: BAR, BLS

Zophosis (Hologenosis) gracilis Fåhraeus, 1870

Penrith 1982

Accession no: UVICT_ZophB

Distribution: South Africa, eastern Botswana, Zimbabwe

VBR localities: LUD, MAR, BLS

Zophosis (Hologenosis) burkei Deyrolle, 1867

Penrith 1982

Accession no: UVICT_ZophC

Distribution: South Africa, Botswana, Namibia, Zimbabwe, Mozambique, Malawi, Tanzania, Zambia

VBR localities: BAR, GOR, LUD

Zophosis (Oculosis) boei Solier, 1834 Plate 4D

Zophosis delalandi Solier, 1834
Zophosis delelandi Solier, 1834
Zophosis caffer Deyrolle, 1867
Zophosis inexplicta Deyrolle, 1867
Zophosis dregei Deyrolle, 1863
Zophosis angusticostis Deyrolle, 1867
Zophosis solieri, Deyrolle, 1867
Zophosis fugax Fåhraeus, 1870
Zophosis moesta Fåhraeus, 1870
Zophosis atra Fåhraeus, 1870
Zophosis anceps Fåhraeus 1870
Zophosis morula Chatanay, 1917
Zophosis latipennis Chatanay, 1920
Oculosis boei Penrith, 1977
Oculosis angusticostis Penrith, 1977

Penrith 1983

Accession no: UVICT_ZophD

Distribution: Throughout southern Africa, Zambia, south DRC

VBR localities: BAR, BLN

Zophosis (Oculosis) convexiuscula Gerstaecker, 1854

Zophosis excisa Chatanay, 1914

Penrith 1983

Accession no: UVICT-ZophE

Distribution: South Africa (KwaZula-Natal, Mpumalanga, Limpopo), Mozambique, Malawi, Tanzania

VBR locality: BAR

Zophosis (Oculosis) nitidisternalis Penrith, 1983

Penrith 1983

Accession no: UVICT_ZophF

Distribution: southern Zimbabwe, Mozambique, Zambia, DRC

VBR localities: BAR, BEN

Zophosis (Oculosis) sp. 1

Accession no: TN8/29

VBR localities: BAR

Cryptochilini Solier, 1840

The tribe Cryptochilini is very poorly represented in the VBR, as their centre of diversity is the arid south-west of Africa, occurring especially in the Northern Cape, Namibia and Angola. Penrith & Endrody-Younga (1994) revised the tribe.

Cychrochile **Koch, 1953**

Small to medium sized beetles, extremely hairy with 10-segmented antennae bearing one to two distal clubs (Penrith & Endrody-Younga, 1994).

Cychrochile pluricostata Penrith, 1994

Penrith & Endrody-Younga 1994

Accession no: CSS-08

Distribution: South Africa (N. Limpopo)

VBR locality: LM

STENOCHINAE

Strongyliini

This group is hardly studied in South Africa.

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Strongilium **Kirby, 1819**

Strongilium sp. A
Accession no: CSS-MS8
VBR locality: MAS

TENEBRIONINAE Latreille, 1802

The Tenebrioninae are characterized by the lack of an intersegmental membrane between the distal segments (Scholtz & Holm, 1985). Unlike Pimeliines which are more often than not globular in shape, Tenebrioninae show much greater diversity in shape and size. Members include ground dwelling and arborial species. Twelve of the tribes spread across Africa delimited by Koch (1956) as Opatrinae (including Pedinini and Opatrini) are now included in Tenebrioninae (Bouchard *et al*., 2005). Many endemics occur in the Namib Desert (Koch, 1953, 1954).

Opatrini Brullé, 1832

Iwan & Kamiński (2016) provide a revised classification of the tribe.

Gonocephalum **Solier, 1834**

Members of the genus are known as dusty surface beetles (Mlambo, 1983), *Gonocephalum* occurs throughout the whole African continent (Koch, 1956). Iwan *et al*. (2010) provides a checklist of the genus world-wide.

Gonocephalum sp. A
Accession no: Teneb15-LM7b

VBR localities: LM, RM, VM

Note: this species is very likely *G. simplex* which is common and known to damage maize seedlings in Southern Africa (Drinkwater, 1999).

Microstizopus **Koch, 1963**

Small beetles, light-brown in colour; the elytra are smooth with intermittent darker patches. Members of this genus are restricted to South Africa and southern Namibia. *Microstizopus transvaalensis* occurs only in the Soutpansberg and Blouberg (Iwan & Schimrosczyk, 2009).

Microstizopus transvaalensis Koch, 1963
Iwan & Schimrosczyk 2009
Accession no: Teneb32/TV6e
Distribution: South Africa (Limpopo)
VBR localities: MAR, BLN, BLS, BRI, LUD, TV

Pedinini Eschscholtz, 1829

The anterior tibia of Platynotina Mulsant and Rey, 1853, the most common subtribe of Pedinini in southern Africa (Iwan, 2000), is generally strongly to triangularly dilated (Koch 1956). Platynotina are flightless. The subtribe's centre of radiation is largely Southern Africa although other genera occur farther up in Africa. In Melambiina the diversity of the Palaearctic component is the same as the Afrotropical one which has been reviewed by Kaminsky (2011, 2015a). All Platynotina and Eurynotina of the Pedinini have a stridulatory gula, a distinctive feature of these subtribes (Kaminsky, 2016). In South Africa there are no representatives of Pedinina, Dendarina, or Loensina. Iwan (2002) has produced a world catalogue of the Platynotina. The African Pedinini has been extensively reviewed by Iwan, 1999, Iwan *et al*., 2011, Iwan & Kamiński 2014, Kamiński, 2011, 2012, 2013, 2015a, 2016, Kamiński & Ras, 2012.

***Anchophthalmus* Gerstaecker, 1854**

=*Oxythorax* Fåhraeus, 1870 syn. by Gebien (1938)

=*Oncotiphallops* Koch, 1956 syn. by Iwan (2002a)

Kaminsky (2015) summarizes the information available on this, and related genera.

Anchophthalmus algoensis Péringuey 1904 Plate 3B
Kamińsky & Iwan 2013, Kamińsky 2015
Accession no: Teneb60-BEN1b
Distribution: southern and eastern Africa
VBR localities: BEN, BLS, BRI

***Anomalipus* Latreille, 1846**

= *Heteroscelis* Latreille, 1829 hom. by Endrody-Younga (1988)

= *Ectatocnemis* Horn, 1866 syn. by Endrody-Younga (1988)

Large or very large beetles of dull or black colour. The lateral margin of the anterior tibia has a large process (Endrody-Younga, 1988). The mentum is very large, concealing the base of the maxillary palps; the presence of a stridulatory gula is unique to this genus (and *Gonopus*, which it resembles). The pronotum is often as broad as or broader than the elytra – elytral sculpturation is usually species or sub-species specific. Endrody-Younga (1988) wrote a valuable monograph on the genus. Besides of the species listed below eight different “morphospecies” were collected and are available with the following accession no: sp. A UVICT_AnA VBR locality: MAA; sp. B UVICT_AnB VBR localities: BLN, GOR; sp. C UVICT_AnC VBR locality: BLS; sp. G UVICT_AnG VBR locality: GOR; sp. L UVICT_AnL VBR locality: BEN.

Anomalipus cf. *carinatus* Oertzen 1897
    Anomalipus amblipennis Péringuey, 1904
    Anomalipus subacutangulus Hesse, 1935
Endrody-Younga 1988; Iwan 2002
Accession no: Teneb9/MAA6c
Distribution: South Africa, Zimbabwe, Botswana
VBR locality: MAA

Anomalipus cf. *granocostatus* Fairmaire, 1894

Anomalipus deceptor Péringuey, 1904
Anomalipus hypocrita Péringuey, 1904

Endrody-Younga 1988; Iwan 2002

Accession no: Teneb57/TN14/BEN5e

Distribution: South Africa (Mpumalanga, Limpopo, KwaZulu-Natal), Mozambique, Swaziland

VBR locality: BEN

Notes: five sub-species described for South Africa (Endrody-Younga, 1988)

Anomalipus cf. *variolosus* (Solier, 1836)

Heteroscelis variolosus Solier, 1836

Endrody-Younga 1988; Iwan 2002

Accession no: Teneb4/MAS6e

Distribution: South Africa (Limpopo, KwaZulu-Natal, Eastern Cape)

VBR locality: MAS

Notes: The Vhembe region may represent the northernmost locality of this species yet recorded

Anomalipus elephas Fåhraeus, 1870 Plate 2A

Endrody-Younga 1988, Iwan 2002

Accession no: TN5/BEN3d

Distribution: South Africa, Zimbabwe, Botswana, Namibia

VBR localities: BEN, BLN, BLS, GON, MAA

Anomalipus expansicollis Fairmaire, 1891 Plate 2B

Anomalipus thoracicus Oertzen, 1897
Anomalipus asidoides Oertzen, 1897
Anomalipus selatinus Péringuey, 1904
Anomalipus crassicauda Fairmaire, 1894

Endrody-Younga 1988, Iwan 2002

Accession no: Teneb58/TN17/BEN7c

Distribution: South Africa (Limpopo), southern Mozambique

VBR localities: BEN, LM, VM

Anomalipus sculpturatus Péringuey, 1886 Plate 2C

Anomalipus marshalli Péringuey, 1886

Anomalipus costatus Oertzen, 1897

Anomalipus granatus Fairmaire, 1897

Endrody-Younga 1988, Iwan 2002

Accession no: Teneb3/MAS4e

Distribution: South Africa (Limpopo)

VBR localities: GON, MAS

Anomalipus seriatus Oertzen, 1897 Plate 2D

Anomalipus spectandus Péringuey, 1904

Anomalipus hybridus Oertzen, 1897

Anomalipus variabilis Oertzen, 1897

Endrody-Younga 1988, Iwan 2002

Accession no: Teneb8/VM6d

Distribution: South Africa (Soutpansberg)

VBR locality: VM

Note: This species may be restricted to the Vhembe Region.

Anomalipus meles Fåhraeus, 1870

Endrody-Younga 1988, Iwan 2002

Accession no: CSS-09

Distribution: South Africa (Mpumalanga, Limpopo), Lesotho, S Botswana

VBR locality: TV

Anomalipus lemur Fåhraeus, 1870

Endrody-Younga 1988, Iwan 2002

Accession no: CSS-10

Distribution: South Africa (Mpumalanga, Limpopo, KwaZulu-Natal, Free State)

VBR locality: TV

Bantodemus Koch, 1955

Iwan & Banaszkiewicz (2006) review the genus; Iwan (2000) provides a key with illustrations to the species in South Africa; *Bantodemus* is a southern African endemic.

Bantodemus lucidus Koch, 1955
Iwan 2000, 2002
Accession no: Teneb35/BLS2b
Distribution: South Africa (Limpopo), Zimbabwe
VBR locality: BLS

Bantodemus. *lajumaiensis* Kamiński & Schoeman, 2018b
Kamiński & Schoeman, 2018b
Distribution: Soutpansberg (Limpopo)
CBR locality: LF, LM

Gonopus Latreille, 1829

Similar in general appearance to *Anomalipus*, the elytra of *Gonopus* are more rounded however, and the anterior margin of the pronotum is broader than the posterior margin articulating with the base of the elytron (Endrody-Younga, 2000). Other separating characters are the deep, collar-like anterior margin of the prosternum; the protibia bearing 2-6 lateral teeth or corresponding undulations, and a stridulatory gula. Endrody-Younga (2000) revised the genus.

Gonopus cf. *deplantus* Fåhraeus, 1870 Plate 3A
    Gonopus costatus Fåhraeus, 1870
    Gonopus agrestis Fåhraeus, 1870
Endrody-Younga 2000, Iwan 2002
Accession no: Teneb12/BRI7c
Distribution: Zimbabwe, Mozambique, Namibia, Botswana, South Africa.
VBR localities: BLN, BRI

Gonopus hirtipes Fåhraeus 1870

Endrody-Younga 2000, Iwan 2002
Accession no: Teneb13/MAA2b
Distribution: Namibia, South Africa
VBR localities: BLN, MAA
Notes: most widely occurring of *Gonopus* species

Gonopus tibialis (Fabricius, 1789)
  Blaps tibialis Fabricius, 1798
  Gonopus sulcatus Solier, 1848
  Gonopus ventricosus Bertoloni, 1849
  Gonopus exaratus Gerstaecker, 1854
  Gonopus ater Fåhraeus, 1870
Endrody-Younga 2000, Iwan 2002
Accession no: Teneb14/GON8a
Distribution: Namibia, Botswana, Zimbabwe, South Africa, Mozambique
VBR locality: GON

***Zoutpansbergia* Koch, 1956**

This genus is endemic to the Soutpansberg, with only two species known from localities north of Lajuma. Kamińsky & Schawaller, 2018 describe a new species named after the author.

Zoutpanbergia schoemani Kamińsky & Schawaller, 2018
Kamińsky & Schawaller, 2018
Distribution: Soutpansberg (Limpopo Province)
VBR locality: LM, GOR
Note: a highly localized endemic

Amarygmini Gistel, 1856

These beetles are arboreal, ovate in shape and black in colour. Many have a thorn-like projection on the fore-femora and the head is sometimes concealed from above by the pronotum. The membrane between the frontal margin of the clypeus and the labrum is nearly always freely visible (Bremer & Lillig, 2014). The head is orthognathous, with the eyes reniform, and the head narrowed on the frons. Antennae are filiform without a separate club, reaching beyond the base of the pronotum. The prosternum is very short before the coxae and shorter than the pronotum, with a bordered anterior margin (Schawaller & Bremer, 2013). Myrmecophilous forms also occur (Schawaller, 2007). Ardoin (1962-1969) revised the African species. Bremer & Lillig (2014) have produced a catalogue of the world Amarygmini. This group is in need of revision.

Hoplonyx **Thomson, 1858**

Hoplonyx cristatus Fåhraeus, 1870 Plate 7B
Bremer & Lillig 2014
Accession no: Teneb40/NWA7c
Distribution: Namibia, Botswana, South Africa (N.Limpopo)
VBR localities: BRI, GON, NWA

Hoplonyx (*Nataloplonyx*) *micans* Schaufuss, 1870
Hoplonyx metallicus (Fåhraeus, 1870)
Oplocheirus metallicus Faraeus, 1870
Bremer & Lillig 2014
Accession no: Teneb18/EF7d
Distribution: South Africa (KwaZulu-Natal, Limpopo)
VBR locality: EF

Oplocheirus **Lacordaire, 1859**

Oplocheirus clypeatus Fåhraeus, 1870
Hoplonyx perforatus Péringuey, 1904
Hoplonyx frontalis Gebien, 1910
Bremer & Lellig, 2014
Accession no: CSS-11
Distribution: Tanzania to South Africa
VBR locality: TV

Eupezus Blanchard, 1845

Eupezus longipennis Gerstaecker, 1871
Bremer & Lellig 2014
Accession no: CSS-12
Distribution: South Sudan; Kenya; Uganda; Tanzania; Malawi; Zimbabwe; Mozambique
VBR locality: TV

Helopinini Latreille, 1802

Originally designated Drosochrini (Koch,1958), Bouchard *et al*. (2005) regard this name as an unnecessary replacement name for Helopinini. A predominantly South African tribe, they are wingless and nocturnal and usually found under stones. *Drosochrus* is small to medium sized, while *Micrantereus* is large. Many species can be recognized by seven or more sharply elevated costae (Scholtz & Holm, 1985). Koch (1958) provides an overview of the two genera included here.

Anaxius Fahraeus, 1870

A genus with highly localized endemic species occurring throughout Limpopo Province and Zimbabwe. These are medium sized black beetles typically with bowed hind tibia which is very distinctive (Kamiński & Schoeman, 2018a (Appendix 1)).

Anaxius bloubergensis Kamiński & Schoeman, 2018a
Kamiński & Schoeman, 2018a
Distribution: Blouberg Nature Reserve (Limpopo Province)
VBR locality: BLS, BLN
Notes: a highly localized endemic known to occur only in Blouberg Nature Reserve.

Drosochrus Erichson, 1843

Beetles of small to moderate size, varying from 3 – 12 mm in length, the upper surface bare or pilose, the pronotum and elytra punctured, with intervals sometimes bearing small rows of tubercles or with raised ridges (costate) (Koch 1958).

Drosochrus sp. A

Accession no: TN1/BEN4a

VBR Localities: GOR, BEN

Droschrus sp. C Plate 7D

Accession no: Teneb30/BLS3e

VBR localities: BLS, GON, GOR, LUD, MAA, MAS, NWA, BEN

***Micrantereus* Solier, 1848**

= *Solenomerus* Fåhraeus, 1870 syn. by Fairmaire (1897)

Beetles of medium size, varying (10 – 24 mm) in length, the upper surface sometimes densely pilose, the pronotum punctured; and the elytra costate and somewhat tuburculate. Males display a large tooth-like projection on the mid-femora (Koch 1958).

Micrantereus planatus (?)

Distribution: South Africa

Accession no: UVICT_Mc1

VBR localities: BEN, BLS

Note: author and date not found

Micrantareus sp. 2

Accession no: UVICT_Mc2

VBR locality: NWA

Micrantareus sp. 3

Accession no: UVICT_Mc3

VBR locality: MAA

Micrantareus sp. 7 Plate 7C

Accession no: Teneb53/GON3d

VBR localities: MAS, GON

Scaurini Billberg, 1820

Herpiscius Solier, 1838

Small beetles that have an elongated distal antennal segment, widely separated pronotum and elytra. The head has a peculiar shape with supra-orbital ridges (somewhat resembling the head of an ant) and the front tibia is bowed (Koch, 1958).

Herpiscius gracilis Gerstaecker, 1854 Plate 4C
Koch 1958
Accession no: TN21/BAR1b
Distribution: Mozambique, South Africa (Limpopo)
VBR localities: MAR, BAR, LUD

Discussion

Of the Tenebrionidae 84 species were sampled, of which 23 are unidentified to species level; these were mostly in the tribe Helopinini, and the genera *Anomalipus* and *Phanerotomea*. Of these three are new species, all endemics: *Bantodemus lajumaiensis*, *Anaxius bloubergensis* and *Zoutpansbergia schoemani*.

The proportion of unidentified to identified species is lower than expected, and similar to results for spiders obtained in the region. Only 17% of spiders sampled in the Soutpansberg are unidentified (Foord, pers. comm.), while 21% of the beetles sampled for this study were identified only to morphospecies. However, the proportion of identified to unidentified is much higher than for the Namibian fauna, which has been extensively studied and sampled since the 1960’s (Koch, 1962a; Polis *et al.*, 1998). Furthermore, the Tenebrionidae of the VBR are clearly comparable in diversity to Tenebrionidae in the Namib Desert; a long term monitoring program at Gobabeb in Namibia recorded 82 Tenebrionidae species (Henschel *et al.*, 2003). The VBR beetles do not have the high number of endemics found in the Namib however.

The Soutpansberg Mountain contains a few possible darkling beetle endemics: *Microstyzopus transvaalensis*, and *Zoutpansbergia* (sampled in another study). The Limpopo Valley also contains beetles possibly endemic to the Limpopo Basin: *Cychrochyle pluricostata*. Subsets of the beetle communities of the VBR, especially Tenebrionidae, show strong regional associations, influenced not just by environmental variables, but by biogeography, such as the psammophylous Sepidiini associated with the mega-Kalahari deep-sands (Koch, 1962a), and Platynotina radiations associated with the Bushveld Igneous complex (Endrody-Younga, 1988, Kamiński & Iwan, 2013). Otherwise the taxonomic composition, even at tribal level, is very different as the ground dwelling coleopterous assemblage of the VBR is dominated by summer-rainfall faunas with distributions extending into the tropics: a trend observed in other families as well (Davis *et al*., 2008).

We broadly identify key points that should be the focus of future research in Africa. The Tenebrionidae, together with other speciose ground dwelling beetles, Carabidae and Scarabaeidae, represent an ideal combination of taxa in studying the effects of change, and should be promoted as such to safeguard the future of invertebrate conservation in Africa. There is a need to generate data on species turnover affected by broad scale environmental variables (Hawkins *et al*., 2003), beetle biogeography and zoogeographic provinces in the light of new data (Wharton & Robert, 1982; Holm *et al*., 1984). Furthermore, very little has been done on studying the ecosystem services provided by Tenebrionidae and Carabidae, especially in arid ecosystems where these taxa are particularly prominent.

The major contribution of this study is to highlight the necessity of continuing to sample and compare faunal assemblages between major biogeographic regions or biomes, focusing on poorly sampled regions. The South African National Survey of Arachnida (Dippenaar-Schoeman *et al*., 2015) provides a tried and tested protocol which can be emulated to catalogue and promote the beetle diversity of South Africa, generating biodiversity data that can provide valuable information to the scientific community. An important by-product of this would be to produce checklists, regional guides and keys to re-invigorate ground-dwelling beetle research in one of the most biodiverse countries in the world.

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Plates

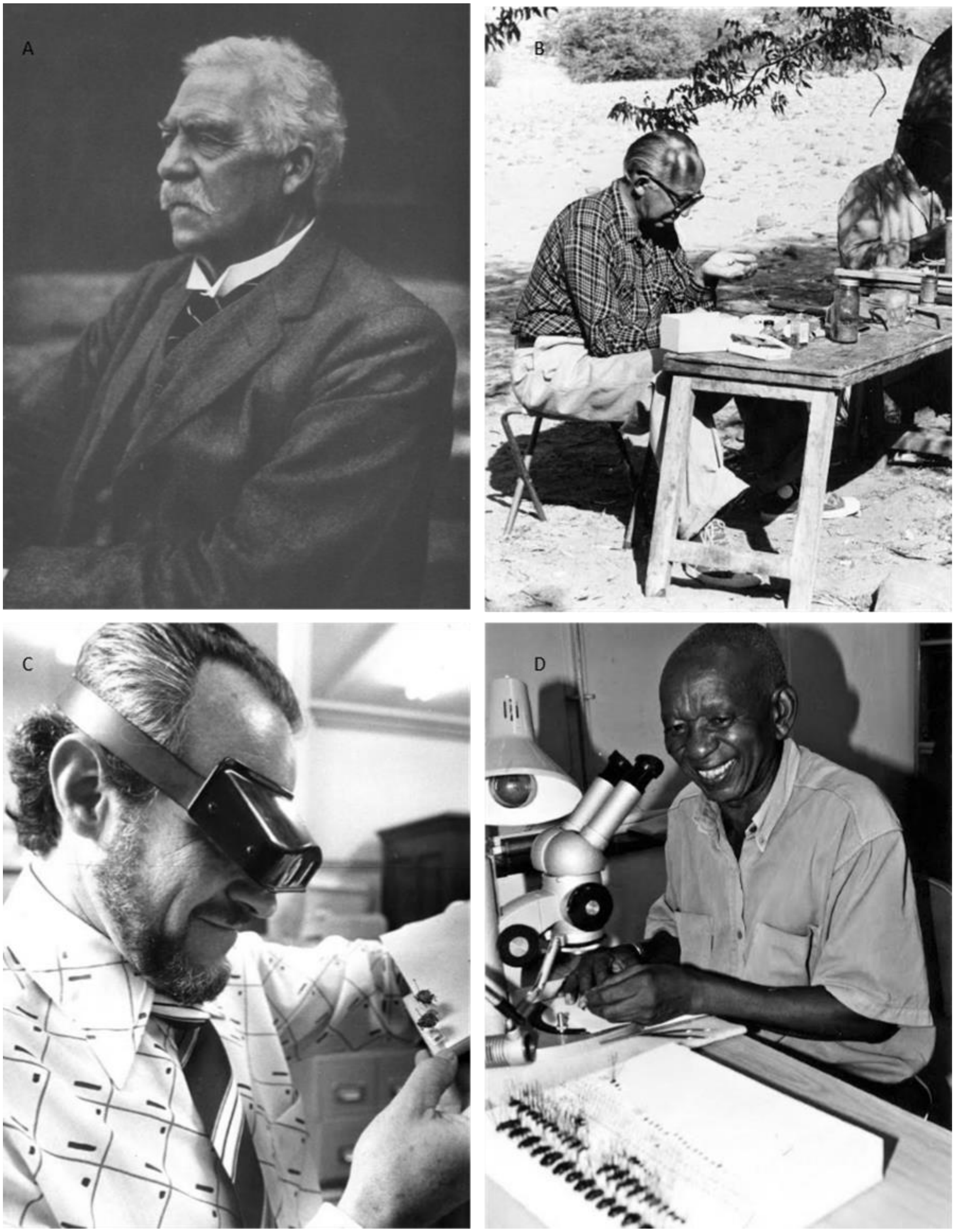

PLATE 1

A. Louis Albert Péringuey, B. Charles Koch, C. Sabastian Endrody-Younga, D. Mathews Mathebathe

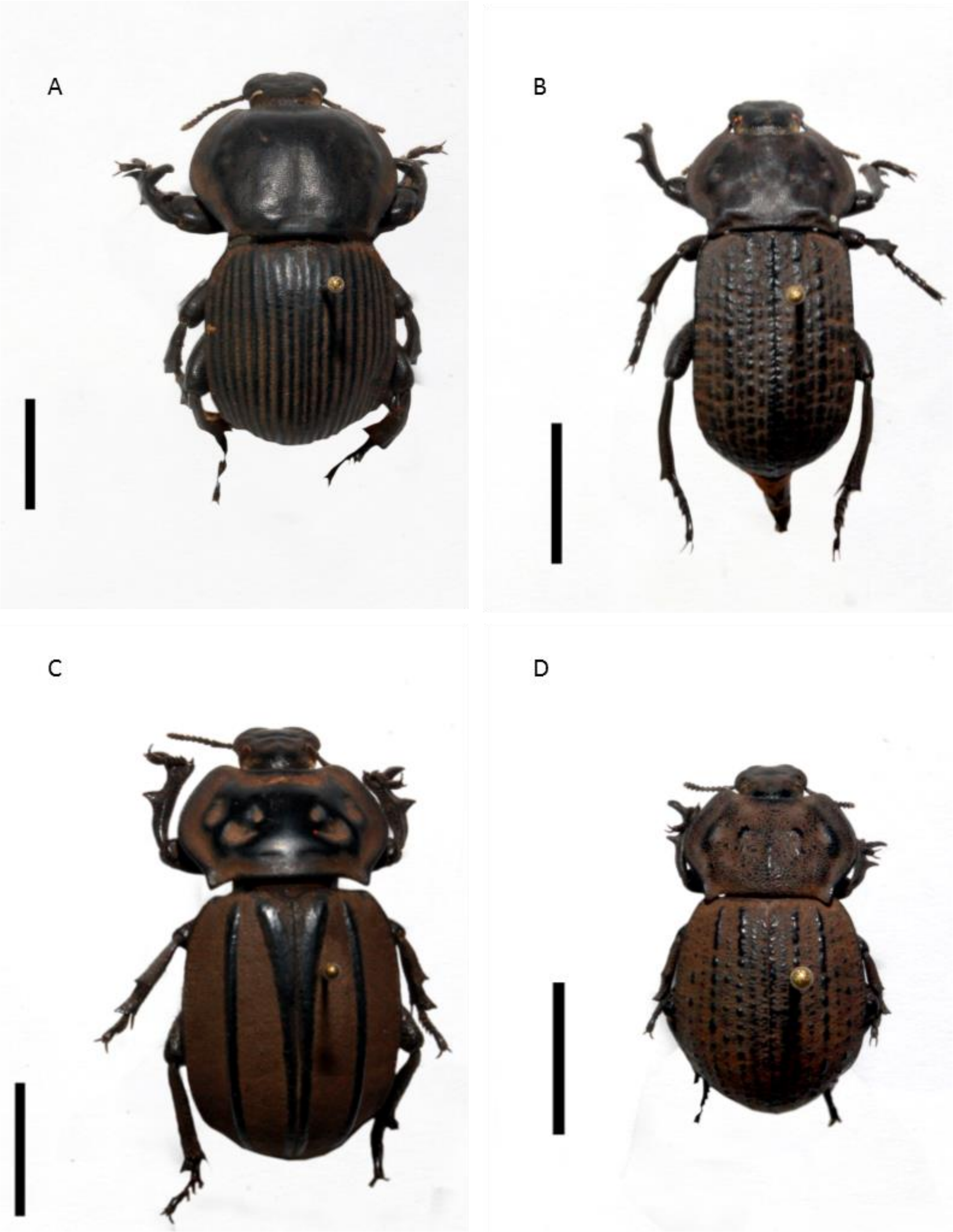

PLATE 2

A. *Anomalipus elephas* B. *A. expansicollis*   C. *A. sculpturatus*   D. *A. seriatus*

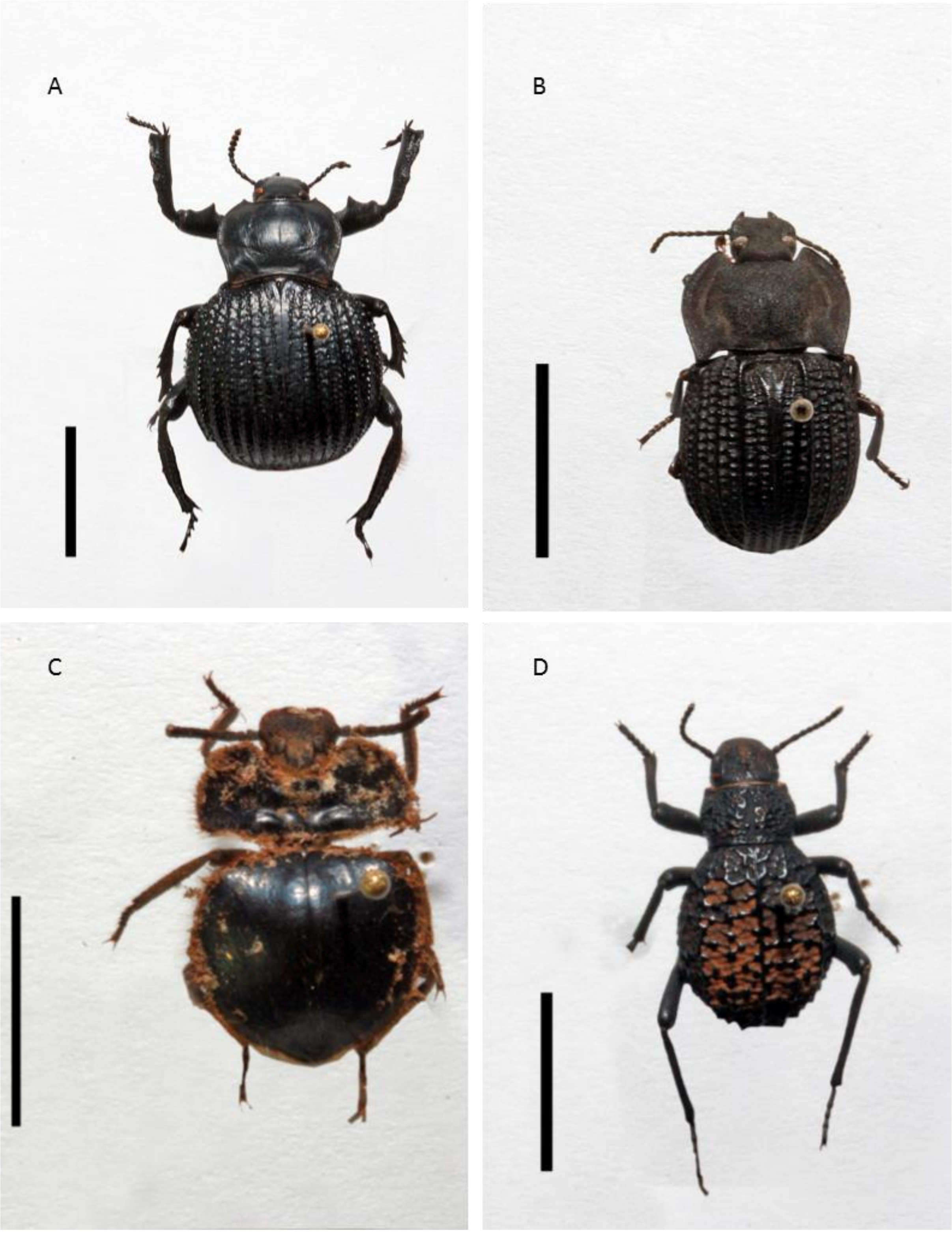

PLATE 3

A. *Gonopus deplanatus* B. *Anchophthalmus algoensis* C. *Eurychora barbata* D. *Renatiella reticulata*

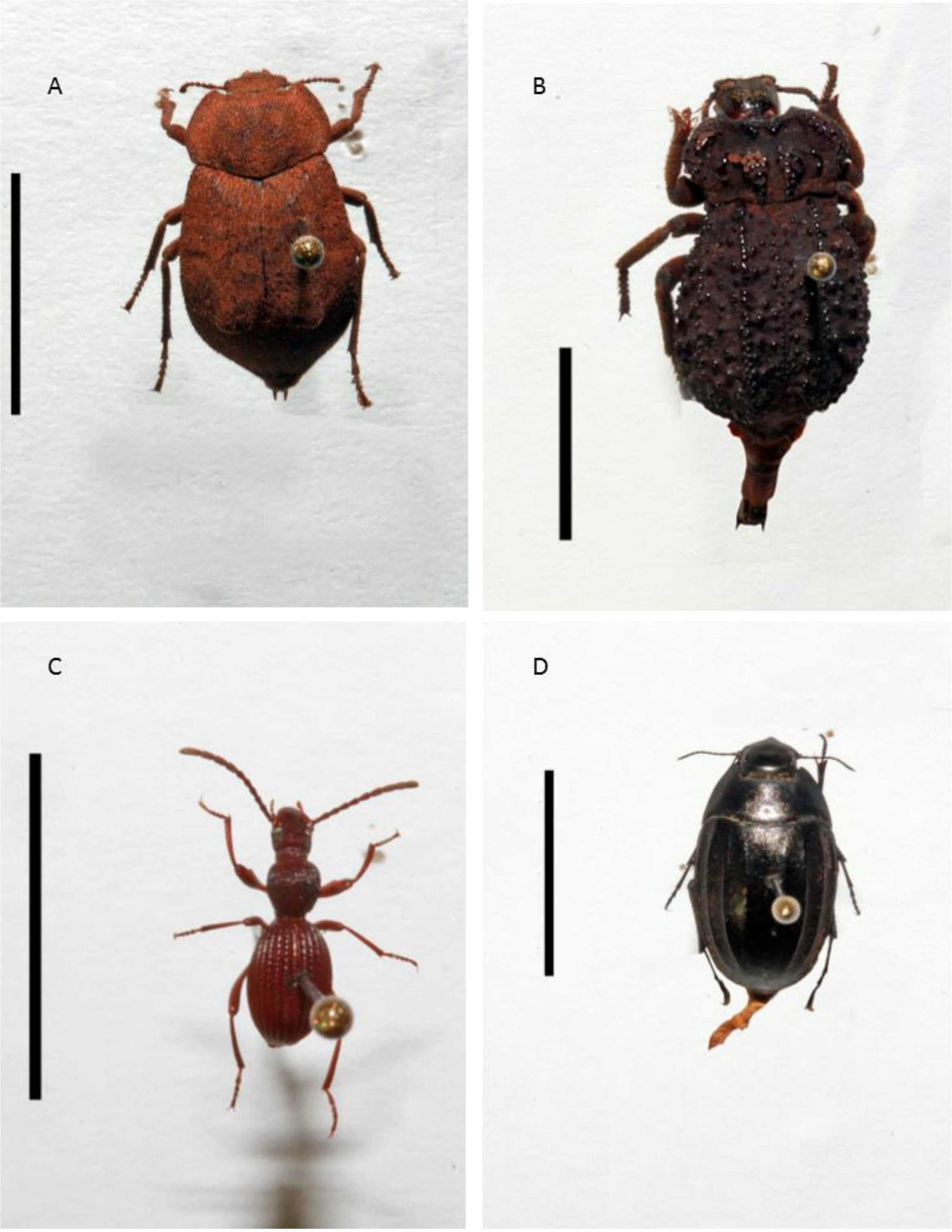

PLATE 4

A. *Machlomorpha cf. mossambica* B. *Amachla* sp. A C. *Herpiscius gracilis* D. *Zophosis (Oculosis) boei*

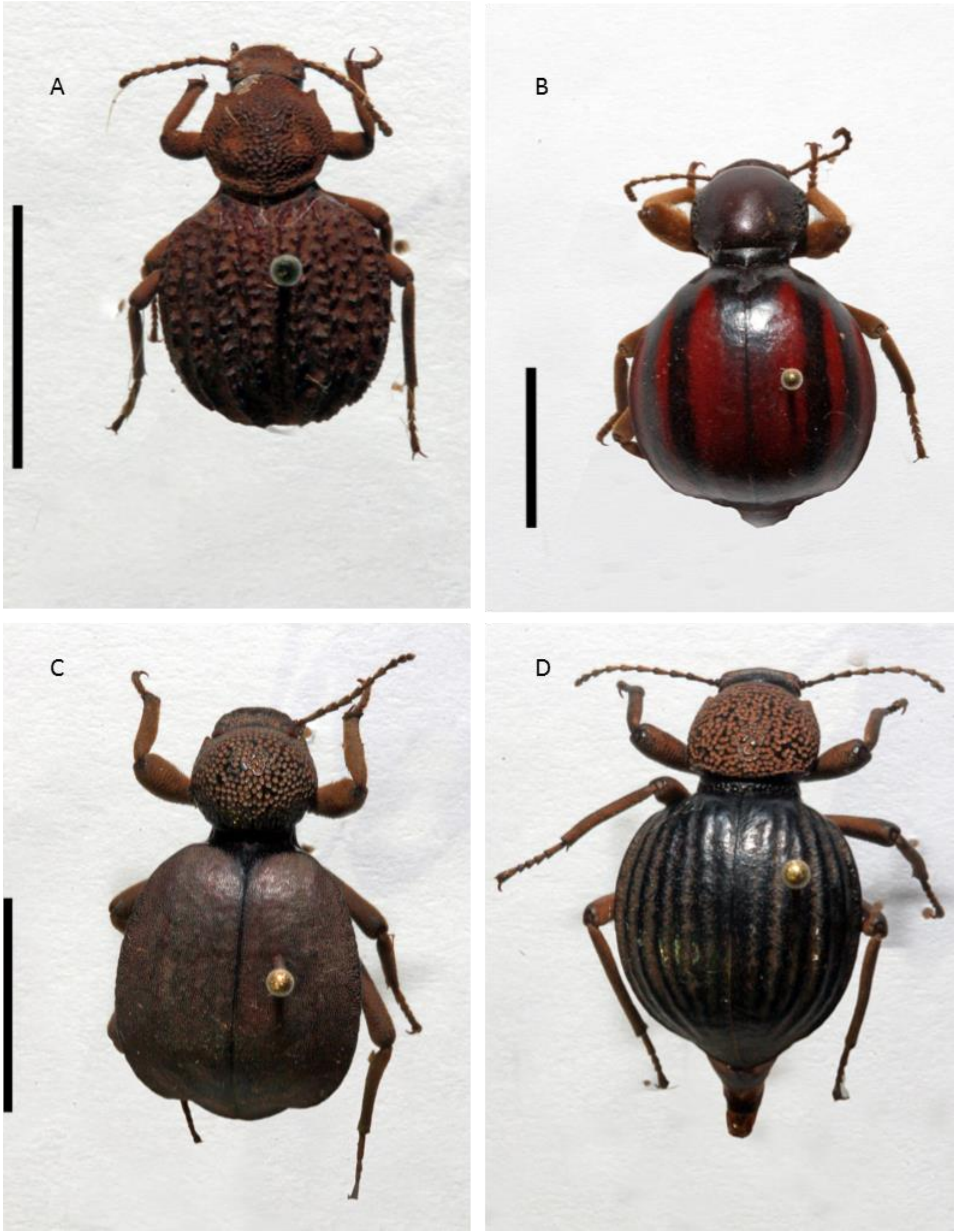

PLATE 5

A. *Amiantus pusilus* B. *Dichtha cubica* C. *Distretus discoideus* D. *Psammophanes* sp.

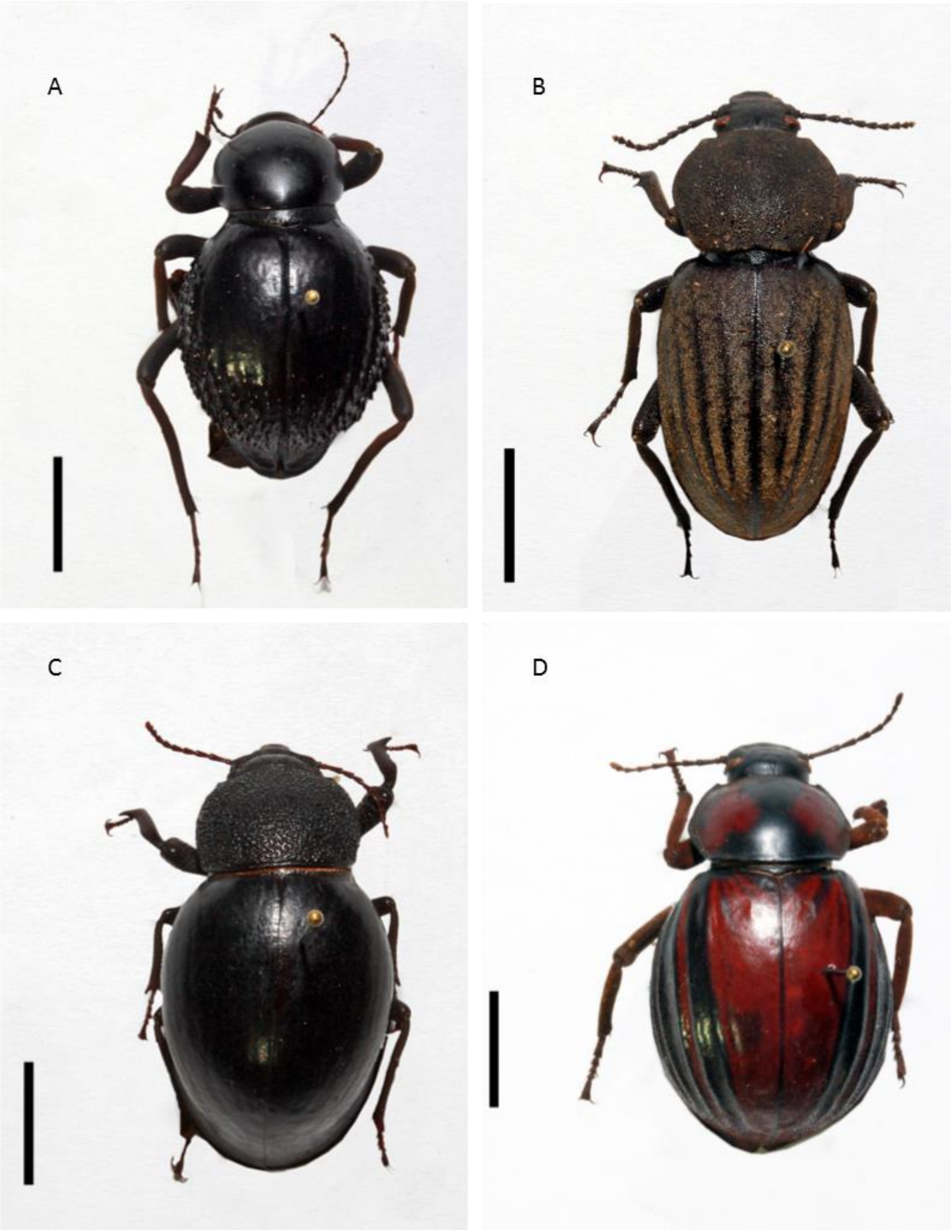

PLATE 6

A. *Psammodes vialis* B. *Phanerotomea rowleianium* C. *Phanerotomea scrobbicolis* D. *Psammodes* cf. *ventrocosus*

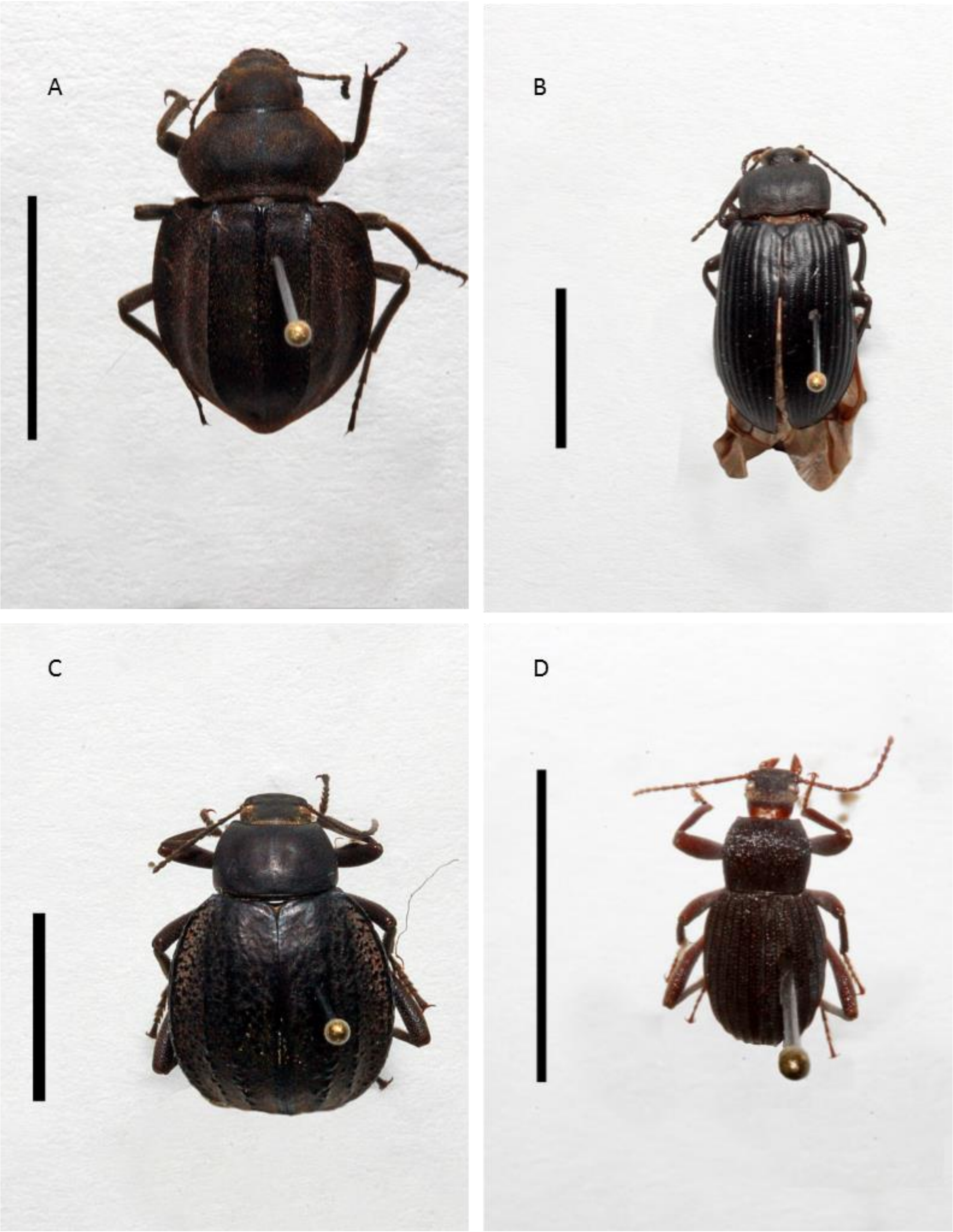

PLATE 7

A. *Somaticus varicollis* B. *Hoplonyx cristatus* C. *Micrantereus* sp. ‘7’ D. *Drosochrus* sp. ‘C’

Gazetteer

Abbreviation	Site	Vegetation type	latitude	longitude
BAR	Barries Farm	Musina Mopane Bushveld	-22.48	29.41
BEN	Ben Lavin Nature Reserve	Makhado Sweet Bushveld	-23.13	29.92
BGM	Bluegumspoort (Farm)	Soutpansberg Summit Sourveld	-22.96	29.89
BLN	Blouberg NR North	Roodeberg Bushveld	-22.98	29.12
BLS	Blouberg NR South	Roodeberg Bushveld	-23.02	29.09
BRI	Bristow Farm	Makhado Sweet Bushveld	-23.17	29.76
EF	Entabeni State Forest	Northern Mistbelt Forest	-23.01	30.24
GON	Gondeni (Communal land)	Soutpansberg Mountain Bushveld	-22.91	30.06
GOR	Goro Game Reserve	Soutpansberg Mountain Bushveld	-22.93	29.42
HLF	Hanglip State Forest	Northern Mistbelt Forest	-22.99	29.88
LF	Lajuma Forest	Northern Mistbelt Forest	-23.03	29.44
LM	Lajuma Mistbelt	Soutpansberg Summit Sourveld	-23.02	29.43
LUD	Ludwig's Lust Farm	Limpopo Ridge Bushveld	-22.25	29.78
MAA	Mara Research Station	Makhado Sweet Bushveld	-23.14	29.55
MAR	Maremani Game Reserve	Limpopo Ridge Bushveld	-22.39	30.23
MAS	Mashovela Lodge	Soutpansberg Mountain Bushveld	-22.93	29.89
NWA	Nwanedi Game Reserve	Soutpansberg Mountain Bushveld	-22.64	30.37
RM	Happy Rest	Soutpansberg Summit Sourveld	-23.01	29.75
TV	Thatevondo State Forest	Northern Mistbelt Forest	-22.91	30.33
VM	Vhuvha (Communal land)	Soutpansberg Summit Sourveld	-22.99	30.18

CHAPTER 6

ANNOTATED CHECKLIST OF CARABIDAE (INSECTA: COLEOPTERA) OF THE VHEMBE BIOSPHERE RESERVE, SOUTH AFRICA[5]

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Abstract

A checklist of genera and species of the Carabidae (Insecta: Coleoptera) of the Vhembe Biosphere Reserve is provided. We briefly summarize what is known of the biology of the tribes and genera of Carabidae in South Africa. A total of 53 species are covered in this checklist.

Keywords

Ground-beetles, biological notes, Savanna Biome, Limpopo Province, Soutpansberg,

Introduction

Of the ground-living beetles, Carabidae (ground beetles, ant guest beetles and tiger beetles), Scarabaeidae (dung beetles), and Tenebrionidae (darkling beetles) are among the most abundant and diverse (Vohland *et al*., 2005). The Staphylinidae are also an extremely diverse component of epigaeic faunal communities (Martins da Silva *et al*., 2011). Ground beetles (Carabidae) are exceptional in that they are polyphagous predators on arthropods, including ants and collembolans (Kotze *et al*., 2011), with the exception of some representatives of Harpalinae which are seed-feeding (Thiele, 1977).

Although Carabidae are often included in assemblage studies in Europe and the USA (Kotze *et al*., 2011), the single greatest impediment to using them as indicators is the lack of taxonomic expertise and of good field guides in South Africa.

Nineteen subfamilies divided into 40 tribes have been recorded from southern Africa. Over 250 genera and 1400 species have been recorded from the region (Scholtz & Holm, 1985). The first comprehensive account of the Carabidae was by Péringuey (1896) who catalogued 165 genera. Since then other groups have been reviewed by Basilewsky (1958, 1962, 1977, 1959), Straneo (1958, 1963, 1983, 1991) and Schüle (2008, 2009).

A valuable internet database (Carabidae of the World.org) is maintained by Anechenko *et al*. (2016). Erwin *et al*. (2012) provides a key which is useful for the identification of the more cryptic tribes.

The latest summary on the natural history, taxonomy and biology of Carabidae in Africa is from Scholtz & Holm (1985), which is out of date, and lacks detail at the tribal level. The goal and scope of this work is therefore to provide a more detailed summary of basic information available on the group, to update the information in Scholtz & Holm (1985) in addition to providing a checklist of the ground-dwelling carabid fauna of the Vhembe Biosphere Reserve. The checklist covers the Vhembe Biosphere Reserve which is known to have rich plant (Hahn, 1994) and spider (Foord *et al*., 2002) diversity, but with significant gaps in our knowledge of other hyper-diverse taxa in the region.

This checklist of the ground-dwelling carabid beetles of the VBR is the first published record of the major ground-dwelling beetle families (Carabidae, Tenebrionidae and Scarabaeidae) for the region. It is also the first checklist of major beetle families for any of the biosphere reserves in South Africa. Only those species that were recorded from the VBR are covered, and a brief overview is provided of the South African fauna at the level of the genera and tribe. In so doing we have collated the widely scattered biological information available for this family with the goal of increasing the usefulness of the checklist.

Methods and Materials

Study area

The Vhembe Biosphere Reserve (VBR), situated in Limpopo Province, South Africa, was established in 2009, and is by far the largest in the country with a size of 3 070 000 ha. Vhembe is located in the far northernmost reaches of South Africa and includes the Soutpansberg, Blouberg, the Limpopo Valley and the Pafuri region (Fig. 1). It covers the entire Vhembe District of Limpopo Province, Blouberg Local Municipality and the northern part of the Kruger National Park (Pool-Stanvliet, 2013).

Twenty sites in the VBR were sampled using pitfall traps (maps were drawn using vector layers from DIVA-GIS) (Fig. 1). The sites covered different habitat types (Figs. 2-3) identified using Mucina & Rutherford’s (2006) vegetation classification (Table 1). Collecting took place during the southern Hemisphere summer months of 2012: December, January, February, March. Within each site, we selected eight a-priori sampling points, hereafter referred to as sampling units (SU’s). These SU’s were spaced between 300 - 2000 m from each other.

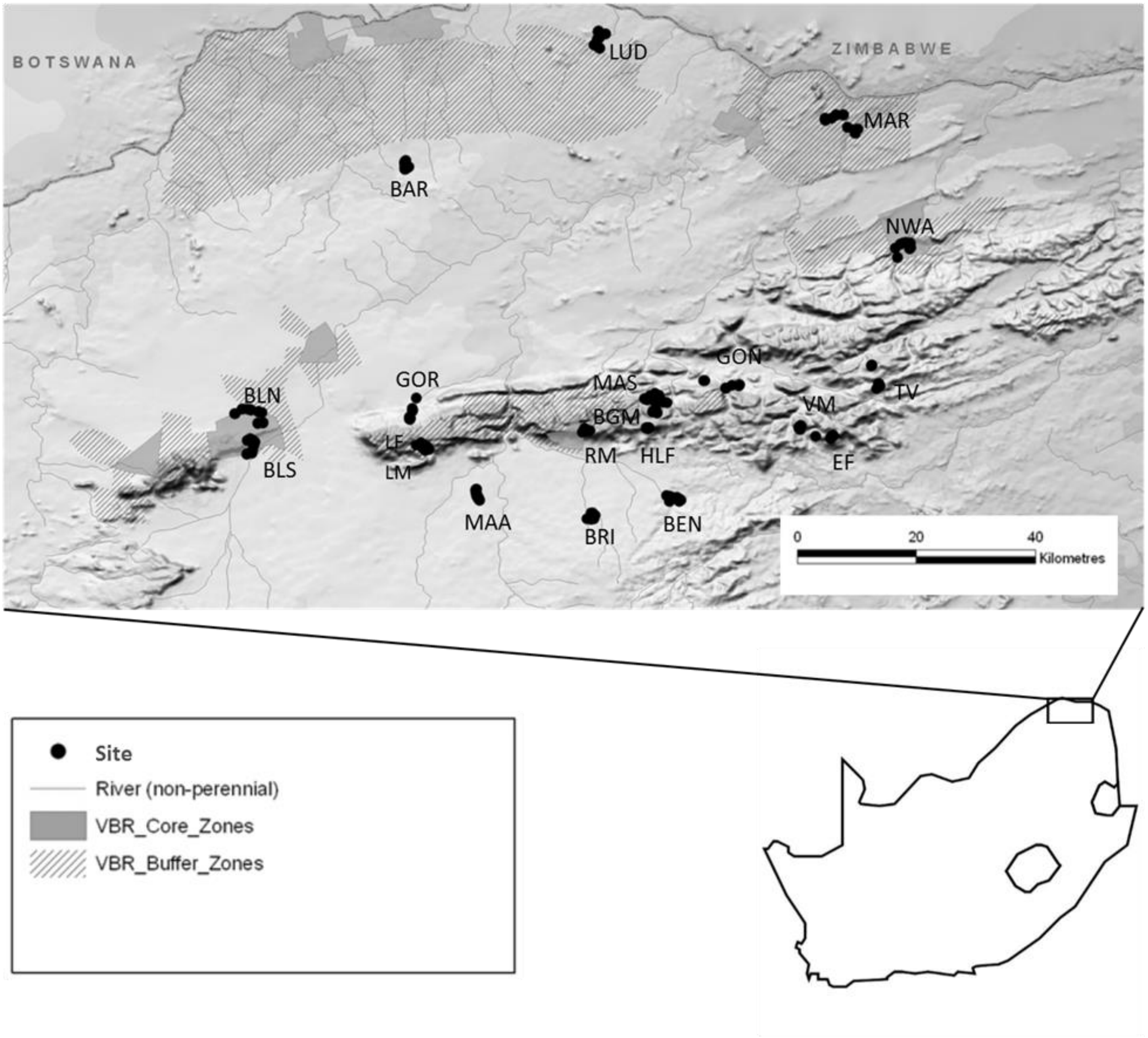

Fig. 1. Map of the Vhembe Biosphere in South Africa with locality of site names used in text and the gazetteer.

Each SU comprised five pitfalls, placed in a circle, with a diameter of 10 m. Pitfall traps (7 cm diameter, `12 cm deep) were dug into the ground and a quarter filled with propylene glycol. Propylene glycol is non-toxic, and does not repel or attract animals through smell (Agosti *et al*., 2000). It also acts partly as a preservative until specimens can be processed and stored in alcohol. Using pitfalls is a thorough method of sampling epigaeal invertebrates. Pitfalling expends the least amount of input with a greater comparable output than any other sampling method (Agosti *et al*., 2000). Left out for seven days, as was done here, it is possible to attain inventory completion for each point. Moreover, we wished to capture as much variation in the immediate habitat as possible and were careful to place our pitfalls in such a way as to consider microscale-heterogeneity.

After collection, the contents of each trap were washed using a fine net, and stored in 96% ethanol. Thereafter, the specimens from each trap were sorted into pill vials with acquisition numbers placed in each. This was an initial step before sorting each taxonomic group into morphospecies.

Beetles were sorted initially to families and subfamilies using Scholtz & Holm (1985). The most diverse beetles found in the pitfall samples were Tenebrionidae, Scarabaeidae and Carabidae. All Carabidae were pinned and labelled and identified using Carabidae.org (Anichtchenko *et al*., 2016). Identifications were then confirmed to genus and species level by Ruth Muller (Ditsong National Museum of Natural History). Vouchers of each species of Carabidae are housed in the Coleoptera Collection of the Ditsong Museum of Natural History and in the UNIVEN Natural History Collection.

There are 7 plates, depicting 28 species of Carabidae found in the VBR (Plates 1-7). The photos were taken with a Kodac digital camera at the Soutpansberger Newspaper offices (Louis Trichardt, Limpopo).

Authorities with dates, synonymns, general distribution records (where these are known (Cochrane, 1995) and Vhembe Biosphere localities (Gazetteer and Fig. 1) are given for each species and morphospecies. Synonyms were obtained from primary references, as well as electronic resources: Carabidae of the World (Anitchenko *et al*., 2016) and Catalogue of Life (Roskov *et al*., 2016). The nomenclature used is that of Lorenz (2005). For this checklist the order of subfamilies, tribes and genera are arranged alphabetically.

We include suspected species (designated with cf.) and morphospecies (identified to genus and tribe) in the checklist. Including these unidentified species also highlights future taxonomic research needs.

Fig. 2. a. Mara Research Station, b. Ben Lavin Nature Reserve, (Makhado Sweet Bushveld); c. Lajuma Mountain Retreat d. Vuvha Tribal Authority (Soutpansberg Summit Sourveld); e. Lajuma Mountain Retreat, f. Hanglip Forest, (Northern Mistbelt Forest).

a

b

c

d

e

Fig. 3. a. 'Barries' Farm' (Musina Mopane Bushveld); b. Maramani Game Reserve; c. 'Ludwig's Lust' Farm, (Limpopo Ridge Bushveld); d. Blouberg Nature Reserve (Roodeberg Bushveld); e. Goro Game Reserve; f. Gondeni Tribal Authority (Soutpansberg Mountain Bushveld).

f

Results

CARABIDAE

According to Scholtz & Holm (1985) the first abdominal sternite is divided by the coxae; the notopleural suture beneath the lateral margin of the pronotum is clearly visible; and a comb organ occurs on the fore-tibia. Many species have lost their wings and have fused elytra – although most are capable of flight. The body of carabid beetles is divided between a definite fore- and hind-body, the head is prognathous and mandibulate. They are generally dark or black in colour, but many species have striking white or yellow colour patterns on the pronotum or the elytra. The antennae are 11-segmented, except for Paussinae, which have fewer than 11-segments.

ANTHIINAE Bonelli, 1813

The Anthiinae occur in mainly tropical regions of the world (Häckel & Farkač, 2013b), but are abundant and particularly diverse in Africa (Scholtz & Holm, 1985). They are often found running over the ground hunting small caterpillars and other prey (Péringuey, 1896).

Anthiini Bonelli, 1813

The Anthiini are known as ‘oogpisters’, and are usually large, black, flightless, somewhat elongated beetles that can spray highly acidic secretions at attackers (Mawdsley *et al*., 2011). Most species are apterous, nocturnal and predaceous (Häckel & Farkač, 2013b). The elytral ridges are often clothed with fine hairs or pubescence, while *Cypholoba* have a series of pits running along the elytral interstices. *Anthia* and *Termophilium* include very large and conspicuous species of diurnal, crepuscular or nocturnal habits (Mawdsley *et al*., 2011). Formiciform or ant-shaped members are found in *Netrodera*, and *Atractonotus* (Péringuey, 1896). They are especially numerous in arid, sandy regions of the bushveld. *Anthia*, *Termophilium* and *Netrodera* feed on termites (Häckel & Farkač, 2013b). The genera recorded from Limpopo Province and Botswana are *Anthia, Atractanotus*, *Baeoglossa*, *Calanthia*, *Cycloloba*, *Cypholoba, Eccoptodera, Gonogenia, Netrodera and Termophilum* (Häckel & Farkač, 2013). South African *Anthia* and *Cypholoba* have been reviewed by Mawdsley *et al*. (2011, 2012).

***Anthia* Weber, 1801**

= *Pachymorpha* Hope, 1838
= *Thoracolobus* Gistel, 1857
=*Calanthia* Obst, 1901
=*Odontanthia* Obst, 1901

The species of this genus are some of the largest and most conspicuous members of the ground-dwelling African beetle fauna (Mawdsley *et al*., 2011). Members of the genus resemble *Termophilium*, but in *Anthia* the pronotum often has broad lateral and or posterior flanges with patches of yellow or brown setae and the lateral margins of the elytra have a thin band of setae. Mawdsley *et al*. (2011) provides a key to the four species in South Africa and a set of photographic plates.

Three species were recorded in VBR during this study, and Mawdsley *et al*. (2011) recorded a fourth, the widespread *Anthia maxillosa* (Fabricius, 1781) from "Grootdraai, Soutpansberg".

Anthia cinctipennis cinctipennis Lequien, 1832 (Plate 1A)
Mawdsley *et al*. 2011, Häckel & Farkač 2013
  Anthia marginipennis Castelnau, 1834
  Anthia limbipennis Chaudoir, 1861
  Anthia pachyoma Chaudoir in Obertur, 1883
  Anthia hottentota Olliff, 1889
  Anthia ooptera Bates, 1889
  Anthia dissimilis Obst, 1901
  Anthia fairmairei Sternberg, 1907
Distribution: Angola, Botswana, Namibia, South Africa, Swaziland, Zimbabwe, Zambia
VBR localities: BAR, BRI

Anthia thoracica thoracica (Thunberg, 1784) (Plate 1B)

Mawdsley *et al*. 2011, Häckel & Farkač 2013

Carabus thoracica Thunberg, 1784
Carabus fimbriatus (Thunberg, 1784)
Anthia maculicollis Perroud, 1846
Anthia portentosa Dohrn, 1882
Anthia stigmodera [chaudoir in litt.] Péringuey, 1896
Anthia dohrni Rousseau, 1906

Distribution: Zimbabwe, Malawi, Botswana, Mozambique, Namibia, South Africa, Swaziland, Tanzania, Zambia

VBR localities: BLS, BRI

Anthia circumscripta Klug, 1853

Mawdsley *et al*. 2011, Häckel & Farkač 2013b

Anthia striatopunctata Guerin-Meneville, 1847
Anthia duparqueti Lucas, 1867
Anthia vitticollis Bates, 1878
Anthia burdoi Fairmaire, 1882
Anthia ovampoensis Péringuey, 1892
Anthia fochi Benard, 1919

Distribution : Democratc Republic of the Congo (Zaire), S. Kenya, Botswana, Malawi, Mozambique, Namibia, Tanzania, Zimbabwe, Zambia

VBR locality: BAR

***Atractonotus* Perroud, 1846**

= *Atractonota* Lacordaire, 1854 in error

This genus (Häckel & Farkač, 2013b) includes elongated beetles that resemble *Netrodera* in being formiciform or ant-like, but which are slightly larger in size. The head and pronotum are especially elongated, and the elytra have lightly coloured white spots and bands on the posterior half (Péringuey, 1896). There is another species described in the genus from Zambia, *Atractonotus puncticollis* (Schüle & Heins, 2013)

Atractonotus mulsanti Perroud, 1846 (Plate 2D)

Häckel & Farkač 2013b

Anthia minima Bertoloni, 1857

Anthia baucis Dohrn, 1881

Atractonotus sansibarica Kolbe, 1898

Atractonotus perturbatus Basilewsky, 1980

Distribution: Mozambique, Angola, Botswana, Namibia, Republic of South Africa (Free State, Mpumalanga, Limpopo), Tanzania, Zimbabwe, Zambia.

VBR locality: BLS

Cypholoba **Chaudoir, 1850**

= *Thermophila* Bertoloni, 1849

= *Polyhirma* Chaudoir, 1850

= *Diabatus* Gistel, 1857

Most species in this genus are black with many species having white setal patches, thought to have evolved through mimicry of Mutillidae, Formicidae, and other stinging Hymenoptera, (Marshall & Poulton 1902, *in* Mawdsley *et al*. 2012). They are typically anthiine appearance, but elytral pits are deeply impressed, oval to round. Mawdsley *et al*. (2012) provides a key to the species in South Africa and a set of photographic plates. Certain species and subspecies are highly localized; of these, three are known to occur in the VBR: *C. amatonga* Péringuey, 1892, *C. gracilis scrobiculata* (Bertoloni, 1847) (Soutpansberg) and *C. rutata* (Péringuey, 1892) (Pafuri region: Kruger National Park).

Cypholoba alveolata alveolata (Brême, 1844) Plate 1C

Mawdsley *et al*. 2012, Häckel & Farkač 2013b

Anthia alveolata Brême, 1844

Thermophila ranzanii (Bertoloni, 1849)

Anthia minima Bertoloni, 1857

Polyhirma plantii (Chaudoir, 1861)

Polyhirma consobrina Péringuey, 1896

Polyhirma algoensis Péringuey, 1896

Polyhirma dohrni [sn. Chaudoir 1850] Sternberg, 1907

Distribution: Botswana, South Africa, Zimbabwe, Mozambique, Malawi

VBR localities: BAR, BLN, BLS, BRI, GON, GOR, MAS, NWA

Cypholoba caillaudi boucardi (Castelnau, 1835)

Häckel & Farkač 2013b

Anthia caillaudi Castelnau, 1835
Anthia polioloma Chaudoir, 1848
Anthia septemcostata Dohrn, 1883
Polyhirma boucardi (Chaudoir,) 1883
Polyhirma biscutellata (Fairmaire,) 1887
Polyhirma bozasi (Sternberg,) 1907
Polyhirma kolbei Sterneberg, 1907
Polyhirma roeschkei Sternberg, 1907
Polyhirma dohrni Sternberg, 1908
Polyhirma neumanni Sternberg, 1908
Polyhirma clausi Kuntzen, 1913
Polyhirma goetzei Kuntzen, 1913
Polyhirma littoralis Kuntzen, 1913
Polyhirma massaica Kuntzen, 1913
Polyhirma ukerewensis Kuntzen, 1913
Polyhirma usagarensis Kuntzen, 1913
Cypholoba punctata Bénard, 1921
Polyhirma clathratipennis Bénard, 1923
Polyhirma erythreensis Bénard, 1924
Cypholoba ledouxi Strohmeyer, 1928
Cypholoba glauningi Strohmeyer, 1928
Cypholoba guruana Strohmeyer, 1928
Cypholoba harrarensis Strohmeyer, 1928
Cypholoba holtzi Strohmeyer, 1928
Cypholoba neumanniana Strohmeyer, 1928
Cypholoba rhodesiana Strohmeyer, 1928
Cypholoba saramica Strohmeyer, 1928
Cypholoba seineriana Strohmeyer, 1928
Cypholoba teteana Strohmeyer, 1928
Cypholoba tiesleri Strohmeyer, 1928
Cypholoba zenckei Strohmeyer, 1928

Cypholoba mirei Basilewsky, 1963
Cypholoba dilagala Basilewsky, 1980

Distribution: Zambia, South Africa (Limpopo), Sudan, Kenya, Tanzania

VBR locality: BRI

Note: Mawdsley *et al*., (2012) lists this species as a synonymn of *C. alveolata*. Häckel & Farkač (2013) list *C. caillaudi* as a valid species. Kleinfeld & Puchner (2012) note that only this subspecies occurs in South Africa. Its distribution also includes Zimbabwe and Tanzania. The typical subspecies occurs in Ethiopia, Eritreia, Sudan and Somalia and the ssp. *biscutellata* Fairmaire occurs in Kenya and Tanzania.

Cypholoba chaudoiri (Péringuey, 1892)

Häckel & Farkač 2013b

Polyhirma chaudoiri (Péringuey, 1892)
Polyhirma ellenbergeri (Benard, 1925)

Distribution: Botswana, Zambia, Zimbabwe, South Africa, Mozambique

VBR locality: BLN

Note: Mawdsley *et al*. (2012) lists this as a synonymn of *C. amatonga* Péringuey, 1892. Häckel & Farkač (2013) list *C. chaudoiri* as a valid name however, which occurs widely throughout Limpopo Province, Gauteng and neighbouring Zimbabwe and Botswana.

Cypholoba gracilis gracilis (Dejean, 1831)

Mawdsley *et al*. 2012, Häckel & Farkač 2013

Anthia gracilis Dejean, 1831
Anthia fossulata Perroud, 1846
Anthia scrobiculata (Bertoloni, 1847)
Anthia clathrata Klug, 1885
Atractonota gallemaertsi Rousseau, 1905
Cypholoba simbabyana Strohmeyer, 1928
Cypholoba damara Strohmeyer, 1928

Distribution: Namibia, Botswana, South Africa, Zimbabwe, Zambia, Lesotho, Mozambique

VBR localities: BEN, BGM, RM

Note: This species was split into 41 subspecies by Strohmeyer (1928) and Mawdsley *et al*. (2012) suggested that many of these may be distinct species. Two of the subspecies were recorded from Limpopo Province, and one of these, *C. g. scrobiculata* (Bertoloni, 1847), only recorded from the Soutpansberg, was thought to be distinct from *C. gracilis* (Mawdsley *et al*., 2012).

Cypholoba graphipteroides graphipteroides (Guérin-Méneville, 1845) Plate 1D
Mawdsley *et al*. 2012, Häckel & Farkač 2013
Anthia suturata Perroud, 1846
Polyhirma bilunata (Boheman, 1860)
Polyhirma alternata (Raffray, 1885)
Cypholoba tiesleriana Strohmeyer, 1928
Cypholoba tschifumbasica Strohmeyer, 1928
Cypholoba fischeri Strohmeyer, 1928
Cypholoba stuhlmanni Strohmeyer, 1928
Distribution: Angola, Botswana, Kenya, Malawi, Mozambique, DRC, Zambia, Zimbabwe, South Africa
VBR localities: BEN, MAA, MAS
Notes: Strohmeyer (1928) and Kleinfeld & Puchner (2012) recognized 20 subspecies in *C. graphipteroides*, respectively some of which are highly localized.

Cypholoba macilenta (Olivier, 1795)
Mawdsley *et al*. 2012, Häckel & Farkač, 2013
Carabus macilenta Olivier, 1795
Cypholoba foveata Perroud, 1846
Cypholoba exarata Boheman, 1848
Anthia dregei Guérin-Méneville, 1849
Polyhirma bennettii Marshall, 1902
Distribution: Botswana, Namibia, Zambia, South Africa, Mozambique, Zimbabwe
VBR locality: BRI

Netrodera **Chaudoir, 1850**

A genus containing three species restricted to southern Africa, one of them occurring in South Africa (Häckel & Farkač, 2013). They are very small, black, with elongated elytra and an ant-like or formiciform head (Péringuey, 1896).

Netrodera formicaria formicaria (Erichson, 1846)
  Anthia formicaria Erichson, 1846
Häckel & Farkač 2013
Distribution: South Africa (North-West, Limpopo), Zimbabwe
VBR locality: BRI

Termophilium **Basilewsky, 1950**

= *Thermophila* Hope, 1838
= *Thermophilum* (misspelling)

Termophilum and *Anthia* representants are almost similar and is closely related, but the former differ in that the pronotum is cordiform, or heart-shaped, and without flanges and projections. Colour patterns on the body are similar to those of *Anthia* (Mawdsley, 2011).

Termophilium cephalotes (Guerin-Meneville, 1845) Plate 2B
Häckel & Farkač 2013
  Anthia cephalotes Guerin-Meneville, 1845
  Anthia bimaculatum (misspelling)
  Anthia bimaculata Perroud, 1846
  Anthia immaculata Wallengreen, 1881
  Anthia torva Péringuey, 1896
  Anthia sternbergi Obst, 1903
Distribution: South Africa (Limpopo), Botswana
VBR locality: BRI

Termophilium burchelli burchelli (Hope, 1832) Plate 2C

Häckel & Farkač 2013

Anthia nuda Sternberg, 1906

Anthia maculata Sternberg, 1906

Distribution: South Africa, Botswana, Namibia, Zimbabwe, Zambia, Malawi, Tanzania, Democratic Republic of the Congo

VBR localities: BLN, GOR

Termophilium massilicatum (Guérin-Méneville, 1845) Plate 3B

Häckel & Farkač 2013

Anthia natalensis Perroud, 1846

Anthia massilicatzi Boheman, 1848

Termophilum damarensis Kuntzen, 1919

Termophilum laevithorax Bénard 1922

Distribution: Zambia, South Africa, Zimbabwe, Mozambique, Zambia, Angola, Botswana

VBR localities: BLS, GON, GOR, NWA

Termophilium homoplatum homoplatum (Lequien, 1832) Plate 2D

Häckel & Farkač 2013

Anthia homoplata in error

Anthia mellyi De Brême, 1844

Anthia algoensis Péringuey, 1892

Anthia cupiens Péringuey, 1892

Anthia heres Péringuey, 1892

Anthia intempestiva Péringuey, 1892

Anthia vagans Péringuey, 1892

Anthia modesta Obst, 1901

Distribution: South Africa, Zimbabwe, Zambia, Botswana, Mozambique, Angola

VBR locality: BLS

BRACHININAE Bonelli, 1810

According to Péringuey (1896) all species have, on each side of the head, a long bristle above the labrum which is fringed with six hairs, another bristle above the eye and a third one on the outer margin of the prothorax at its broadest base. The first antenomeres have each a pair of setae, the inner one longer than the outer. They are generally ochrous yellow and black in colour; with seven to eight abdominal visible sternites (other Carabidae subfamilies have six or less visible abdominal segments) (Péringuey, 1896; Erwin *et al*., 2012). They audibly emit a caustic fluid when irritated which has earned them the name “bombardier beetles” (Skaife, 1979).

Brachinini Bonelli, 1810

The Brachinini are characterized by the presence of a fringe of hairs on the apical margins of the elytra (Basilewsky, 1962). This feature though is highly variable between species, though Basilewsky (1962), considers it always present. The tribe occurs worldwide; Basilewsky (1962) provides a key to African genera based on the labium of the mouthparts.

***Brachinus* Weber, 1801**

Brachinus are medium sized beetles, the elytra is disproportionate in size to the rest of body, as the length of the head and the pronotum together is half the length of the elytra. The head and pronotum and legs are red-orange in colour, the elytra is black with two ochrous spots on the posterior half (Péringuey, 1896). Many species within subgenus *Metabrachinus* have carinate elytral interstria and a larger apical membrance (Basilewsky, 1962).

Brachinus (*Metabrachinus*) cf. *armiger* Dejean, 1831
Péringuey 1896, Basilewsky 1962
    Brachinus parvulus Chaudoir, 1843
    Brachinus venator Klug 1862
Distribution : Namibia, South Africa (Eastern Cape, KwaZulu-Natal, Mpumalanga, Limpopo)
VBR localities: LM, RM

Crepidogastrini Jeannel, 1949

A predominantly African tribe that has been revised by Basilewsky (1959).

***Crepidogaster* Boheman, 1848**

They are flightless; similar in general appearance and colouration to *Brachinus*, only much smaller, the distal segment of the labial palp is enlarged (Basilewsky, 1959). The head and pronotum are ochrous yellow, with orange and black patterns on the shortened elytra, thus exposing the posterior two to three abdominal segments (Péringuey, 1896).

Crepidogaster insignis Péringuey, 1896 Plate 3D
Péringuey 1896, Basilewsky 1959
Distribution : South Africa (Free State; Limpopo: Soutpansberg)
VBR localities: BAR, LUD, NWA

Crepidogaster protuberata Basilewsky, 1959 Plate 3C
Basilewsky 1959
Distribution : South Africa (Limpopo)
VBR localities: MAR, NWA

CARABINAE Latreille, 1802

The carabid ground beetles belonging to the subfamily are predominantly apterous and beautifully colored, especially in European and Asian species. They are therefore popular with collectors. They are distributed throughout the world (Su *et al*., 1996). The Carabinae consist of about 1299 extant pecies mainly inhabiting the Northern Hemisphere (Lorenz, 2005).

Carabini Latreille, 1802

Many species are hind-wingless or have reduced hindwings, and cannot fly. Representatives of *Calosoma* however are capable of flight. They are widely distributed throughout the world (Su *et al*., 1996).

***Calosoma* Weber, 1801**

Calosoma is common in the northern bushveld of South Africa (Basilewsky, 1958). They are large beetles (2-3 cm), with a very convex, broad hind body (that covered by the elytra) – the shape is tenebrionid-like. The pronotum is almost heart-shaped, broader anteriorly than posteriorly. *Calosoma* species are specialized caterpillar feeders (Erwin *et al*., 2012).

Calosoma planicolle Chaudoir, 1869 Plate 4A
Péringuey 1896, Häckel *et al*. 2016
  Calosoma procerum Harold, 1880
Distribution: Angola, Botswana, D. R. of the Congo, Zambia, South Africa, Lesotho, Swaziland, Zimbabwe, Malawi, Uganda, Mozambique, Tanzania, Kenya, Ethiopia, Somalia and Madagascar
VBR localities: BLN, BLS, GOR

CICINDELINAE Latreille, 1802

Important regional checklists of tiger beetles include ones of the Kruger National Park (Mawdsley *et al*. 2012b) and Angola (Serano & Capela, 2013). New species continue to be described (Serano *et al*., 2015) and *Chaetodera* (Mawdsley, 2011) and *Dromica* (Mawdsley, 2009; Schüle, 2011) have recently been revised.

Cicindelini Latreille, 1802

Most southern African tiger beetles belong to this tribe, of which *Dromica*, *Lophyra* and *Chaetodera* are the most common (Scholtz & Holm, 1985). *Lophyra*, recorded from the VBR, but not sampled in our traps, is larger and more robustly built than *Dromica*, the neck and prothorax are clothed with short white setae, the elytra is patterned in distinct black and orange-yellow patterns. *Chaetodera* Jeannel, 1946 is very closely related to *Lophyra*, but haa distinctly different elytral markings, important differences in the position and number of setae, particularly on the antennae, and are generally larger (Mawdsley, 2011). The tribe also has rare and isolated forms in Namibia (Scholtz & Holm, 1985) and Angola (Serano *et al*., 2015).

***Dromica* Dejean, 1826**

The body is black, slightly elongated, with flecks of white on either side of the rugose elytra. The legs are spindly, and the antennal segments appear to be somewhat flattened.

Dromica brzoskai Cassola, 2002
Cassola 2002
Distribution : South Africa (Limpopo)
VBR locality: NWA

Dromica concinna Péringuey, 1904
Cassola 2002
Distribution : South Africa (Limpopo), Zimbabwe
VBR localities: BEN, MAS

Dromica costata Péringuey, 1892 Plate 4C
Cassola 2002, Mawdsley & Sithole 2012
Distribution: Botswana, South Africa (Limpopo)
VBR localities: BLS, MAS, MAA

Dromica laticollis Horn, 1903 Plate 4B
Cassola 2002, Mawdsley & Sithole 2012
Distribution: Botswana, Mozambique, South Africa, Zimbabwe, Zambia
VBR localities: BEN, BRI

Dromica sexmaculata Chaudoir, 1860

Cassola 2002, Mawdsley & Sithole 2012

? *simplex* Bates, 1878
? *cordicollis* (Péringuey, 1892)
? *gruti* Péringuey, 1892

Distribution: Mozambique, Swaziland, South Africa (Limpopo)

VBR localities: BEN

Note: genus names of synonymns missing

Dromica tenella (Péringuey, 1893)

Mawdsley & Sithole 2012

Distribution: Zimbabwe (Manicaland, Masvingo), South Africa (Limpopo,; Mpumalanga), Mozambique (Maputo).

VBR localities: BLS, BRI

Dromica sp. Y

Accession no.: UVICC_Dro1

VBR locality: BEN

Manticorini Csiki, 1907

Representants of this tribe are widespread in central, southern and eastern Africa (Marĕs 2002)

***Manticora* Fabricius, 1792**

Members are very large, black species, with massive heart-shaped, bulbous hind bodies. The mandibles are enlarged and asymmetrical in males, and are thought to be used for holding females when mating (Skaif, 1979). Oberprieler & Arndt (2000) reviewed the biology of *Manticora*.

Manticora scabra Klug, 1849 Plate 5A

Marĕs 2000, Mawdsley & Sithole 2012

Manticora herculeana Klug, 1849

? latipennis Bertoloni, 1849

Manticora manicana Péringuey, 1898

Distribution : Mozambique, South Africa (Limpopo), Tanzania (Uhehe, Kilwa, Lindi), Malawi, Zimbabwe, Botswana.

VBR localities: BAR, BEN, BLN, LUD

Megacephalini Laporte, 1834

The tribe is widespread in Africa, but represented by only a few species in southern Africa (Scholtz & Holm, 1985).

Megacephala **Latreille, 1802**

Megacephala representants are larger than *Dromica* and *Lophyra*; the prothorax is nearly cordiform or heart-shaped, the dorsum is darkly coloured with a metallic green, purple or blue sheen, especially on the elytra, which in African species seems to have an uneven surface sculpture. The genus was revised by Basilewsky (1966).

Megacephala regalis regalis Boheman, 1848 Plate 4D

Basilewsky 1966, Mawdsley & Sithole 2012

Distribution: sub-Saharan Africa

VBR localities: MAS, BLS

HARPALINAE Bonelli, 1810

Possibly the most speciose group of Carabidae, with good flyers and with many species still being described (Facchini, 2016). Genera occurring in South Africa also occur in the rest of sub-Saharan Africa, with monotypic genera having mostly been described from equatorial regions.

Some highly localized species are found in Namibia. Péringuey (1896) recorded 19 genera to occur in South Africa. Basilewsky (1950b) revised the subfamily.

Harpalini Bonelli, 1810

The posterior margin of the prothorax is roughly equal to the width of the elytral base, fits compactly and not loosely as in Anthiines (Basilewsky, 1958). Only one supra-orbital seta occurs on the head; the prothoracic setae either occur in one pair (always on the latero-anterior margin of the prothorax), or two pairs.

***Omostropus* Péringuey, 1896**

Omostropus species species are small, black beetles, with one supra-orbital seta above each eye, and one pair of setae on the lateral margin of the pronotum. The pronotum fits in broadly with the anterior margins of the elytra. The clypeus bears two long setae on the fronto-lateral margin, the labrum with six setae on the anterior margin above the mandibles (Basilewsky, 1958).

Omostropus sp.
Accession no: mspp84.2-BLS7a
VBR localities: BGM, BLS, GON, LM, MAA
Note: Basilewsky (1958) records that *Omostropus palangoides* Reiche occurs in Limpopo Province and southern Zimbabwe. We were unable to confirm whether our specimen was this particular species.

***Platymetopus* Dejean, 1829**

Platymetopus figuratus Boheman, 1848
Basilewsky 1950b, Basilewsky 1958, Facchini 2016
Distribution: Namibia, southern Angola, Zimbabwe, Mozambique, Botswana, South Africa (Limpopo, KwaZulu-Natal, Eastern Cape)
VBR locality: NWA

LEBIINAE Bonelli, 1810

This is a large subfamily with many genera distributed within four or five tribes in South Africa (Péringuey, 1896). The head bear two supra-orbital setae, the clypeus has at least one seta on each side, the prothorax somewhat heart-shaped and bearing two setae, the waist is narrower than the neck in dorsal view; the last abdominal segment (pygidium) is exposed.

Cyclosomini Laporte, 1834

A predominantly African group, with a few genera reaching into Asia (Anichtchenko *et al*., 2016).

***Graphipterus* Latreille, 1802**

Graphipterus is a diverse and very distinctive genus, containing small to medium-sized diurnal beetles with velvet pubescence and vivid colour patterns on their elytra (Péringuey, 1896). The genus is characterized by three setae on the labial palps pointing inwards (Péringuey, 1896). Their representants are flightless. The prothorax is broader than long. They are endemic to Africa, abundant and particularly diverse in southern Africa (Scholtz & Holm, 1985). Along with *Anthia*, *Graphipterus* is one of the most conspicuous ground beetles of sub-saharan Africa. The genus was revised by Basilewsky (1977).

Graphipterus cf. *endroedyi* Basilewsky, 1977
Basilewsky 1977
Distribution: South Africa (Limpopo, Transvaal, Natal)
VBR localities: BEN, BLS

Graphipterus lateralis lateralis Boheman, 1848 Plate 6A
Basilewsky 1977
Distribution: Botswana, Zimbabwe, South Africa (N. Limpopo)

VBR localities: BAR, BEN, BLN, BLS, BRI, GON, MAA, MAS, NWA

Graphipterus cordiger cordiger Dejean, 1831 Plate 6B

Basilewsky 1977

Distribution: Namibia, Tanzania, South Africa (N. Limpopo)

VBR localities: BLS, MAA

Notes: Basilewsky (1977) distinguished 9 subspecies, including the nominal one; *Graphipterus cordiger cordiger* is proper to South Africa (Traansval, Orange, Lesotho and Cape Province).

Graphipterus fasciatus fasciatus Chaudoir, 1870 Plate 6C

Basilewsky 1977

Distribution: South Africa (Traansval, Natal), Swaziland

VBR localities: BEN

Graphipterus incanus quadrilineatus Brullé, 1834 Plate 6D

Graphipterus consocius Péringuey, 1896

Basilewsky 1977

Distribution: South Africa (N. Limpopo)

VBR locality: BEN

Pieza Brullé, 1834

The prothorax is longer than broad (Péringuey, 1896). These beetles are black in colour, larger than *Graphipterus* which it resembles in general appearance, but without velvety pubescence on the elytra. The genus was revised by Basilewsky (1981).

Pieza cf. *algoensis* Péringuey, 1896 Plate 7A

Basilewsky 1981

Distribution: Mozambique, South Africa (Limpopo), Botswana

VBR locality: MAS

Lebiini Bonelli, 1810

Lebiini are medium sized, very dark brown beetles with reddish brown legs; the lateral margins of the pronotum and elytra are distinctly emarginated. The head bears two supra-orbital setae above the eyes, and narrows into a neck before articulating with pronotum. The pronotum is broad and short, and the elytra are somewhat depressed (Péringuey 1896). They are mostly southern African in distribution. Basilewsky (1958) provides a checklist to the South African species.

***Hystrichopus* Boheman, 1848**

= *Aspastus* Péringuey, 1896:
= *Assotatus* Péringuey, 1896:
= *Assoterus* Péringuey, 1896:
= *Astus* Péringuey, 1896:
= *Ctenoncus* Chaudoir, 1850

Hystrichopus sp. Plate 5D
Accession no.: carabd-BEN4d
VBR localities: BEN, HLF, RM, TV, VM
Note: Basilewsky (1958) records one species of this genus as occurring country-wide, including Limpopo, *Hystrichopus atratus* Caudoir, 1850. We were unable to determine whether our specimen matches this species, but it is highly likely that it is the same based on the locality records.

***Pseudomasoreus* Desbrochers des Loges, 1904**

= *Cymindis* Fairmaire & Laboulbene, 1854

Preudomasoreus shows a disjunct distribution, occurring in the Mediterranean, then Madagascar, the Cape and Drakensberg (Basilewsky, 1958). Basilewsky (1958) shows no record of the genus from Limpopo however.

Pseudomasoreus sp.
Accession no: mspp71-LF5b
VBR locality: LF

LICININAE Bonelli, 1810

Like Harpalines, this tribe has one supra orbital seta but this occurs along the posterior half of the eye; on the other hand there is one prothoracic seta or setae absent. They are arboreal in habit. To enable them to walk on smooth leaf surfaces, they possess specialized claws or adhesive lobes and pads on the underside of their tarsi (Scholtz & Holm, 1985). Some species have flattened bodies which allow them to move under bark and in narrow crevices in wood.

Chlaeniini Brulle, 1834

Occur worldwide and in a wide variety of different habitats (Erwin, 1984).

***Chlaenius* Bonelli, 1810**

= *Rhysotrachelus* Boheman, 1848

The representants of this genus are often metallically coloured (Scholtz & Holm, 1985), especially the pronotum, which is punctate and in all cases has a small depression on either side of the postero-lateral region. Sometimes a broad orange-brown band occurs along the lateral margins of the elytra, thickening towards the posterior margin, especially on specimens with darkly coloured elytra. Burgeon & Banninger (1937) list and describe a few species from Africa. Kirschenhofer (2010) describes the known species from Africa and provides a key.

Chlaenius (*Pachydinodes*) *bipustulatus* Boheman, 1848 Plate 7B
Péringuey 1896, Alluaud 1939
Distribution : Angola, Namibia, Zimbabwe, Mozambique,South Africa (N. Limpopo)
VBR localities: BLS, GON, GOR

Chlaenius (*Amblygenius*) *cyanipennis* Boheman, 1848
Péringuey 1896, Kirschenhofer 2010
Distribution : South Africa (N. Limpopo)
VBR locality: RM

Chlaenius (*Lissauchenius*) *perspicillaris* Erichson, 1843
Péringuey 1896, Kirschenhofer 2010
Distribution : Botswana, South Africa (N. Limpopo)
VBR locality: BLS

Chlaenius (*Rhysotrachelus*) *quadrimaculatus* (Boheman, 1848)
Péringuey 1896, Kirschenhofer 2010
Rhysotrachelus quadrimaculalus Boheman, 1848
Distribution : South Africa (N. Limpopo)
VBR locality: BGM

ORTHOGONIINAE Schaum, 1857

Very little is known of this group in Africa. Three tribes are recorded: Amorphomerini, Idiomorphini and Orthogoniini (Anichtenko *et al*. 2016).

Orthogoniini Schaum, 1857

Occur in sub-Saharan Africa and Oriental regions (Erwin, 1984).

***Orthogonius* Macleay, 1825**

= *Apsectra* Schmidt-Gobel, 1864
= *Haplopisthius* Chaudoir, 1850
= *Maraga* Walker, 1858

Their representants are somewhat flattened, small to medium sized beetles with truncate elytra (Erwin 1984). They are generally brown in colour, the pronotum is emarginate and small in relation to the entire body; the head sculpture is reticulo-punctate. Péringuey (1896) lists this as the only genus of the tribe to occur in southern Africa, and catalogued four species.

Orthogonius capucinus Boheman, 1848
Distribution: South Africa (N. Limpopo)
VBR locality: BAR

PANAGAEINAE Bonelli, 1810

Beetles showing great variability in size, with some showing striking colourations. Three tribes are known to occur in southern Africa: Panagaeini, Peleciini and Bascanini. A catalogue and an addenda of the world fauna of this family was published by Häckel & Farkač (2012, 2013a).

Panagaeini Bonelli, 1810

This tribe occurs in tropical and warm temperate regions worldwide (Erwin, 1984). Seven genera occur in southern Africa, including *Microcosmodes* Strand, 1936, which has been recorded from the VBR.

***Tefflus* Leach, 1819**

= *Archotefflus* Kolbe, 1903
= *Mesotefflus* Kolbe, 1903
= *Stictotefflus* Kolbe, 1903
= *Heterotefflus* Kolbe, 1904
= *Alexotefflus* Basilewsky, 1935

The genus *Tefflus* Leach contains 15 (Lorenz, 2015) species widely distributed throughout sub-Saharan Africa. They can be recognized by their large body size (24-55 mm in length) and their distinctive body form. *Tefflus* are predators of land snails, particularly the giant land snails in the genus *Achatina* Lamarck (Gastropoda: Achatinidae) (Mawdsley *et al*., 2011b). Other important morphological features are the terminal segments of the palps which are securiform (axe-shaped) and attached eccentrically to the preceding segment (Péringuey 1896). The prothorax is hexagonal in dorsal view. The abdomen is enclosed entirely by the deeply punctate-striate elytra. Mawdsley *et al*. (2011b) reviewed information on *Tefflus*.

Tefflus cf. *meyerlei* (Fabricius, 1801) Plate 7C

Carabus meyerlei Fabricius, 1801

Mawdsley *et al*. 2011b, Häckel & Farkač 2012, 2013a

Distribution : sub-Saharan Africa

VBR locality: TV

PAUSSINAE Latreille, 1807

Paussinae are highly specialized inquilines of ant colonies, hence their common name ant-guest beetle. Their members have antennae of 10-segments or less (except for the Ozaenini, a rare basal tribe of Paussines that still have 11-segmented antennae) (Basilewsky, 1962). The Ozaenini are unrecorded for South Africa. Scholtz & Holm (1985) state that all Paussinae have two antennal segments - although this state is common with ant-guest beetles, common genera like *Cerapterus* have 10 segmented antennae. The shape of the antennae is flattened, reportedly to serve as handles by which the beetles are dragged about by ants. Paussines appease ants by secreting a volatile substance from the prothorax and in some cases the antennae. Some species rely on the ants' food distribution system through trophallaxis (Scholtz & Holm, 1985). Luna de Carvalho (1989) published a world monograph on this subfamily.

Paussini Latreille, 1807

Many genera occur in this tribe; members are pantropical in distribution (Erwin, 1984). Their classification has changed considerably in recent years (Anichtenko *et al*., 2016).

***Cerapterus* Swederus, 1788**

= *Orthopterus* Westwood, 1838
= *Euthysoma* J.Thomson, 1860
= *Ceratopterus* Girard, 1873
= *Eucerapterus* H.Kolbe, 1926

Very stoutly built beetles with 10 segmented antennae; the antennae are extremely broad and compact, the legs are flattened and dorsolaterally expanded (Scholtz & Holm, 1985). The surface of the beetle is very smooth and a rich brown in colour. They ejects a volatile fluid that stains the skin a dark-brown when handled.

Cerapterus sp. Plate 7D
Accession no: Car-LTT1
VBR locality: BEN

***Cochliopaussus* Kolbe, 1927**

= *Fimbriopaussus* H.Kolbe, 1927
= *Dollmanipaussus* H.Kolbe, 1933
= *Marshallipaussus* H.Kolbe, 1933
= *Spinipaussus* H.Kolbe, 1933
= *Angolapaussus* Luna de Carvalho, 1989
= *Strombipaussus* Luna de Carvalho, 1989

Lorenz (2005) considers this genus as a subgenus of *Paussus* Linnaeus, 1775). Their representants are very peculiar paussines, with small heads, and 2-segmented antennae, the last segment is very large and almost leaf-shaped with serrated margins. The prothorax bears a lateral thorn or tooth anterior to the front legs, with tufts of setae behind on the pronotum. The elytra are posteriorly truncate, exposing the last abdominal sternite. The genus occurs in Africa, the Arabian Peninsula and India (Luna de Carvalho, 1989).

Cochliopaussus cf. *cucullatus* Westwood, 1850

Luna de Carvalho 1989, Nagel 2006

Distribution: Zambia, Botswana, South Africa (N. Limpopo)

VBR locality: BRI

PLATYNINAE Bonelli, 1810

A very large subfamily with three tribes, with only Platynini known to occur in southern Africa (Anichtchenko *et al*. 2016).

Platynini Bonelli, 1810

Two subtribes occur in southern Africa: Platynina and Enoicina.

***Orthotrichus* Payron, 1856**

= *Trichotarus* Motschulsky, 1865
= *Metagonum* Jeannel, 1948
= *Kalchtacha* Morvan, 2002

The species of this genus are small to medium dark beetles, with lightly coloured orange legs; the pronotum is emarginated; two supra-orbital setae occur above the eyes, one pair of setae occurs on the pronotum, both elytra have a row of three short setae along the first and second elytral stria situated medially.

Orthotrichus gilvipes (Boheman, 1848) Plate 5B

Basilewsky 1950a

Distribution: Ethiopia, Mozambique, Zimbabwe, Burundi, Rwanda, D. R. of the Congo, Angola, Botswana, South Africa (N. Limpopo)

VBR localities: BGM, EF, HLF, LF, LM, RM. TV, VM

PTEROSTICHINAE Bonelli, 1810

Representants of this subfamily present two supra-orbital setae and two prothoracic setae. Moreover they do not generally have the last abdominal segment exposed, as the elytra enclose the abdominal tergites. The most important feature of the group is the internal plica, an infolding of each elytron along the postero-lateral margin. Straneo (1958, 1963) revised the South African fauna. Straneo (1963) writes that there are a high number of endemic species in southern Africa.

Pterostichini Bonelli, 1810

This tribe occurs world-wide, and is adapted to all zones and regions. They mostly live in leaf litter and decaying wood. Some are arboreal (Erwin, 1984).

Wahlbergiana **Bousquet, 2002**

= *Wahlbergia* Tschitscherine, 1896

Medium sized beetles; the entire body is black, the head and pronotum are shiny, while the tarsi, antennae and palps are dark red. The prothorax is only a little narrower than the elytra; with the interstices raised and tectiform (Straneo, 1963).

Wahlbergiana alternans Straneo, 1951 Plate 3A
Straneo 1963
Distribution : South Africa (Soutpansberg)
VBR localities: EF, HLF, TV, VM
Note: Straneo (1963) recorded only this species in the genus. It apprears to be restricted to forests in the Soutpansberg, and is very likely a local endemic.

Abacetini Chaudoir, 1872

Occurs world-wide in different regions (Anichtenko *et al*. 2016).

Abacetus Dejean, 1828

The genus *Abacetus* is characterized chiefly by the following characters: the shape of the labium; the second joint of the antennae eccentrically inserted in the basal joint; no scutellary stria on the base of the elytra; interstice three of the elytra with a single puncture; and male protarsi with the joints not obliquely truncate (Straneo, 1963). Three prominent setae are also visible on the postero-lateral margins of the elytra. Straneo (1963) provides keys for the South African species, however species level identification poses considerable difficulty without access to types.

Abacetus sp.
Accesion no: mspp84-BLS7a
VBR localities: BLS, LF, LM, RM, VM

Aristopus Laferté-Sénectère, 1853

= *Celioschesis* Tschitscherin, 1898

These are very small, lightly coloured beetles, with two setae on the lateral margins of pronotum, and two supra-orbital setae above the eyes; the clypeus has two anterolateral margins, and the labrum has four setae on the anterior margin. No setae occur on the postero-lateral margins of the elytra however. The entire fifth elytral interstice forms a light band on the elytron (Straneo, 1963).

Aristopus decorus (Straneo, 1956)
Straneo 1958
Distribution : South Africa (Limpopo, Cape)
VBR locality: HLF
Note: synonymn missing

SCARITINAE Bonelli, 1810

This is a well represented group of beetles in southern Africa. The tribe is characterized by an elongated first segment of the antennae, hence elbowed antennae. The prothorax and hind body are joined by a narrow peduncle. The head and prothorax are deeply grooved; the legs are short and stout and adapted for digging (Péringuey, 1896), and burrowing in loose soil where they hunt larvae and other insects (Scholtz & Holm, 1985). The related Promecognathinae is similar in appearance, but members of this group are smaller is size, and the peduncle between prothorax and the hind body is broader (Basilewsky, 1962).

Scaritini Bonelli, 1810

Péringuey (1896) records twelve genera in the tribe in southern Africa. The most common genus in the northern bushveld is *Scarites*.

***Scarites* Fabricius, 1775**

The genus is found worldwide. They are completely black, large beetles, with deeply grooved mandibles. The mentum almost obscures the insertions of the labial palps in dorsal view. The mentum is also deeply grooved with a prominent median projection; the eyes are small, with the head fitting broadly into the anterior margin of the pronotum. The anterior tibia bears a spur nearly as long as the tarsi (Péringuey, 1896).

Scarites sp. A Plate 5C
Accession no.: mspp88-BAR4c
VBR localities: BAR, GOR, MAS, NWA
Note: This species closely matches the description of *Scarites natalensis* Boheman, 1848 in Péringuey (1896). It is also the species in the genus with the widest distribution.

Scarites sp. B

Accession no: UVICC_Sca2

VBR locality: LM

Note: This species closely matches the description of *Scarites molossus* Klug, 1853 found in Péringuey (1896).

Discussion

For this study we sampled 53 ground beetle species in total, of which one, *Wahlbergiana alternans* is a confirmed local endemic. There are 8 morphospecies, identified to genus that we could not determine to species level; we cannot confirm at this point whether these are new species. The Vhembe Biosphere Reserve carabid fauna is dominated by Anthiinae, Cicindelinae and *Graphipterus*. It is difficult to compare this assemblage to other regions in South Africa as very little assemblage studies have been done on Carabidae in the region, but the species we found are large, spectacular and often beautifully coloured. Only a small proportion of the assemblage we collected is small and cryptic.

The Carabidae (along with Tenebrionidae, Scarabaeidae, ground-dwelling Curculionidae and Staphylinidae) is one of the major components of the ground dwelling beetle assemblage. The group needs to feature more prominently in assemblage studies. This checklists highlights the richness and complexity of the ground beetle fauna of the bushveld. It also provides a summary of what is known of their basic biology and overall taxonomy, intended to supplement the information available in Scholtz & Holm (1985) and acts as a point of departure for coleopterists keen to pursue studies on South African Caraidae. This is possible because of the excellent Carabidae collections available in South African natural history museums. We recommend that a basic field guide to the Carabidae fauna of South Africa also be written, and that more revisions be undertaken to facilitate the identification of Carabidae by non-specialists.

Acknowledgments:

The collection that forms the basis of this checklist took four years to sort and assemble. During that time Ruth Muller, the Collection Manager of Coleoptera at the Ditsong Museum of Natural History, determined the genera, species and morphospecies of Carabidae. She provided valuable comments on their taxonomy and higher phylogeny, providing insights which we have incorporated into the text. We wish to dedicate this checklist to her in acknowledgement of her expertise and tireless support which has made this publication possible.

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Plates

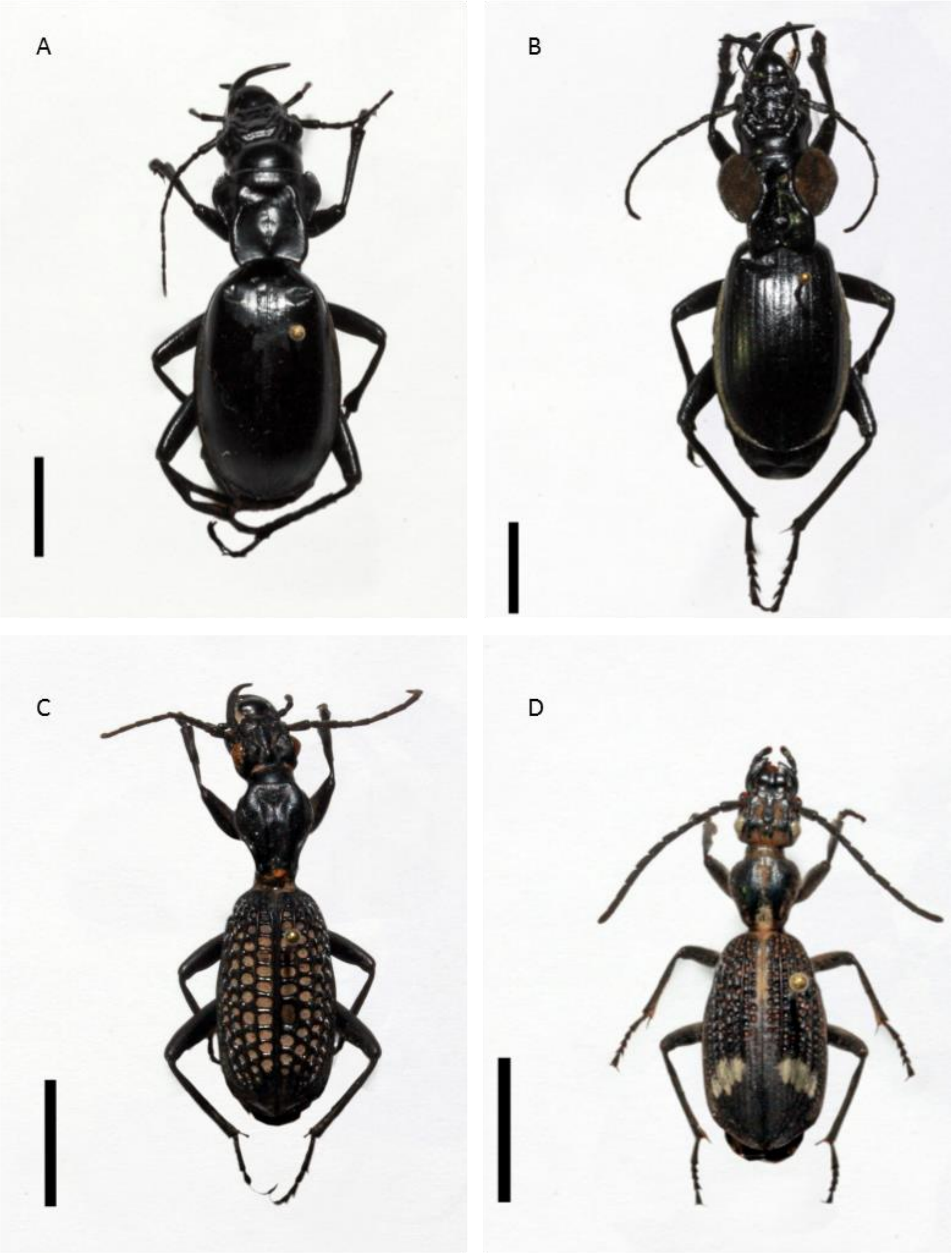

PLATE 1

A. *Anthia cinctipennis* B. *Anthia thoracica* C. *Cypholoba alveolata* D. *Cypholoba graphipteroides.* Scale bar 1 cm.

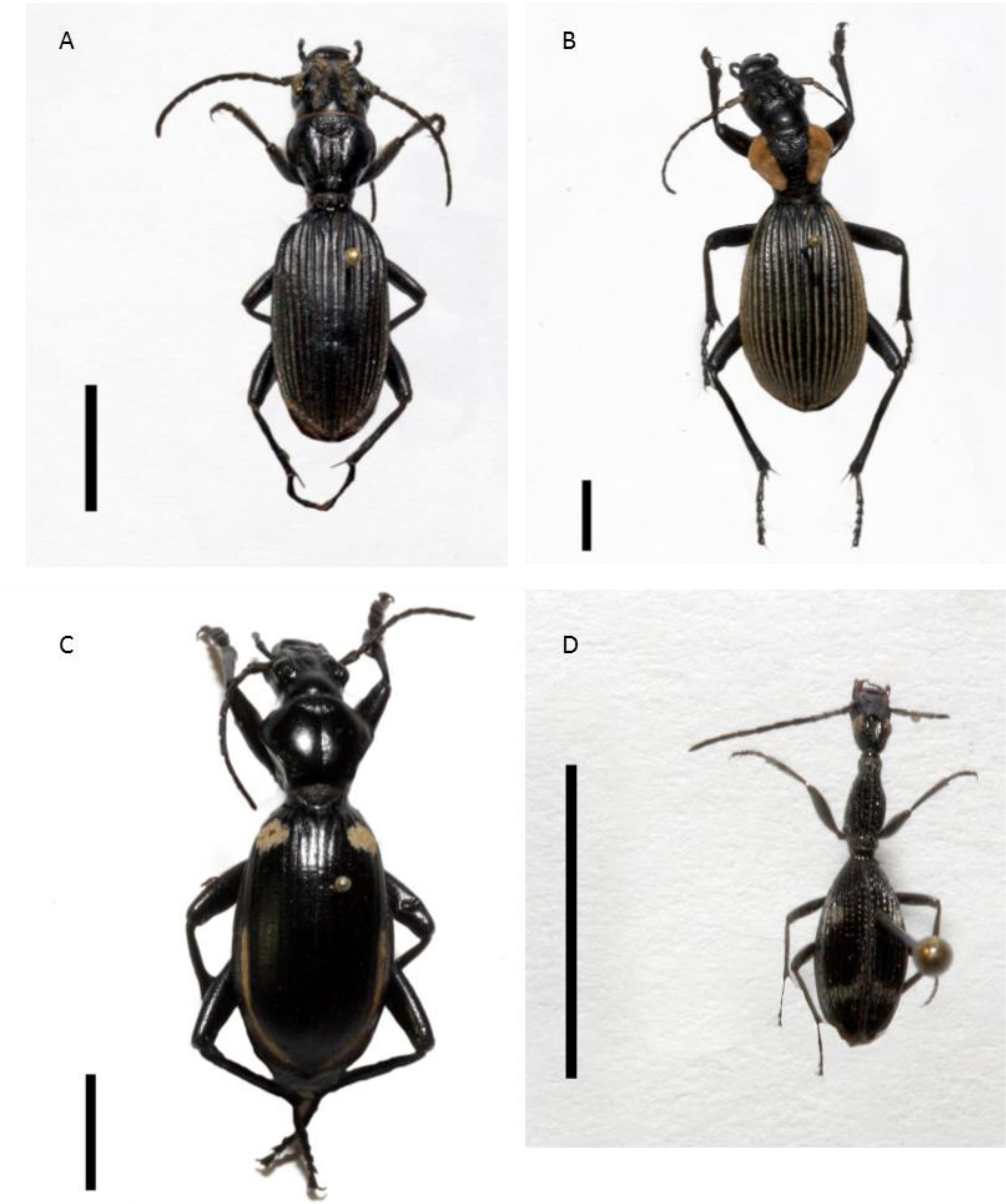

PLATE 2

A. *Termophilium bimaculatum* B. *T. burchelli* C. *T. cephalotes* D. *Atractonotus mulsanti.* Scale bar 1 cm.

PLATE 3

A. *Wahlbergiana alternans* B. *Termophilium massilicatum* C. *Crepidogaster protuberata* D. *Crepidogaster insignis.* Scale bar 1 cm.

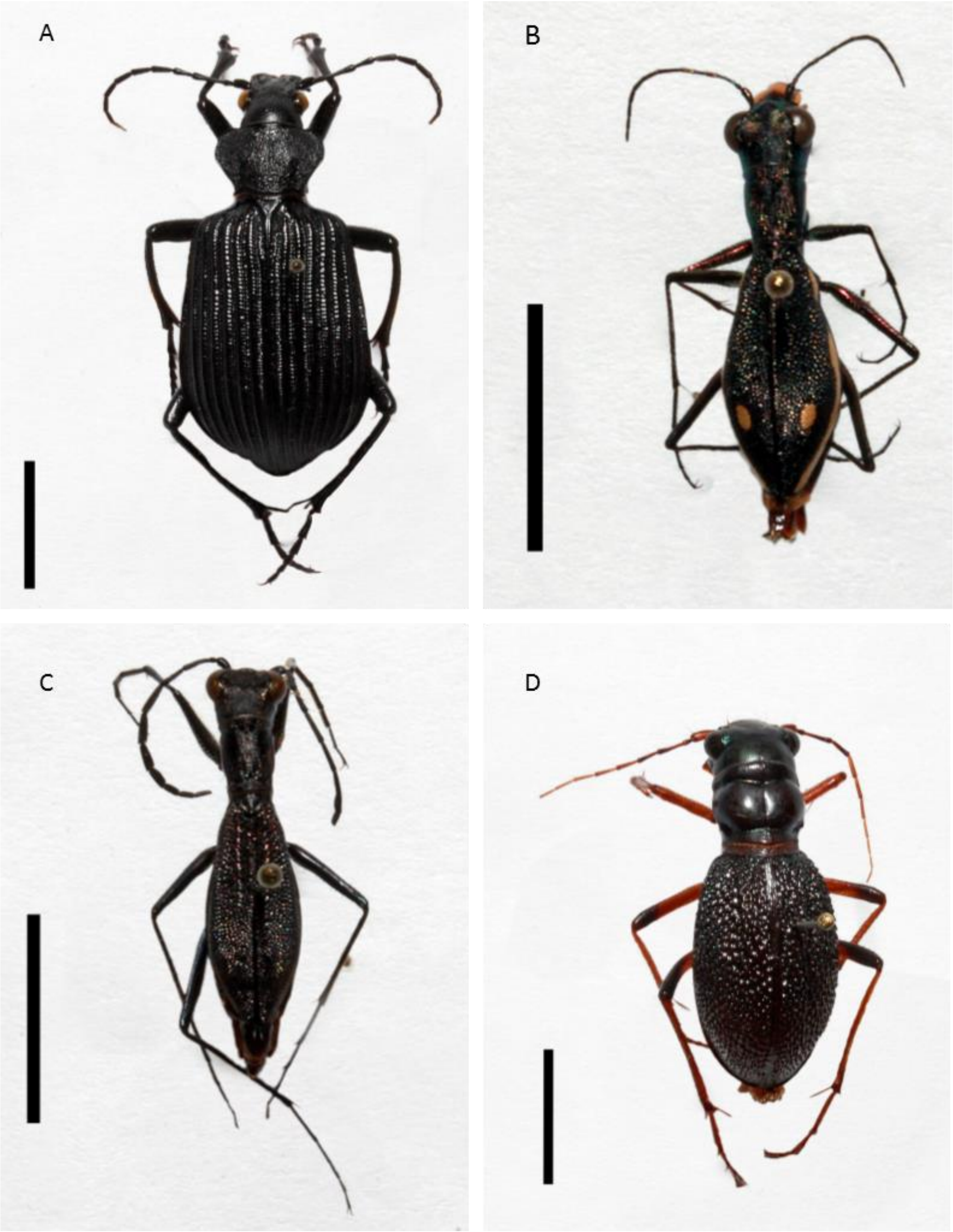

PLATE 4

A. *Calosoma planicolle* B. *Dromica latticolis* C. *Dromica costata* D. *Megacephala regalis*. Scale bar 1 cm.

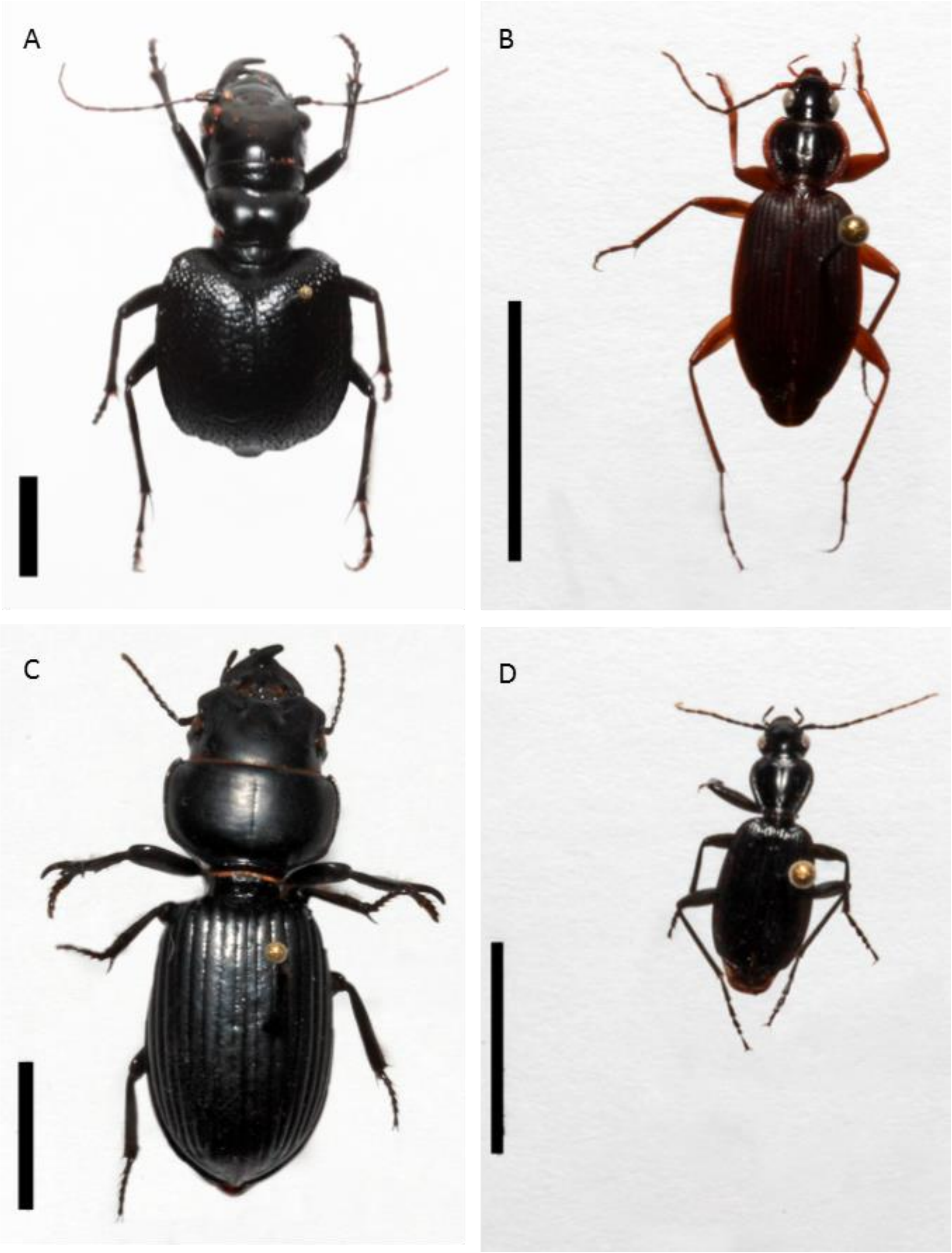

PLATE 5

A. *Mantichora* cf. *scabra* B. *Orthotrichus gilvipes* C. *Scarites* sp. A D. *Hystrichopus* sp. Scale bar 1 cm.

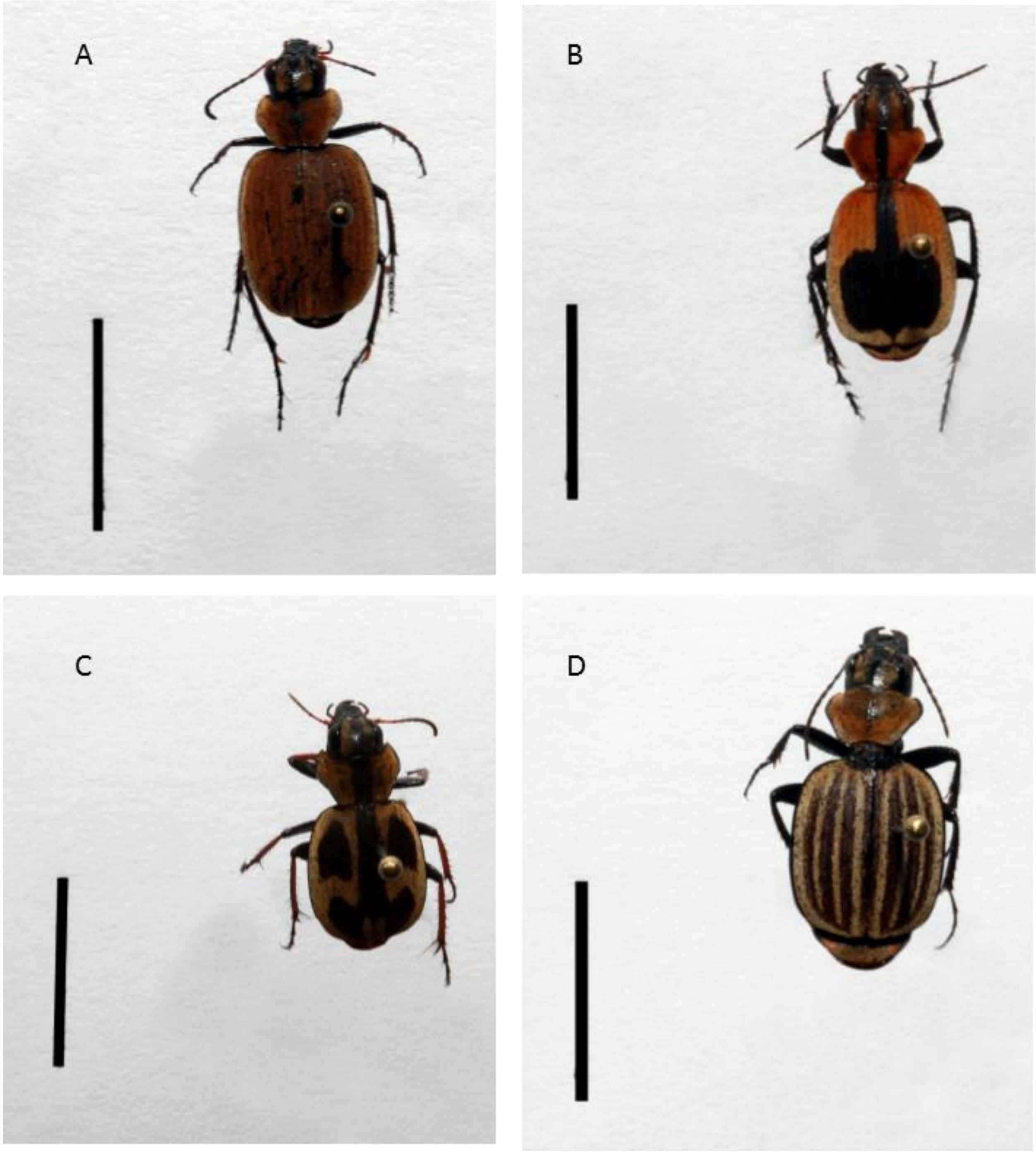

PLATE 6

A. *Graphipterus lateralis* B. *Graphipterus cordiger* C. *Graphipterus fasciatus* D. *Graphipterus incanus* Scale bar 1 cm.

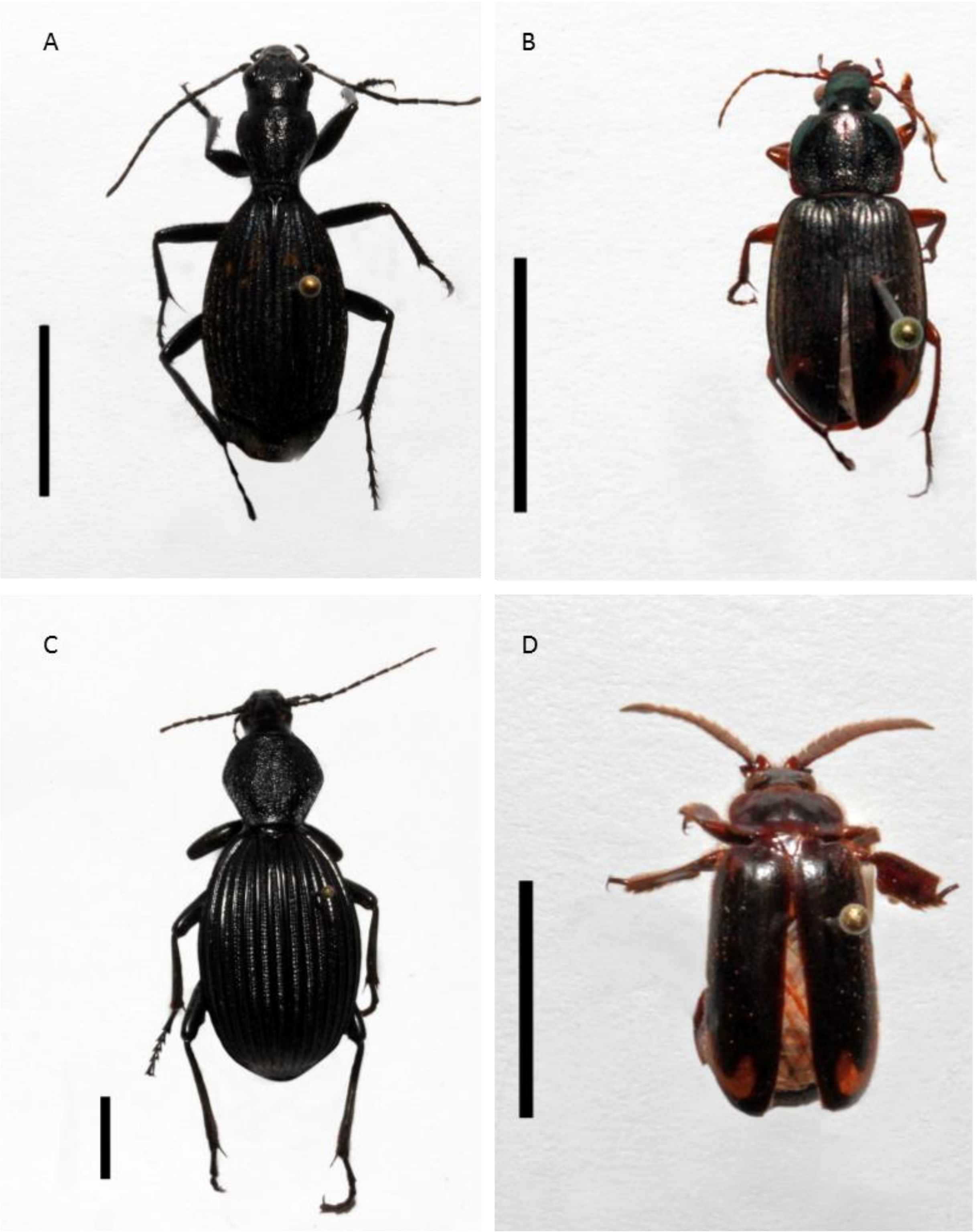

PLATE 7

A. *Pieza algoensis* B. *Chlaenius bipistulatus* C. *Tefflus* cf. *meyerlei*. D. *Cerapterus* sp. Scale bar 1 cm.

Gazetteer

Abbreviation	Site	Vegetation type	latitude	longitude
BAR	Barries Farm	Musina Mopane Bushveld	-22.48	29.41
BEN	Ben Lavin Nature Reserve	Makhado Sweet Bushveld	-23.13	29.92
BGM	Bluegumspoort (Farm)	Soutpansberg Summit Sourveld	-22.96	29.89
BLN	Blouberg NR North	Roodeberg Bushveld	-22.98	29.12
BLS	Blouberg NR South	Roodeberg Bushveld	-23.02	29.09
BRI	Bristow Farm	Makhado Sweet Bushveld	-23.17	29.76
EF	Entabeni State Forest	Northern Mistbelt Forest	-23.01	30.24
GON	Gondeni (Communal land)	Soutpansberg Mountain Bushveld	-22.91	30.06
GOR	Goro Game Reserve	Soutpansberg Mountain Bushveld	-22.93	29.42
HLF	Hanglip State Forest	Northern Mistbelt Forest	-22.99	29.88
LF	Lajuma Forest	Northern Mistbelt Forest	-23.03	29.44
LM	Lajuma Mistbelt	Soutpansberg Summit Sourveld	-23.02	29.43
LUD	Ludwig's Lust Farm	Limpopo Ridge Bushveld	-22.25	29.78
MAA	Mara Research Station	Makhado Sweet Bushveld	-23.14	29.55
MAR	Maremani Game Reserve	Limpopo Ridge Bushveld	-22.39	30.23
MAS	Mashovela Lodge	Soutpansberg Mountain Bushveld	-22.93	29.89
NWA	Nwanedi Game Reserve	Soutpansberg Mountain Bushveld	-22.64	30.37
RM	Happy Rest	Soutpansberg Summit Sourveld	-23.01	29.75
TV	Thatevondo State Forest	Northern Mistbelt Forest	-22.91	30.33
VM	Vhuvha (Communal land)	Soutpansberg Summit Sourveld	-22.99	30.18

CHAPTER 7

CONCLUSION

This thesis consisted of two parts. First a synopsis that provides the background, conceptual framework, objectives, the main findings of the thesis and some perspectives, followed by three data chapters on how drivers and predictors at varied scales can be used to explain and act as surrogates for invertebrate biodiversity as well as provide a framework for effective zonation in biosphere reserves. The first paper deals specifically with predictors of invertebrate species richness and turnover, the second investigates surrogacy by exploring cross taxon surrogacy between woody vegetation and ground dwelling invertebrate richness and community complimentary (or beta diversity), and the third specifically tests effectiveness of the current Vhembe Biosphere zonation in representing invertebrate diversity across the region. Uniting these three papers is the use of spatial data over a large geographic area to explore the performance of the drivers and correlates we measured. One of the major constraints of this study was the sheer abundance of invertebrate specimens that were sampled in pitfalls. My original intention was to work simply on the ants, but this was impossible, as the obvious diversity of beetles clearly exceeded ant diversity. We therefore only sorted and identified beetles, spiders and millipedes from these samples. To summarize we found that:

1. Vegetation units or types were the best predictor of richness and community structure for spiders and beetles in the region. Richness was negatively affected by increases in ruggedness and canopy cover while community structure was also strongly influenced by temperature and elevation.
2. Woody plant richness and composition was not a very suitable surrogate for beetle and spider diversity, and was a poor surrogate for millipedes. In terms of complimentarity, higher taxonomic surrogates performed best in the Surrogacy Accumulation Index, indicating the genus level identities are suitable proxies for species level determination in biodiversity surveys.
3. The current zonation of core areas conserved approximately 50% of the invertebrates species recorded in this study, and was significantly more effective than if core areas were to be selected at random conserving an unusually high diversity of beetles, spiders and millipedes in relation to the area covered. We found that the current zonation of core zones must be adjusted to take biodiversity data into account, as displayed by the proposed core areas which shows greater potential in conserving regional fauna despite challenges in its application.

The second part of this thesis consists of two checklists of the darkling beetles (Tenebrionidae) and ground beetles (Carabidae) of the Vhembe Biosphere Reserve. Because very few biodiversity surveys report on these two taxa I began to collect and gather all the information that I could on these groups. The checklists summarize all the current literature of these two groups in South Africa, and therefore provides a much needed conspectus of a highly neglected fauna in Africa. I did not provide a similar treatment for dung beetles (Scarabaeinae) as they are relatively well-known (Davis *et al*. 2008). As part of this initiative, many specimens which became the basis for a large Coleoptera collection were pinned and are housed in four new cabinets in the Natural History Collection at the University of Venda. This collection contains all identified species in their genera, tribes and families, and has proven invaluable in providing information to a number of specialists in Coleoptera (Kamiński & Schoeman, 2018a, 2018b; Kamiński & Schawaller, 2018).

Because many of the specimens obtained in biodiversity surveys are rare, endemic or new, they have immense value for taxonomy. Not contributing specimens used as morphospecies in some way to taxonomic efforts is wasteful and can be unethical. However, new species from two darkling beetle genera, *Bantodemus* and *Anaxius*, collected during this study, are described and revised respectively.

Recommendations

1. We recommend that conservationists and decision makers use vegetation types as the coarsest biodiversity unit in which new areas can be selected for conservation (Schaffers *et al*., 2008).
2. Vegetation units, at least for savanna ecosystems, can be used as appropriate proxies for conserving invertebrate biodiversity (Martínez *et al*., 2017).
3. If we conserve original vegetation cover and invertebrates we are in fact conserving basic ecological processes without which larger organisms, often the target of conservation action, wouldn’t survive.
4. This is one of the few studies that shows that core and buffer zones are effective at conserving invertebrates.

5. Invertebrate conservation must go hand in hand with sound taxonomy. It is important to provide detailed descriptions of regional fauna because this is the hard currency that gives value to conservation efforts (Mace, 2004; Strayer, 2006; Cardoso *et al*., 2011).

Future directions

The network of protected areas in the savanna biome in Africa is one of the most extensive in the world, conserving over 17% of habitat cover (Juffe-Bignoli *et al*., 2014). This network represents the most iconic wilderness areas in the world (Scholte, 2011) and comprises 10 major protected area clusters (Fig. 1). These protected areas have been relatively effective at conserving biodiversity within their borders (Gross *et al*., 2013), yet habitat degradation and land cover change outside of them has led to increasing isolation (Clerici *et al*., 2007). Other more direct threats to African protected areas in the savanna biome are downgrading and poor management of parks (Watson *et al*., 2014; Juffe-Bignolli *et al*., 2014; Lewis *et al*., 2017). In Uganda, oil exploration and development is occurring inside protected areas, including the western portion of Murchison Falls National Park (Watson *et al*., 2014). The World Heritage Site Selous Game Reserve in Tanzania was reduced to allow for uranium mining (Watson *et al*., 2014). Mining is also a major threat to the biosphere reserves of Limpopo, including the World Heritage Site Mapungubwe National Park in the Vhembe Biosphere Reserve (Steenkamp, 2018). With population growth and pressures on natural ecosystems increasing more species and ecosystems are becoming predominantly confined to protected areas – including invertebrates (Watson *et al*., 2014). Transformation of habitat between protected areas is especially acute for South Africa (Wegmann *et al*., 2014) especially within semi natural and partially degraded areas in the African savanna (Schoeman & Foord, 2012; Foord *et al*., 2018). The few remnant habitats that persist within these degraded rural landscapes are protected within small nature and game reserves (Rogo & Odulaja, 2001; Wegmann *et al.*, 2014). Very few protected areas consider broad-scale patterns on invertebrate diversity, but this study has shown that information on this mega-diverse group can and should guide conservation initiatives in Africa. In particular, it highlights the importance of targeting areas that have existing frameworks and structures for conservation and complementing with conservation targeted conservation initiatives in areas that does have similar infrastructure support.

As available habitat is being reduced, areas that are available for conservation are becoming smaller and smaller (Keller & Largiader, 2003; UNEP-WCMC & IUCN, 2016). And one question that interests me is, if an area is too small to support 'Big 5' animals, what then is the use of conserving a small plot of land? For me the answer is that there is still a community of plants, meso-carnivores, small mammals and invertebrates that continue to provide ecosystem services (Duflot *et al.*, 2015). Studies that explore how fragmented and transformed habitats conserve species often find that a much greater proportion of species than the authors expected is conserved (Erős & Campbell-Grant, 2015; Suggitt *et al.*, 2015; Hanski *et al.*, 2017; Foord *et al.*, 2018). Of course, we may be seeing an extinction debt in such cases – or communities are in fact more resilient than we give them credit for (Chiquetto-Machado *et al.*, 2018).

Fig. 1. Clusters of protected areas in the savanna biome of Africa. As an example, the Kruger Cluster includes, Kruger National Park, Kruger to Canyons and Vhembe Biosphere Reserves, Limpopo National Park (Mozambique) and Gonorazhou National Park (Zimbabwe). For more details on the composition of other protected area clusters see https://www.protectedplanet.net/

A number of old reserves that have acted as flagship reserves in the past have become increasingly isolated in (Newmark, 2008). It would be very interesting to see how beetle assemblages are persisting in highly modified rural landscapes in South Africa, Zimbabwe, Zambia, Tanzania and Kenya. Sub-Saharan Africa also remains largely unexplored and many new species await discovery. It is also important to understand how isolation, edge effects from surrounding rural communities, and habitat degradation in the African landscape act as drivers of species loss in reserves that often protect the last remnants of original vegetation cover. Moreover, I would like to know how much of the original invertebrate assemblage has become restricted to protected areas, and what effect this species loss has on the provision of ecosystem services in the surrounding landscape mosaic, especially in countries where a large proportion of the population continues to rely directly on natural resources.

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APPENDICES

TAXONOMIC REVISION OF A DARKLING BEETLE GENUS *ANAXIUS* (TENEBRIONIDAE: PEDININI: HELOPININA).

TAXONOMY OF THE GENUS *BANTODEMUS* KOCH, 1955 (COLEOPTERA: TENEBRIONIDAE: PLATYNOTINI): *LUCIDUS* AND *LETHAEUS* SPECIES-GROUPS.

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Taxonomic revision of a darkling beetles genus *Anaxius* (Tenebrionidae: Pedinini: Helopinina)

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Abstract

The genus *Anaxius* Fåhraeus, 1870 (Tenebrionidae: Helopinina) is revised to include seven Southern African species, four of which are new. A taxonomic treatment of the genus is provided including a morphological study, new species descriptions, keys, illustrations, and notes on species distributions. The following species are treated: *Anaxius bloubergensis* **sp. nov.**, *A. campbellae* Koch, 1958, *A. limpopoensis* **sp. nov.**, *A. meletsensis* **sp. nov.**, *A. obesus* Fåhraeus, 1870, *A. prozeskyi* Koch, 1958, and *A. pseudoloensus* **sp. nov**. A lectotype is designated for *Anaxius obesus* Fåhraeus, 1870 to fix the taxonomic status of this species. *Anaxius montiscaerulei* Koch, 1958 is considered as a synonym of *A. campbellae*.

Key words: Southern Africa, Limpopo, Blouberg Nature Reserve, new species, morphology, female terminalia

Introduction

A recently conducted phylogenetic analysis (Kamiński *et al*. 2018) revealed a close affiliation between Helopinina Latreille, 1802 (treated previously as a separate tribe), Leichenina Mulsant, 1854 and Pedinina Eschscholtz, 1829. This relation is supported by the following morphological characters (Fig. 2A): supraorbital crest flat or carinate; mentum with lateral wings clearly visible; middle part of mentum with longitudinal keel; palpifer smaller than basistipes, situated laterally; cavities of labial palpi separated by a small distance (distance between them ca. 0.3 of the ligula width). Additionally, many representatives of this taxonomic grouping are characterized by having bipartite aedeagal tegmina with the basal piece much shorter than the apical one (Kamiński & Iwan 2017). This feature does not occur in other closely related groups of darkling beetles, such as Dendarini and Platynotini (Kamiński *et al*. 2018). Taking into consideration the above mentioned facts, Kamiński *et al*. (2018) proposed to include Helopinina, Leichenina and Pedinina within a single tribe, named Pedinini. Additionally, in the same paper the previously designated subtribes (Aptilina Koch, 1958, Micrantereina Reitter, 1917, and Oncosomina Koch, 1958) were merged with the nominal one.

The most comprehensive morphological study of the beetles currently classified within Helopinina was conducted by Koch (1958), who was the first to study male terminalia of this group. Based on the analysis of ~7,000 specimens, he proposed new diagnoses for all generic and subtribal components, and identified nearly 300 new species, most of which he planned to describe in subsequent papers. However, Koch stopped working on this group after 1958. For the next 40 years only a few authors published small contributions (e.g. Schulze 1968a, Kaszab 1971, Ferrer 1999). Within this period the most important paper was authored by Schulze (1968b), who described the larval morphology of selected species representing different genera. She provided support for the classification system previously presented by Koch (1958). In 2001, Robiche started working on *Amatodes* Dejean, 1834 (=*Oncosoma* Westwood, 1843; see Bousquet & Bouchard 2013) and related genera. This resulted in a series of taxonomic papers (Robiche 2001, 2004a, b, 2005, 2008, 2012, 2013).

Several genera representing Helopinina remained untreated for the last 60 years, with *Anaxius* Fåhraeus, 1870

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being one example. Up to now, this genus contained four species, which were known from a total of ten specimens (Koch 1958). During recent identification work, new specimens of *Anaxius* were identified within the entomological collection of the Ditsong National Museum of Natural History (Pretoria). A close investigation revealed that they, *inter alia*, represent four new species described below. Additionally, the taxonomy of the previously described species is revised.

Material and methods

This study was based on material from the Ditsong National Museum of Natural History, Pretoria, South Africa (TMNH) and the Museum and Institute of Zoology of the Polish Academy of Sciences (MIZ PAS). The original label data for the specimens is given in quotation marks and separated by a comma. Each line of the original label data is separated by a forward slash. Morphological terminology follows that of Matthews *at al.* (2010), with additional specialized terms used for the male and female terminalia (Iwan & Kamiński 2016). Terminalia were investigated using standard methodologies (see Iwan & Kamiński 2016). Morphological measurements were recorded using a filar micrometer. Images were taken using a Canon 1000D body with accordion bellows and a Canon Macro Lens EF 100 mm, and with a Hitachi S-3400N SEM in MIZ PAS. The distribution of species was illustrated using Quantum GIS (QGIS) v. 2.4, while the vector layers were downloaded from the Natural Earth web-page (www.naturalearthdata.com). The division of the Afrotropical Realm into ecoregions follows Olson *at al.* (2001). The list of all investigated localities is presented in Appendix 1.

Taxonomy

Genus *Anaxius* Fåhraeus, 1870

Anaxius Fåhraeus, 1870: 307.- Koch 1958: 208.
Type species. *Anaxius obesus* Fåhraeus, 1870; by monotypy.

Diagnosis. According to Koch's (1958) hypothesis, this genus is close to *Aptila* Fåhraeus, 1870 and *Asidodema* Koch, 1958 based on pronotal shape (subparallel sided; flat disc) and male terminalia (relatively short tegmen; clavae as large as penis). All three genera were previously classified within a single subtribe Aptilina. From *Aptila* and *Asidodema*, *Anaxius* can be distinguished by having widened protarsi and the apical segment of the maxillary palpus enlarged in males. Moreover, it differs from *Aptila* by the lack of scale-like vestiture on the upper surface of the body, while the relatively reduced prosternum differentiates it from *Asidodema* (see Koch 1958).

***Species included* (7)**. *bloubergensis* **sp. nov.**, *campbellae* Koch, 1958, *limpopoensis* **sp. nov.**, *meletsensis* **sp. nov.**, *obesus* Fåhraeus, 1870, *prozeskyi* Koch, 1958, *pseudoloensus* **sp. nov.**

Distribution. Representatives of this genus have been collected in the following ecoregions of Namibia, Mozambique, South Africa and Zimbabwe (Fig. 5): Drakensberg montane grasslands, woodlands, and forests; Highveld grasslands; Kalahari xeric savanna; Southern Africa bushveld; and Southern Miombo woodlands.

Anaxius was recorded from localities distributed between 874 and 1544 meters in elevation (Fig. 6).

Note. During the present investigation 49 *Anaxius* specimens were studied. Among this number a total of three females was identified. Because of this the following key includes only the male morphology.

Key to the species of the genus *Anaxius* (males only).

1. Intercoxal process of prosternum strongly depressed in apical part (lateral view). Elytron with setation composed of short, yellowish bristles and elongate black stiff setae (Fig. 1C, F). Protarsus slightly dilated (Fig. 1F). Metafemora with small denticles (Fig. 2D) 2

-. Intercoxal process of prosternum straight or slightly depressed in apical part (lateral view). Elytron bare or with inconspicuous bristles (Fig. 1A, B, D–G). Protarsus distinctly dilated (at least basal tarsomere) (Fig. 1A). Metafemora not covered with small denticles. 3

2. Mesotibia flattened apically, with rounded protuberance present medially (Fig. 2C). Underside of profemora with fringe of

bristles in apical part (Fig. 1B). Inner side of mesofemora with preapical denticle (Fig. 1F) . . . . *prozeskyi*
-. Mesotibia evenly curved (Fig. 1C). Underside of profemora not covered with bristles. Inner side of mesofemora without preapical denticle (Fig. 1C). . . . . *limpopoensis*
3. Elytron covered with small, shiny, tubercles (Fig. 1A, 2E). Only basal tarsomere of protarsus widened, remaining tarsomeres extremely narrow (Fig. 1A). Mesotarsus with apical tarsomere widened (Fig. 2F). Mesotiba flattened laterally (Fig. 2F) . . . . *bloubergensis*
-. Elytron covered with punctures. Basal tarsomere of protarsi widened, with subsequent tarsomeres slightly narrower (Fig. 1E). Mesotarsus with relatively narrow first tarsomere. Mesotibia not flattened laterally. 4
4. Protibia with deep median cavity (Fig. 2G). Metatibia bent inwards (Fig. 1D, E). 5
-. Protibia without or with shallow median cavity. Metatibia not bent inwards. 6
5. Meso- and metafemora simple. Metatibia bent more medially (Fig. 1D). *meletsensis*
-. Mesofemora with preapical denticle (Fig. 1E). Metafemora with fringe of bristles on underside. Metatibia bent more basally (Fig. 1E) . . . . *obesus*
6. Body size = 6.5–7.0. Mesofemora with preapical denticle (Fig. 1B). Aedeagal tegmen narrowed periapically (Fig. 3B) . . . . *campbellae*
-. Body size ca. 4.5. Mesofemora simple. Aedeagal tegmen evenly narrowed towards apex (Fig. 3E) . . . .*pseudoloensus*

Anaxius bloubergensis **sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:81D10A96-9238-4501-AF69-048DFF06453F
(Figs. 1A, 2E, F, 3A, 5)

Type data. Holotype, male (TMSA): "S. Afr.; Limpopo Prov. / Blouberg Nat. Res. / 22.59 S–29.08 E", "25–27.11.2016E-Y:3987 / day, sandy bushveld / leg. Ruth Müller". **Paratypes**, 3 males (TMSA): same data as holotype; male (TMSA) and male (MIZ PAN): "S. Afr.; Limpopo Prov. Blouberg NR North / dd22 98S, dd29.12E", "6.12.2012; 866m, BLN1 / Roodeberg Bushveld / leg. Colin Schoeman"; male (MIZ PAN): "Blouberg NR / Rodeberg Bushveld / -22.98; 29.12", "leg. Colin Schoeman / BLN7c / I".

Etymology. The name refers to the type locality, Blouberg Nature Reserve (Limpopo, South Africa).

Diagnosis. This species is distinguished from all other congeners by a unique structure of pro- (first tarsomere extremely widened, following tarsomeres narrow; Fig. 1A), mesotarsi (first tarsomere widened; Fig. 2F), mesotibiae (flattened laterally; protruding outwards apically; Fig. 2F), and aedeagal tegmen (without basal gap; Fig. 3A).

Description. Body—length = 8.0-9.0 mm. Habitus as in Fig. 1A.

Dorsal side of head covered with fine confluent punctures (0.5–1.0 diameters apart). Frontoclypeal suture rough. Canthus rounded at base; narrower than head at level of eyes. Clypeal emargination shallow (clypeal emargination width: depth ratio ca. 8.0). Labrum narrow (width: length ratio ca. 1.1); strongly emarginate medially; with basal membrane exposed. Ligula exposed, not covered by mentum. Mentum widest in apical part; with well-developed medial keel; with exposed lateral lobes; not covering cardo or basistipes; apically with median indentation. Submentum pentagonal; short. Apical segment of maxillary palpus trapezoidal; with sensory field occupying whole proximal edge. Second segment of maxillary palpus elongate (length: width ratio ca. 2.4). Palpifer located laterally on basistipes. Anterior tentorial pit circular. Eye not dorsally shielded by any keel. Margin between maxillary fossa and antenna insertion well marked. Antenna relatively long (antenna: pronotum length ratio ca. 1.4); third antennomere short (3rd: 2nd antennomere length ratio ca. 3.0); fifth antennomere elongated (length: width ratio ca. 2.0).

Pronotum narrower than elytra (elytra: pronotum width ratio ca. 1.3); relatively narrow (length: width ratio of pronotal disc ca. 0.7); disc dull, covered with fine punctures (3–4 diameters apart). Lateral sides of pronotal disc straight. Disc widest in basal half; without apophyseal depressions. Basal and lateral emargination of pronotal disc present; anterior interrupted in middle. Base of pronotum straight. Posterior angles not protruding beyond base. Pronotal hypomeron dull; without punctures; covered with very fine longitudinal rugosities; without submarginal indentation. Intercoxal process of prosternum depressed apically (lateral view); apically with oval depression on ventral surface; slightly protruding towards first abdominal segment. Procoxae narrowly separated (procoxa: intercoxal process width ratio ca. 2.0).

Elytral striae and intervals not clearly visible. Elytron covered by shiny tubercles (0.1 diameters apart) displayed on dull surface. 1st, 3rd, 5th and 7th intervals protruding on disc; transforming into sparsely (1–2 diameters apart) distributed, large, tubercles on elytral apex. Elytral base straight; not emarginate. Elytral humerus rounded. Epipleuron slightly narrowing apically, then of constant width; basally covering all elytral intervals (ventral view). Scutellum relatively large; triangular. Metathoracic wings absent.

Metaventrite extremely short (metacoxal cavity: metaventrite (between insertions of meso- and metacoxae) length ratio ca. 10.0). Process of first abdominal ventrite wide (distances between mesocoxae: metacoxae ratio ca. 0.9). Fifth abdominal ventrite without submarginal sulcus; covered with fine punctures (4–5 diameters apart).

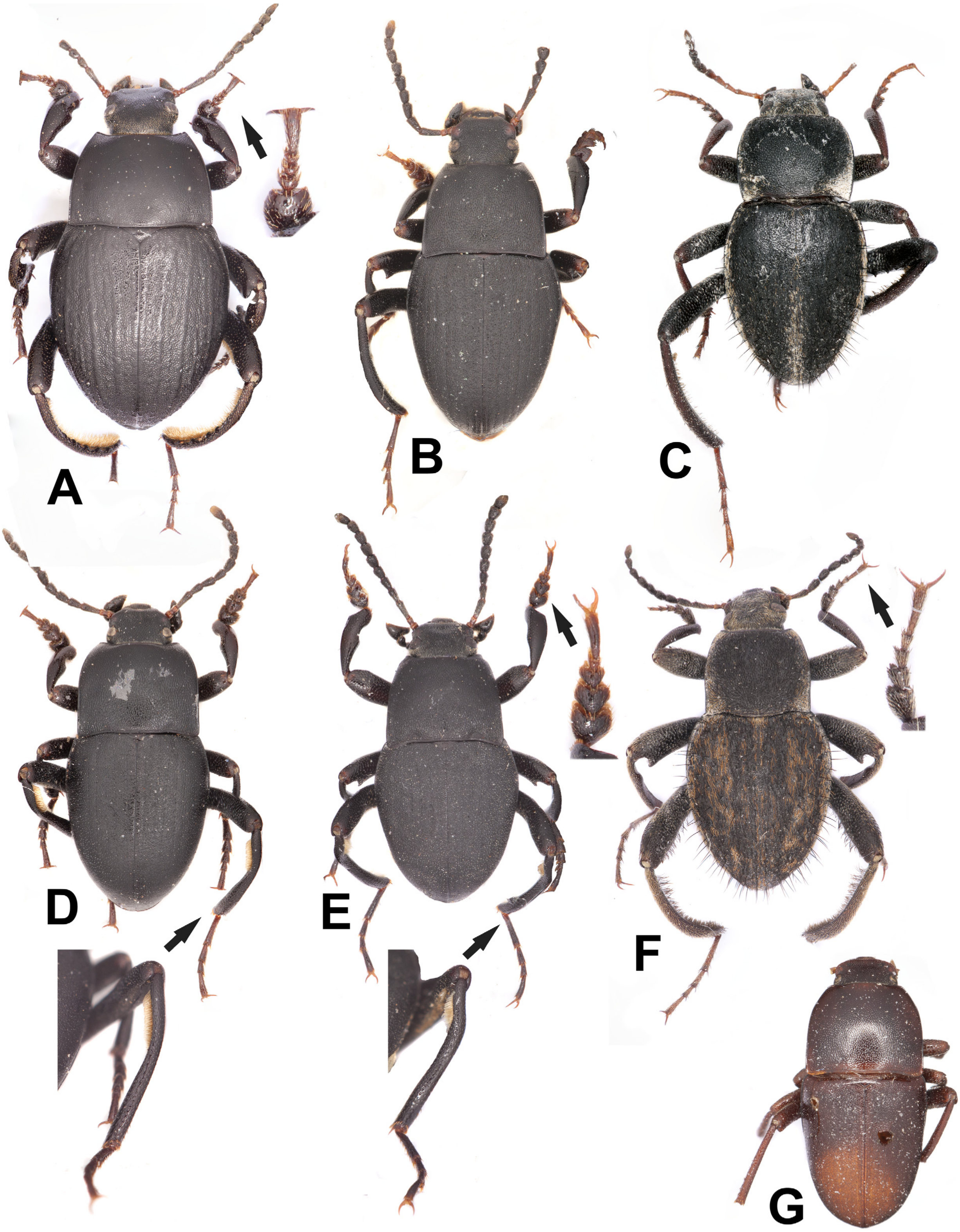

FIGURE 1. Habitus images of the studied species. *Anaxius bloubergensis* (A), *A. campbellae* (B), *A. limpopoensis* (C), *A. meletsensis* (D), *A. obesus* (E), *A. prozeskyi* (F), and *A. pseudoloensus* (G).

Male pro- and mesotarsi with basal tarsomere widened. Protibia with deep longitudinal cavity. Profemora simple. Mesotibiae flattened laterally; protruding outwards apically. Mesofemora with internal extension in apical part. Metatibia and metafemora with fringe of setae distributed on whole length. Metatibia curved inwards. First tarsomere of metatarsi elongated (1.5× longer than 4th one). Length of metatarsus equal to half of metatibial length.

Aedeagal tegmen widest in middle; unipartite; without basal gap. Apical part divided (up to 0.15 of whole tegmen length). Clava straight. Penis of even width along most of its length; with apical part not covered by tegmen, exposed dorsally. Basal apophyses of penis relatively short (ca. 0.4 of whole tegmen length).

Distribution. This species has been collected in the following ecoregions of South Africa (Fig. 5): Drakensberg montane grasslands, woodlands and forests; and Southern African bushveld.

Anaxius campbellae **Koch, 1958**

(Figs. 1B, 2A, H, 3B, 4, 5)

Anaxius campbellae Koch, 1958: 213.
=*Anaxius montiscaerulei* Koch, 1958: 214 **syn. nov.**

Notes. The original descriptions of *A. campbellae* and *A. montiscaerulei* were laconic, and as a result information concerning many features was omitted. Moreover, the newly available material revealed much variability within the diagnostic features proposed for both these species. No new characters separating *A. campbellae* and *A. montiscaerulei* were found, therefore a synonymy is proposed.

The studied female specimen was classified within this species based on the presence of orange bristles on the elytra, which seems to be a unique feature of *A. campbellae.*

Material studied. *Anaxius campbellae* Koch, 1958, **holotype**, male (TMSA): "Pienaars / River, 1898. / v. Jutrzencka", "182", "HOLTYPE / Anaxius / CAMPBELLAE". **Paratype**, male (TMSA): "Plat River.I, II:,1903 / (Jutrzencka)".

Anaxius montiscaerulei Koch, 1958, **holotype**, male (TMSA): "BLOUBERG, Tvl. / Leipsig Miss. Stat. / 3–5.I.1955 / Transv.Mus.Exp.".

Other material, 3 males (TMSA): "S. AFRICA, TVL / 25km W Pretoria / 23–29.XI.1984 / H & A Howden"; male (TMSA): "S. Afr.: Transvaal / Pienaars River 8km / 25.17S–28.17E, 28.12.1994; E-Y 3234, on ground / leg. CL Bellamy"; male (TMSA): "6.12.2012; 862m; BLS5 / Roodeberg Bushveld / leg Colin Schoeman", "S. Afr.: Limpopo Prov / Blouberg NR South / dd23.03S, dd29.10E"; male (TMSA): "S. Afr.: N Province / Blouberg / 23.03S–29.04E", "savana: 26.11.1996 / at light / Krüger, Dombrowsky"; male (TMSA): "4.12.2012; GON5 / Soutpansberg / Mountain Bushveld / leg. Colin Schoeman", "S. Afr.; Limpopo Prov / Gondeni; 871m / dd22 91S dd30 03E"; female (TMSA): "Bulawayo / S. Rhodesia / 9.I.1923 / Rhodesia / Museum".

Redescription. Body—length = 5.5–7.5 mm. Habitus as in Fig. 1B.

Dorsal side of head covered with confluent punctures. Frontoclypeal suture smooth. Canthus rounded at base; narrower than head at level of eyes. Clypeal emargination shallow (clypeal emargination width: depth ratio ca. 9.0). Labrum wide (width: length ratio ca. 1.9); slightly emarginate medially; with basal membrane exposed. Ligula exposed, not covered by mentum. Mentum widest in apical part; with well-developed medial keel; with exposed lateral lobes; not covering cardo or basistipes; apically with median indentation. Submentum pentagonal; short. Apical segment of maxillary palpus trapezoidal; with sensory field occupying whole proximal edge. Second segment of maxillary palpus elongate (length: width ratio ca. 2.6). Palpifer located laterally on basistipes. Anterior tentorial pit circular. Eye not dorsally shielded by any keel. Margin between maxillary fossa and antennal insertion well marked. Antenna relatively long (antenna: pronotum length ratio ca. 1.7); third antennomere short (3rd: 2nd antennomere length ratio ca. 2.5); fifth antennomere elongated (length: width ratio ca. 2.0).

Pronotum slightly narrower than elytra (elytra: pronotum width ratio ca. 1.2); relatively narrow (length: width ratio of pronotal disc ca. 0.8); disc shiny, covered with confluent punctures and sparse orange bristles. Lateral sides of pronotal disc straight at basal half. Disc without apophyseal depressions. Basal, anterior, and lateral emargination of pronotal disc present. Base of pronotum straight. Posterior angles not protruding beyond base. Pronotal hypomeron dull; covered with very fine longitudinal rugosities; without submarginal indentation. Intercoxal process of prosternum not depressed apically (lateral view); slightly protruding towards first abdominal segment. Procoxae narrowly separated (procoxa: intercoxal process width ratio ca. 2.0).

Elytral striae visible as nine rows of slightly impressed depressions on each elytron. Intervals covered by coarse and confluent punctures, and sparse orange bristles, that become denser on lateral intervals. Elytral base straight; not emarginate. Elytral humerus rounded. Epipleuron slightly narrowing apically, then of constant width; basally covering all elytral intervals (ventral view). Scutellum relatively large; triangular. Metathoracic wings absent.

Metaventrite extremely short (metacoxal cavity: metaventrite (between insertions of meso- and metacoxae) length ratio ca. 10.0); with rounded tubercle in middle (Fig. 2H). Process of first abdominal ventrite wide (distances between mesocoxae: metacoxae ratio ca. 0.9). Fifth abdominal ventrite without submarginal sulcus; covered with fine punctures (4–5 diameters apart).

Male protarsus widened, with subsequent tarsomeres slightly narrower. Protibia with shallow longitudinal cavity. Pro- and metafemora simple. Mesofemora with apical tooth. Meso- and metatibia curved. Metatibia with fringe of setae distributed on whole length. Female legs simple. First tarsomere of metatarsi elongated (1.7× longer than 4th one). Length of metatarsus equals to 0.75 of metatibial length.

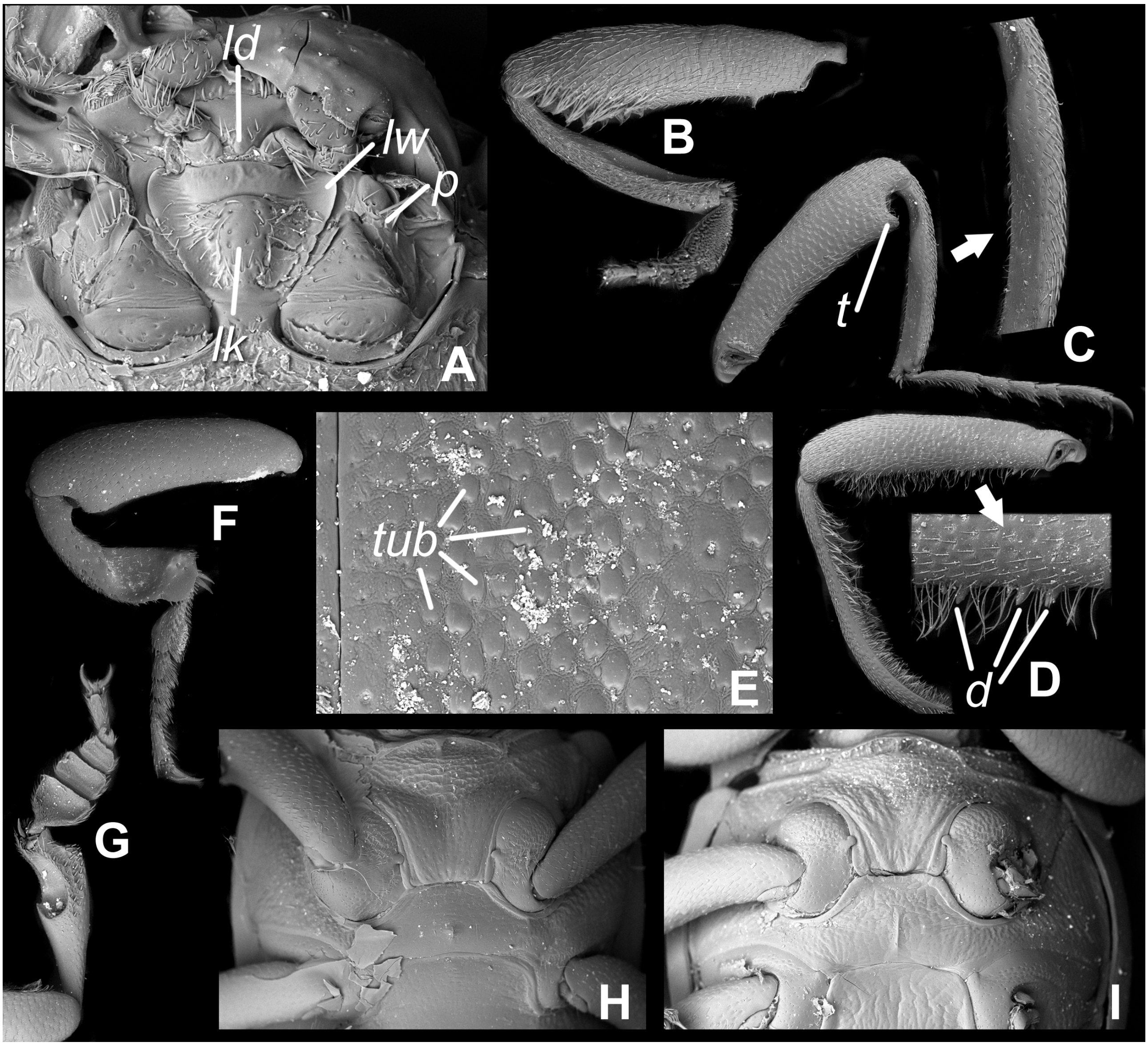

FIGURE 2. Diagnostic characters proposed for *Anaxius*: mentum (A), proleg (B, G), mesoleg (C, F), metaleg (D), metaventrite (H, I). *Anaxius bloubergensis* (E, F), *A. campbellae* (A, H), *A. meletsensis* (G, I), and *A. prozeskyi* (B, C, D). *Abbreviations*: *d*—denticles, *ld*—surface between labial palpi, *lk*—longitudinal keel, *lw*—lateral wing, *p*—palpifer, *t*—apical denticle, *tub*—tubercles.

Aedeagal tegmen narrowing along middle; bipartite; apically curved (lateral view). Apical part slightly divided (up to 0.10 of whole tegmen length). Clava narrowed and curved in apex. Penis of even width along most of its length; with apical part not covered by tegmen, nor exposed dorsally. Basal apophyses of penis relatively short (ca. 0.4 of whole tegmen length).

Ovipositor (Fig. 4) relatively short (body: ovipositor length ratio ca. 3.0). Paraproct much longer than coxites (paraproct: coxites length ratio ca. 1.8); triangular, not shielding valvifer or any other lobes of coxites. Valvifer and second lobe slightly transverse, while third one triangular. Fourth lobe rounded, situated dorsally. Gonostylus located on dorsal side of fourth lobe. Vagina and bursa copulatrix without sclerites. Spermatheca sac-like. Proctiger covering nearly whole ventral side of ovipositor.

Distribution. This species has been collected in the following ecoregions of South Africa and Zimbabwe (Fig. 5): Drakensberg montane grasslands, woodlands and forests; and Southern Africa bushveld.

***Anaxius limpopoensis* sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:0719746F-D175-4BF0-9B46-561914F390E1
(Figs. 1C, 3C, 5)

Type data. Holotype, male (TMSA): "S. Afr.; Limpopo Prov. / Lindani Nat. Res 1336m / 24.02 S–28.23 E", "8.12.2005; E-Y:3687 / single, bushveld / leg. Gusmann, Müller". **Paratypes**, male (TMSA) and male (MIZ PAN): same data as holotype; 2 males (TMSA): "S. Afr. Limpopo Prov. / Mabote farm / 24.07S 28.39 E", "14.11.2009 / Leg. Ruth Müller"; male (TMSA) "S. Afr.; Limpopo Prov. / 25 km N Mookgophong / 24.25 S–28.41 E", "12–15.1.2014 E-Y:3951 / mixed moodland 1185m / leg. Ruth Müller"; male (TMSA): "S. Afr.; Limpopo Prov. / Waterberg Game Res. / 24.11 S–28.20 E", "4–7.11.2002 / leg. B. Dombrowsky".

Etymology. The name refers to the type locality, Limpopo Province (South Africa).

Diagnosis. This species is similar to *A. prozeskyi* by having relatively narrow protarsi in males (like in Fig. 1F), strongly depressed apical part of the intercoxal process of prosternum (lateral view), and dorsal body surface covered with soft and dense bristles, with additional stiff and black setae on elytra (Fig. 1C, F). *Anaxius limpopoensis* can be easily distinguished by having simple mesotibia (curved in *limpopoensis*; flattened apically, protruding in middle in *prozeskyi*) profemora (with fringe of bristles on underside in *prozeskyi*), and mesofemora (with prominent denticle in *prozeskyi*).

Description. Body—length = 5.0–7.0 mm. Habitus as in Fig. 1C.

Dorsal side of head covered with fine confluent punctures (0.5–1.0 diameters apart) and fine yellow bristles. Frontoclypeal suture smooth. Canthus rounded at base; narrower than head at level of eyes. Clypeal emargination shallow (clypeal emargination width: depth ratio ca. 9.0). Labrum wide (width: length ratio ca. 1.5); shallowly emarginate medially; with basal membrane exposed. Ligula exposed, not covered by mentum. Mentum widest in apical part; with well-developed medial keel; with exposed lateral lobes; not covering cardo or basistipes; apically with median indentation. Submentum pentagonal; short. Apical segment of maxillary palpus trapezoidal; with sensory field occupying whole proximal edge. Second segment of maxillary palpus elongate (length: width ratio ca. 2.3). Palpifer located laterally on basistipes. Anterior tentorial pit circular. Eye not dorsally shielded by any keel. Margin between maxillary fossa and antenna insertion well marked. Antenna relatively long (antenna: pronotum length ratio ca. 1.6); third antennomere short (3rd: 2nd antennomere length ratio ca. 3.0); fifth antennomere relatively short (length: width ratio ca. 2.0).

Pronotum narrower than elytra (elytra: pronotum width ratio ca. 1.3); relatively narrow (length: width ratio of pronotal disc ca. 0.7); disc dull, covered with confluent punctures (space between punctures shiny) and yellow bristles, which are becoming denser in posterior anges. Lateral sides of pronotal disc rounded. Disc widest in middle; without apophyseal depressions; with basal depressions. Basal, anterior and lateral emargination of pronotal disc present. Base of pronotum slightly bisinuate. Posterior angles not protruding beyond base. Pronotal hypomeron dull; with fine punctures; covered yellow bristles; without submarginal indentation. Intercoxal process of prosternum depressed apically (lateral view); not protruding towards first abdominal segment. Procoxae narrowly separated (procoxa: intercoxal process width ratio ca. 2.0).

Elytral striae and intervals not visibly distinguishable. Elytron covered by confluent punctures, yellow hair, which become more dense closer to elytral suture and epipleuron, and additional stiff and black setae (Fig. 1C).

Elytral base slightly bisinuate; not emarginate. Elytral humerus rounded. Epipleuron slightly narrowing apically, then of constant width; basally covering all elytral intervals (ventral view). Scutellum relatively large; triangular. Metathoracic wings absent.

Metaventrite extremely short (metacoxal cavity: metaventrite (between insertions of meso- and metacoxae) length ratio ca. 10.0). Process of first abdominal ventrite wide (distances between mesocoxae: metacoxae ratio ca. 0.9). Fifth abdominal ventrite without submarginal sulcus; covered with fine punctures (4–5 diameters apart).

Male protarsi relatively narrow. Protibia with shallow median cavity on inner side. Pro- and mesofemora simple. Meso- and meta curved; with fringe of setae distributed on whole length. Metafemora with fringe of setae distributed along whole length; with three spines. First tarsomere of metatarsi elongated (1.5× longer than 4th one). Metatarsus nearly as long as metatibia.

Aedeagal tegmen widest in middle; bipartite. Apical part divided (up to 0.15 of whole tegmen length). Clava straight. Penis of even width along most of its length; with apical part not covered by tegmen, exposed dorsally. Basal apophyses of penis relatively short (ca. 0.4 of whole tegmen length).

Distribution. This species has been collected in the following ecoregion of South Africa (Fig. 5): Southern Africa bushveld.

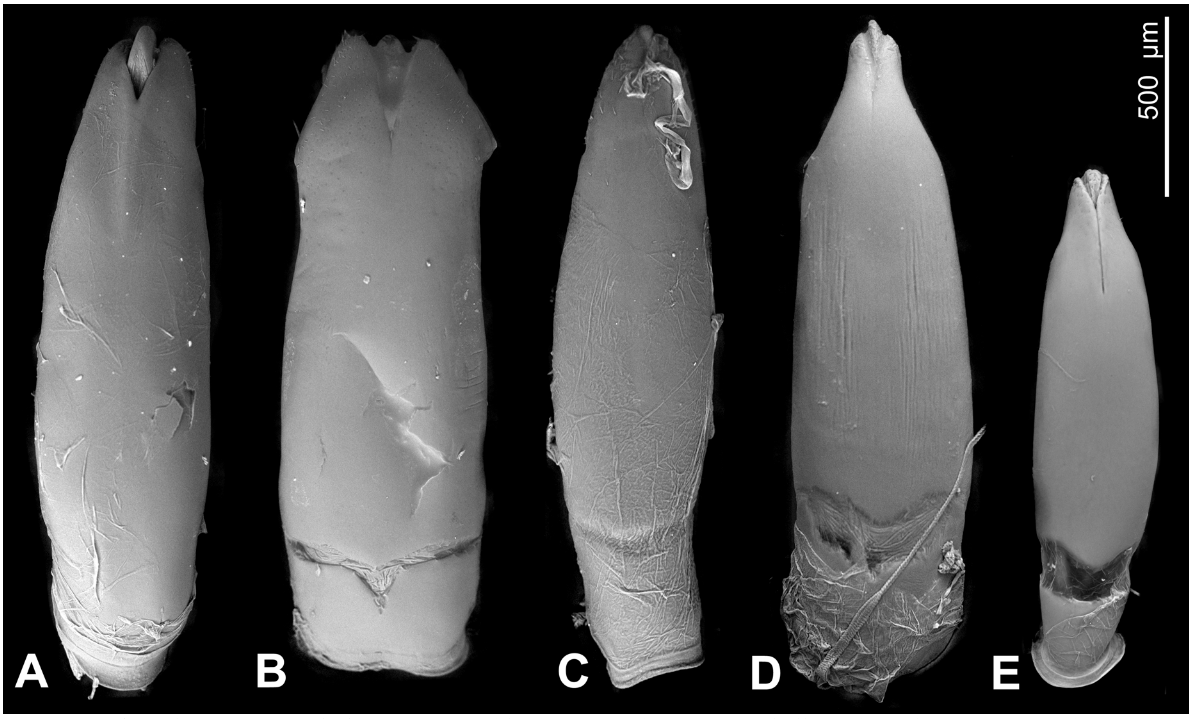

FIGURE 3. Aedeagal tegmen morphology. *Anaxius bloubergensis* (A), *A. campbellae* (B), *A. limpopoensis* (C), *A. meletsensis* (D), and *A. pseudoloensus* (G).

Anaxius meletsensis sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:79A5A46A-8614-410A-A322-AC3CF9933242

(Figs. 1D, 2G, I, 3D, 5)

Type data. Holotype, male (TMSA): "S. Afr.; Limpopo Prov. / Meletse Reserve 1003m / 24.36 S–27.39 E", "27.11.2014; E-Y:3954 / on ground, bushveld / leg. Ruth Müller". **Paratypes**, 2 males and female (TMSA) and male (MIZ PAN): same data as holotype. **Other material**, female (TMSA): "S. Afr.: Waterberg / Geelhoutbush farm / 24.22S–27.33 E", "3.10.1955; E-Y:3143 / singled / Endrödy & Bellamy".

Etymology. The name refers to the type locality, Meletse Reserve (Limpopo, South Africa).

Diagnosis. This species is similar to *A. obesus* by having, *inter alia*, protibia with deep metian cavity (visible laterally) (Fig. 2G), widened protarsus, with subsequent tarsomeres slightly narrower, and not apically depressed intercoxal process of prostenum (lateral view). *Anaxius meletsensis* can be easily distinguished by having simple mesofemora (with preapical denticle in *obesus*) and metafemora (with fringe of bristles on underside in *obesus*).

Moreover, some differences might be observed in the structure of the metatibae of both species, which are curved in the middle in *meletsensis* (Fig. 1D), and more basally in *obesus* (Fig. 1E).

Description. Body—length = 7.0–7.5 mm. Habitus as in Fig. 1D.

Dorsal side of head covered with confluent punctures. Frontoclypeal suture smooth. Canthus rounded at base; narrower than head at level of eyes. Clypeal emargination shallow (clypeal emargination width: depth ratio ca. 9.0). Labrum wide (width: length ratio ca. 1.9); slightly emarginate medially; with basal membrane exposed. Ligula exposed, not covered by mentum. Mentum widest in apical part; with well-developed medial keel; with exposed lateral lobes; not covering cardo or basistipes; apically with median indentation. Submentum pentagonal; short. Apical segment of maxillary palpus trapezoidal; with sensory field occupying whole proximal edge. Second segment of maxillary palpus elongate (length: width ratio ca. 2.6). Palpifer located laterally on basistipes. Anterior tentorial pit circular. Eye not dorsally shielded by any keel. Margin between maxillary fossa and antenna insertion well marked. Antenna relatively long (antenna: pronotum length ratio ca. 1.7); third antennomere short (3rd: 2nd antennomere length ratio ca. 3.0); fifth antennomere elongated (length: width ratio ca. 2.0).

Pronotum slightly narrower than elytra (elytra: pronotum width ratio ca. 1.2); relatively narrow (length: width ratio of pronotal disc ca. 0.9); disc shiny, covered with fine punctures (0.5–1.0 diameters apart). Lateral sides of pronotal disc straight at basal half. Disc without apophyseal depressions. Basal, anterior, and lateral emargination of pronotal disc present. Base of pronotum straight. Posterior angles not protruding beyond base. Pronotal hypomeron dull; covered with very fine longitudinal rugosities; without submarginal indentation. Intercoxal process of prosternum not depressed apically (lateral view); apically with oval depression on ventral surface; slightly protruding towards first abdominal segment. Procoxae narrowly separated (procoxa: intercoxal process width ratio ca. 2.0).

Five elytral intervals finely marked; remaining ones indistinguishable. Elytron covered by fine punctures (0.1 diameters apart; sometimes confluent). Elytral base straight; not emarginate. Elytral humerus rounded. Epipleuron slightly narrowing apically, then of constant width; basally covering all elytral intervals (ventral view). Scutellum relatively large; triangular. Metathoracic wings absent.

Metaventrite extremely short (metacoxal cavity: metaventrite (between insertions of meso- and metacoxae) length ratio ca. 10.0); with longitudinal process at middle in males (Fig. 2I). Process of first abdominal ventrite wide (distances between mesocoxae: metacoxae ratio ca. 0.9). Fifth abdominal ventrite without submarginal sulcus; covered with fine punctures (4–5 diameters apart).

Male protarsus widened, with subsequent tarsomeres slightly narrower. Protibia with deep longitudinal cavity. Mesotibiae, profemora, mesofemora, and metafemora simple. Metafemora similar to that of *A. obesus*. Female legs simple. First tarsomere of metatarsi elongated (1.7× longer than 4th one). Length of metatarsus equal to 0.75 of metatibial length.

Aedeagal tegmen widest in middle; unipartite; with wide basal gap. Apical part slightly divided (up to 0.10 of whole tegmen length). Clava straight. Penis of even width along most of its length; with apical part not covered by tegmen, exposed dorsally. Basal apophyses of penis relatively short (ca. 0.4 of whole tegmen length).

Ovipositor relatively short (body: ovipositor length ratio ca. 3.0). Paraproct much longer than coxites (paraproct: coxites length ratio ca. 1.8); triangular, not shielding valvifer or any other lobes of coxites. Valvifer and second lobe slightly transverse, while third one triangular. Fourth lobe rounded, situated dorsally. Gonostylus located on dorsal side of fourth lobe. Vagina and bursa copulatrix without sclerites. Spermatheca sac-like. Proctiger covering nearly whole ventral side of ovipositor.

Distribution. This species has been collected in the following ecoregion of South Africa (Fig. 5): Southern Africa bushveld.

Anaxius obesus **Fåhraeus, 1870**

(Figs. 1E, 5)

Anaxius obesus Fåhraeus, 1870: 307.- Koch, 1958: 211.

Notes. Fåhraeus (1870) did not specify the number of studied specimens, however from the context it seems to be clear that he was dealing with at least two specimens. Therefore, a lectotype designation is needed to fix the taxonomic status of the genus and the species.

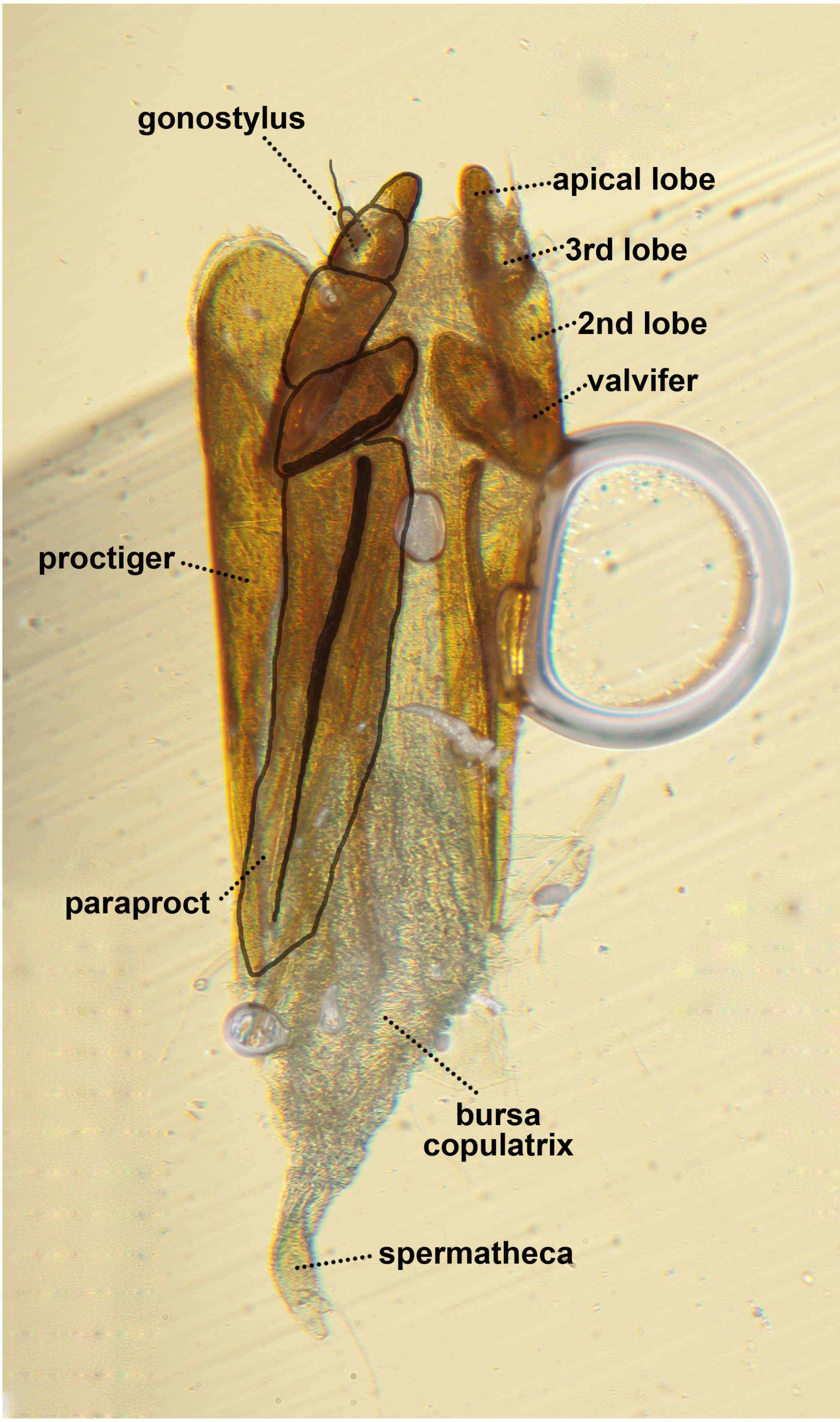

FIGURE 4. Morphology of female terminalia of *Anaxius campbellae.*

Material studied. Lectotype, designated here, male (TMSA): "Caffra- / ria". **Paralectotype**, male (TMSA): same data as holotype. **Other material**, male (TMSA): "Lichtenburg / Transvaal / Dr. Brauns", male (TMSA): "Plansberg / XI.1950 / P.L. Breutz"; 2 males (TMSA): "S. Afr.; Limpopo Prov. / Mabote farm / 24.07 S–28.39E", "12.12.2009 / in the Waterberg / leg. Ruth Müller"; male (TMSA): "S. Afr.: Transvaal / Pienaars River 8km / 25.17S–28.17E, 28.12.1994; E-Y 3234, on ground / leg. CL Bellamy".

Distribution. This species has been collected in the following ecoregions of South Africa (Fig. 5): Highveld grasslands; and Southern Africa bushveld.

Anaxius prozeskyi Koch, 1958

(Figs. 1F, 2C–D, 5)

Anaxius prozeskyi Koch, 1958: 209.

Material studied. Holotype, male (TMSA): "Anaxius / magnificus / Koch / C. Koch det. 195", "Blouberg, Tvl. / N. side, Glenferness / 16–21.I.1955 / Transva.Mus.Exp.", "HOLOTYPE / Anaxius / PROZESKYI". **Paratype**, male (TMSA): "Helopininae / anaxius / ?", "186", ""3811", "3427", "Makgaberg. / - 2.03. / 2457", "PARATYPE / Anaxius / PROZESKYI" **Other material**, 5 males (TMSA) and male (MIZ PAN): "S. Afr.: Limpopo Prov. / Blouberg Nat. Res. / 22.59S–29.08E", "25–27.11.2016 E-Y:3987 / day, sandy bushveld / leg. Ruth Müller"; 3 males (TMSA): "Namibia, Okahandja Dis/ 45 kmSE—Okakarara / 20.56S–17.42E", "4.3.2006; E-Y:3713 / single, sandveld, 1345m, Ruth Müller".

Distribution. This species has been collected in the following ecoregions of Namibia and South Africa (Fig. 5): Kalahari xeric savanna; and Southern Africa bushveld.

Anaxius pseudoloensus sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:13054B1E-F5D9-43A0-BAE0-BAA29297C843

(Figs. 1G, 3G, 5)

Type data. Holotype, male (TMSA): "Espungabera / 80.K.Jutha 1954".

Etymology. The name highlights the morphological resemblance of this species to representatives of the genus *Loensus* Lucas, 1920 (Pedinini: Pedinina).

Diagnosis. This species is similar to *A. campbellae* by having, *inter alia*, protibia with shallow median cavity, widened protarsus, with subsequent tarsomeres slightly narrower, and not apically depressed intercoxal process of prostenum (lateral view). *Anaxius pseudoloensus* can be easily distinguished by its smaller body size (4.5 mm in *pseudoloensus*; 6.5–7.0 in *campbellae*), more slender elytra (Figs 1B vs 1G), and simple mesofemora in males (with preapical denticle in *campbellae*).

Description. Body—length ca. 4.5 mm. Habitus as in Fig. 1G.

Dorsal side of head covered with fine punctures (0.5–1.0 diameters apart). Frontoclypeal suture not visible. Canthus rounded at base; narrower than head at level of eyes. Clypeal emargination shallow (clypeal emargination width: depth ratio ca. 8.0). Labrum wide (width: length ratio ca. 1.9); emarginate medially; with basal membrane exposed. Ligula exposed, not covered by mentum. Mentum widest in apical part; with well-developed medial keel; with exposed lateral lobes; not covering cardo or basistipes; apically with median indentation. Submentum pentagonal; short. Apical segment of maxillary palpus trapezoidal; with sensory field occupying whole proximal edge. Second segment of maxillary palpus elongate (length: width ratio ca. 2.4). Palpifer located laterally on basistipes. Anterior tentorial pit circular. Eye not dorsally shielded by any keel. Margin between maxillary fossa and antenna insertion well marked. Antenna not available for study (broken off holotype).

Pronotum slightly narrower than elytra (elytra: pronotum width ratio ca. 1.1); relatively narrow (length: width ratio of pronotal disc ca. 0.8); disc shiny, covered with fine punctures (0.5–1.0 diameters apart). Lateral sides of pronotal disc straight at basal half. Disc without apophyseal depressions. Basal, anterior, and lateral emargination of pronotal disc present. Base of pronotum straight. Posterior angles not protruding beyond base. Pronotal hypomeron dull; covered with very fine longitudinal rugosities; without submarginal indentation. Intercoxal process of prosternum not depressed apically (lateral view); apically with oval depression on ventral surface; slightly protruding towards first abdominal segment. Procoxae narrowly separated (procoxa: intercoxal process width ratio ca. 2.0).

Five elytral intervals finely marked; remaining ones indistinguishable. First interval elevated in disc. Elytron covered by fine punctures (0.1 diameters apart; sometimes confluent). Elytral base straight; not emarginate. Elytral humerus rounded. Epipleuron slightly narrowing apically, then of constant width; basally covering all elytral intervals (ventral view). Scutellum relatively large; triangular. Metathoracic wings absent.

Metaventrite extremely short (metacoxal cavity: metaventrite (between insertions of meso- and metacoxae) length ratio ca. 8.0). Process of first abdominal ventrite wide (distances between mesocoxae: metacoxae ratio ca. 0.9). Fifth abdominal ventrite without submarginal sulcus; covered with fine punctures (4–5 diameters apart).

Male protarsus widened, with subsequent tarsomeres slightly narrower. Protibia with shallow longitudinal cavity. Metafemora with fringe of setae distributed on whole length. Other leg parts simple. Meso- and metatibiae not avaliable for study (broken out of holotype).

Aedeagal tegmen widest in middle; unipartite; without basal gap. Apical part divided (up to 0.10 of whole tegmen length). Clava straight. Penis of even width along most of its length; with apical part not covered by tegmen, exposed dorsally. Basal apophyses of penis relatively short (ca. 0.4 of whole tegmen length).

Distribution. This species has been collected in the following ecoregion of Mozambique (Fig. 5): Southern Miombo woodlands.

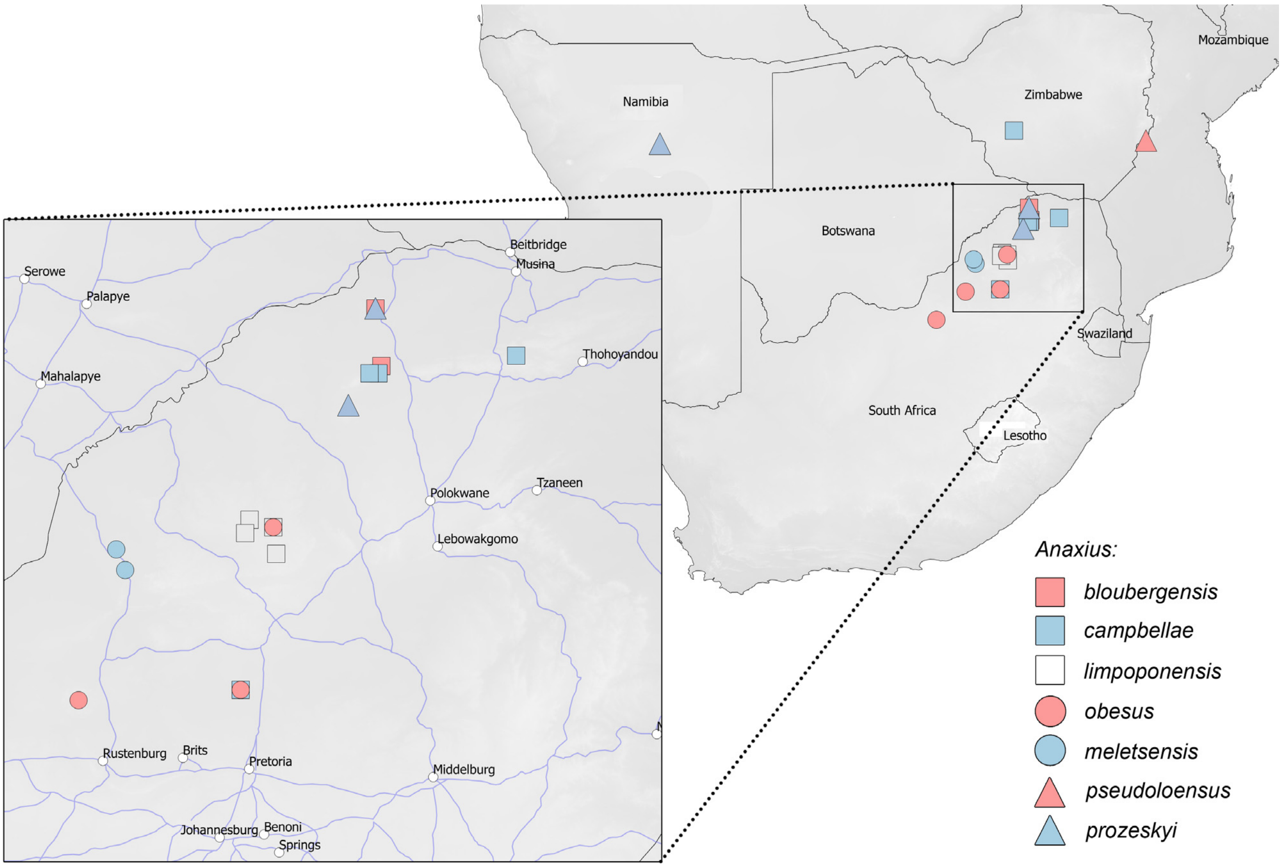

FIGURE 5. Distribution of the species representing *Anaxius*.

Discussion

The newly analyzed material supports the majority of diagnostic characters for the genus *Anaxius* proposed by Koch (1958). Only the presence of the preapical denticle on the male mesofemora was proved to be not stable across the studied species (i.e. is absent in *A. meletsensis* **sp. nov.** and *A. limpopoensis* **sp. nov.**) and should be removed from the list of diagnostic characters for the genus.

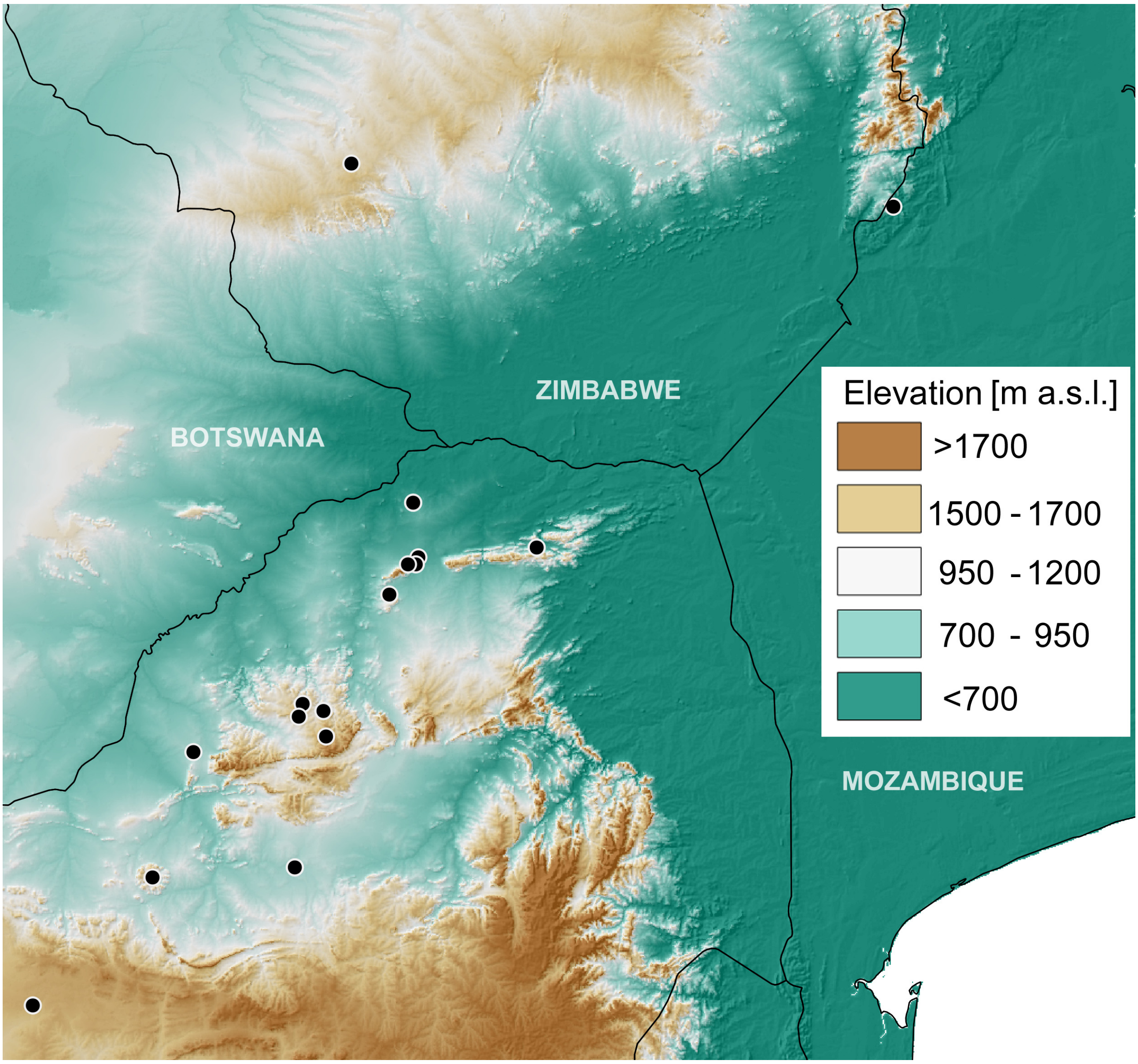

FIGURE 6. Distribution of the genus *Anaxius* in the Limpopo Province.

At the moment, because of the lack of published references, it is impossible to determine if the revealed morphology of the ovipositor and the genital tubes is unique for *Anaxius* within Helopinina. The only paper providing any data on the female terminalia structure within this subtribe was published by Tschinkel & Doyen (1980), who included a single species of *Micrantereus* in their comparative analysis. The general morphology of the ovipositor seems to be consitent with the image presented here for *Anaxius* (paraproct is elongated). However, the information concerning the structure of coxites in *Micrantereus* was insufficiently presented, which inhibits any further comparisons. Moreover, Tschinkel & Doyen (1980) stated that they were unable to dissect the genital tubes. The morphology of the latter structures seems to be peculiar within *Anaxius*. The entire bursa copulatrix is nearly shielded by the paraprocti, while contrary to the other closely related groups (see Banaszkiewicz 2006, Kamiński 2015, 2017, Kamiński *at al.* 2017, Iwan & Kamiński 2016, Iwan & Kamiński 2016, Kamiński & Schawaller 2018) the spermatheca is extremely reduced (Fig. 4). However, it needs to be noted that due to the lack of female specimens—only three females were identified within the set of 49 studied *Anaxius* specimens—the data presented here is highly fragmentary. The cause of the peculiar sex ratio remains uninvestigated. This phenomenon was not observed within other genera representing Helopinina (e.g. Koch 1958, Robiche, 2008, 2012).

Acknowledgments

We acknowledge Aquila Steel (Thabazimbi) Pty. Ltd for allowing the collection of the specimens on their property, and AfricanBats NPC for facilitating and supporting this research. We are grateful to Ruth Müller (TMSA) for sending the specimens used in this study.

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APPENDIX 1. Analysed distributional data in CSV format

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Species name,Country,Locality,Latitude,Longitude,Reference,Notes
bloubergensis,South Africa,Blouberg Nat. Res.,-22.59,29.08,New data
bloubergensis,South Africa,Blouberg Nat. Res.,-22.98,29.12,New data
campbellae,South Africa,Pienaars River,xx,xx,Koch 1958,not georeferenced
campbellae,South Africa,Plat River,xx,xx,Koch 1958,not georeferenced
campbellae,South Africa,BLOUBERG,xx,xx,Koch 1958,not georeferenced
campbellae,South Africa,25km W Pretoria,xx,xx,New data,not_georeferenced
campbellae,South Africa,Pienaars River 8km,-25.17,28.17,New data
campbellae,South Africa,Blouberg Nat. Res.,-23.03,29.10,New data
campbellae,South Africa,Blouberg Nat. Res.,-23.03,29.04,New data
campbellae,South Africa,Gondeni,-22.91,30.03,New data
campbellae,Zimbabwe,Bulawayo,-20.146498,28.604809,New data
limpopoensis,South Africa,Lindani Nat. Res.,-24.02,28.23,New data
limpopoensis,South Africa,Mabote farm,-24.07,28.39,New data
limpopoensis,South Africa,25 km N Mookgopnong,-24.25,28.41,New data
limpopoensis,South Africa,Waterberg Game Res.,-24.11,28.20,New data
meletsensis,South Africa,Meletse Reserve,-24.36,27.39,New data
meletsensis,South Africa,Geelhoutbush farm,- 24.22,27.33,New data
obesus,South Africa,Caffraria,xx,xx,Fåhraeus 1870,not georeferenced
obesus,South Africa,Mabote farm,-24.07,28.39,New data
obesus,South Africa,Pienaars River 8km,-25.17,28.17,New data
obesus,South Africa,Lichtenburg,-26.132573,26.154712,Koch 1958
obesus,South Africa,Pilansberg,-25.240122,27.075533,Koch 1958
prozeskyi,South Africa,Makgabeng,-23.245105,28.896944,Koch 1958
prozeskyi,South Africa,Blouberg,Koch 1958,not georeferenced
prozeskyi,South Africa,Blouberg Nat. Res.,-22.59,29.08,New data
prozeskyi,Namibia, Okahandja Dis.,-20.56,17.42,New data
pseudoloensus,Mozambique,Espungabera,-20.459053,32.772910,New data
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ANNALES ZOOLOGICI (Warszawa), 2018, 68(3): 493-500

TAXONOMY OF THE GENUS *BANTODEMUS* KOCH, 1955 (COLEOPTERA: TENEBRIONIDAE: PLATYNOTINI): *LUCIDUS* AND *LETHAEUS* SPECIES-GROUPS

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Abstract.— A new species of the genus *Bantodemus* is described (*B. lajumaiensis* **sp. nov.**) from the surroundings of the Lajuma Research Centre (Limpopo Province, South Africa). This discovery enforced the revision of some crucial morphological features used for species delimitation within the *lucidus* species-group. As a result a new identification key is provided for this species-group. Furthermore, the male morphology of *Bantodemus montanus* (*lethaeus* species-group) is described for the first time based on the material collected in the Lotheni Nature Reserve (KwaZulu-Natal, South Africa).

⁂

Key words.— 'Opatrinoid' clade, Platynotina, darkling beetles, South Africa, Lajuma Research Centre, Lotheni Nature Reserve

Introduction

A recently conducted molecular phylogenetic analysis revealed a close affiliation between Eurynotina Mulsant & Rey, 1854 and Platynotina Mulsant & Rey, 1853 (Kamiński *et al*. 2018b). From the morphological perspective, this relation is strongly supported by the presence of a stridulatory gula in both tribes (Kamiński 2015b, 2016). The phenomenon of stridulation is relatively rare within Tenebrionidae (see Smith & Wirth 2016), and therefore this feature does not occur in other closely related groups of darkling beetles, such as Dendarini Mulsant & Rey, 1854, Opatrini Brullé, 1832 and Pedinini Eschscholtz, 1829 (Kamiński *et al*. 2018b). Taking into consideration the above mentioned facts, Kamiński *et al*. (2018b) proposed to include Eurynotina and Platynotina within a single tribe, named Platynotini.

The morphological phylogeny of the subtribe Platynotina was conducted by Iwan (2002). Based on the obtained results he designated the three following evolutionary lineages: melanocratoid, platynotoid and trigonopoid. The appropriateness of this subdivision was largely supported by the recently conducted molecular analysis (Kamiński *et al*. 2018b). The only difference concerned the phylogenetic placement of the genus *Gonopus* Latreille 1829, which according to Iwan's hypothesis is a member of the trigonopoid Platynotina, while pursuant to the molecular data it forms a separate evolutionary lineage (sister to all other Platynotina).

Regardless of the above mentioned phylogenetic inconsistencies, the trigonopoid Platynotina with over 200 species is an extremely diverse generic group of Southern African darkling beetles (Kamiński 2017a). Despite intensive taxonomic work, trigonopoid Platynotina are still poorly studied. This phenomenon is best visualized by the high number of species still being described every year (e.g., Endrödy-Younga 2000, Iwan 1998a, b, c, 2001, 2006, 2008, 2016, Iwan & Banaszkiewicz 2006, Iwan & Kamiński 2014, Kamiński 2011a, 2017a).

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Geographic distributions of most of the genera representing trigonopoid Platynotina are restricted to relatively small areas in Southern Africa (e.g. Iwan 2002, Kamiński 2011b, Iwan & Kamiński 2014). Similar distributional patterns were also observed in the case of some closely related tribes and subtribes of the 'Opatrinoid' clade: Eurynotina of Platynotini (Koch 1954a, b, 1956, Kamiński 2016), Melambiina Mulsant & Rey, 1854 of Dendarini (Kamiński 2011a, Kamiński 2015c, 2017b, Kamiński *et al*. 2018a, Kamiński & Schwaller 2018), Stizopina Lacordaire, 1859 of Opatrini Brullé, 1832 (Kamiński 2015a). The commonness of the representatives of the trigonopoid Platynotina in different environments of Southern Africa makes them probably one of the most extensively collected groups of darkling beetles in this area. However, due to the small amount of people interested in this particular taxonomic group this material largely stays undetermined (e.g. Ditsong Museum in Pretoria). Moreover, several species of such genera as *Atrocrates* Koch, 1956, *Bantodemus* Koch 1955 or *Schelodontes* 1956 are extremely difficult to identify without a reliable reference collection.

This paper focuses on the taxonomy of the *lucidus* and *lethaeus* species-groups of the genus *Bantodemus*. During the recent collecting events in South Africa (Limpopo, KwaZulu-Natal) some new and interesting specimens of those lineages were gathered. The subsequent identification work resulted in designation of a new species (*B. lajumaiensis* sp. nov.) and recognition of a male specimen of *B. montanus* Iwan, 2001 (a species previously known only from females). Detailed results are presented below.

MATERIAL AND METHODS

This study was based on material from the Ditsong National Museum of Natural History, Pretoria, South Africa (TMNH) and the Museum and Institute of Zoology of the Polish Academy of Sciences (MIZ PAS). The original label data for the specimens is given in quotation marks and separated by a comma. Each line of the original label data is separated by a forward slash. The morphological terminology follows that of Matthews *et al*. (2010) and Kamiński & Iwan (2017), with additional specialized terms used for the male and female terminalia (Iwan & Kamiński 2016). Terminalia were investigated using standard methodology (see Iwan & Kamiński 2016). Morphological measurements were recorded using a filar micrometer. Images were taken using a Canon 1000D body with accordion bellows and a Canon Macro Lens EF 100 mm, and with a Hitachi S-3400N SEM in MIZ PAS. The distribution of species was illustrated using Quantum GIS (QGIS) v. 2.4, while the vector layers were downloaded from the Natural Earth web-page (www.naturalearthdata.com).

TAXONOMY

Bantodemus Koch, 1955

Type species. *Trigonopus lethaeus* Mulsant & Rey, 1853.

Diagnosis. See Iwan (2002).

Distribution. Republic of South Africa, Lesotho, Mozambique, Swaziland, Zimbabwe

lucidus species-group

Diagnosis. Easily distinguishable species-group based on the presence of an elongated denticle on metatrochantes in males (Fig. 2A) and sloping prosternal process (Fig. 2B). Additionally, all member of this species groups possess an enlarged additional sac in the bursa copulatrix (feature shared with *B. armatus* Mulsant & Rey, 1853).

Remarks. Prior to this study, majority of the taxonomic concepts of the species representing the *lucidus* species-group were partly based on different degree of convexity of elytral intervals (Iwan & Banaszkiewicz 2006), *i.e. B. lucidus* and *B. rectimanus* – intervals flat; *B. mocambiqueus*, *B. vescus*, *B. zoutpansbergianus* – intervals convex. It is worth mentioning that all those species are known from relatively small specimen series. The material recently collected in the surroundings of the Lajuma Research Centre (interpreted as the *B. lajumaiensis* sp. nov.) revealed that the convexity of the elytral intervals can be highly variable and should not be used for species recognition. Taking this into consideration, new diagnostic features are presented in the key below.

Species included (6). *lajumaiensis* sp. nov., *lucidus* Koch, 1955, *mocambiqueus* Koch, 1955, *rectimanus* Koch, 1955, *vescus* Koch, 1955, *zoutpansbergianus* Koch, 1955.

Distribution (Fig. 3). Republic of South Africa (Limpopo), Mozambique and Zimbabwe (see Iwan 2000).

Key to the species of the *lucidus* species-group

1. Base of pronotum deeply emarginate in the middle (Fig. 2C). Male protibia triangularly dilated in the middle of inner surface of ventral side (Fig. 2D). [Notes. Females unknown; species known exclusively from Masiene, Mozambique] .... ***B. mocambiqueus***

–. Base of pronotum not emarginate in the middle. Male protibia obtuse in the middle of inner surface of ventral side **2**

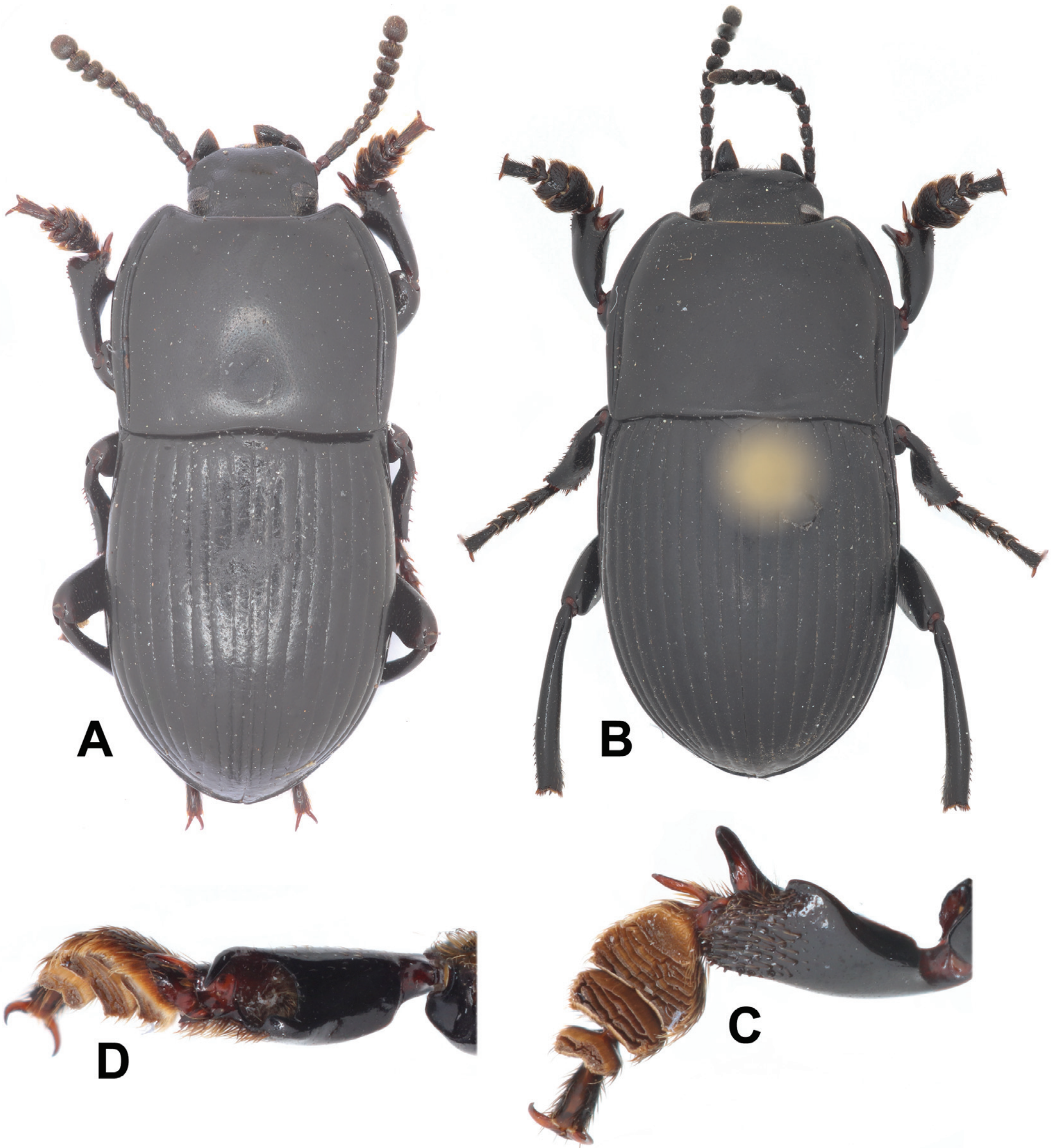

Figure 1. Habitus images of the studied species (A, B). *B. lajumaiensis* sp. nov. (A), *B. montanus* (B-D). Additional features: male protibia (C) and mesotibia (D).

2. Male protibia with an additional apical denticle on the inner side (ventral view) (Fig. 2E) **3**
–. Male protibia obtuse apically on the inner side (ventral view) (Fig. 2G) **4**
3. Body size: 12.2–12.7 mm. Male mesotibia distinctly S-shaped . . . ***B. rectimanus*** [***Notes***. females unknown]
–. Body size: ca. 11.2 mm. Male mesotbia nearly straight . . . . ***B. zoutpansbergianus***
4. Male protibia protruding near base (Fig. 2F). Pronotum elongated (length to width ratio = 0.92–0.96). Elytral intervals moderately convex, while rows sulcate and indistinctly punctured . . . . ***B. lucidus***
–. Male protibia basally straight. Pronotum relatively wide (length to width ratio = 0.82-0.86). When elytral intervals moderately convex, rows always with distinct punctures **5**
5. Body size: ca. 10.5-12.0 mm. Epipleura not covering terminal elytral intervals at the level of metanepisternum (ventral view). Setae distributed only on the middle of the outer edge of profemur (ventral side) . . . . ***B. vescus***
–. Body size: 9.0-10.0 mm. Epipleura covering terminal elytral intervals at the level of metanepisternum (ventral view). Setae evenly distributed on the whole length of the outer edge of profemur (ventral side) . . . . ***B. lajumaiensis*** sp. nov.

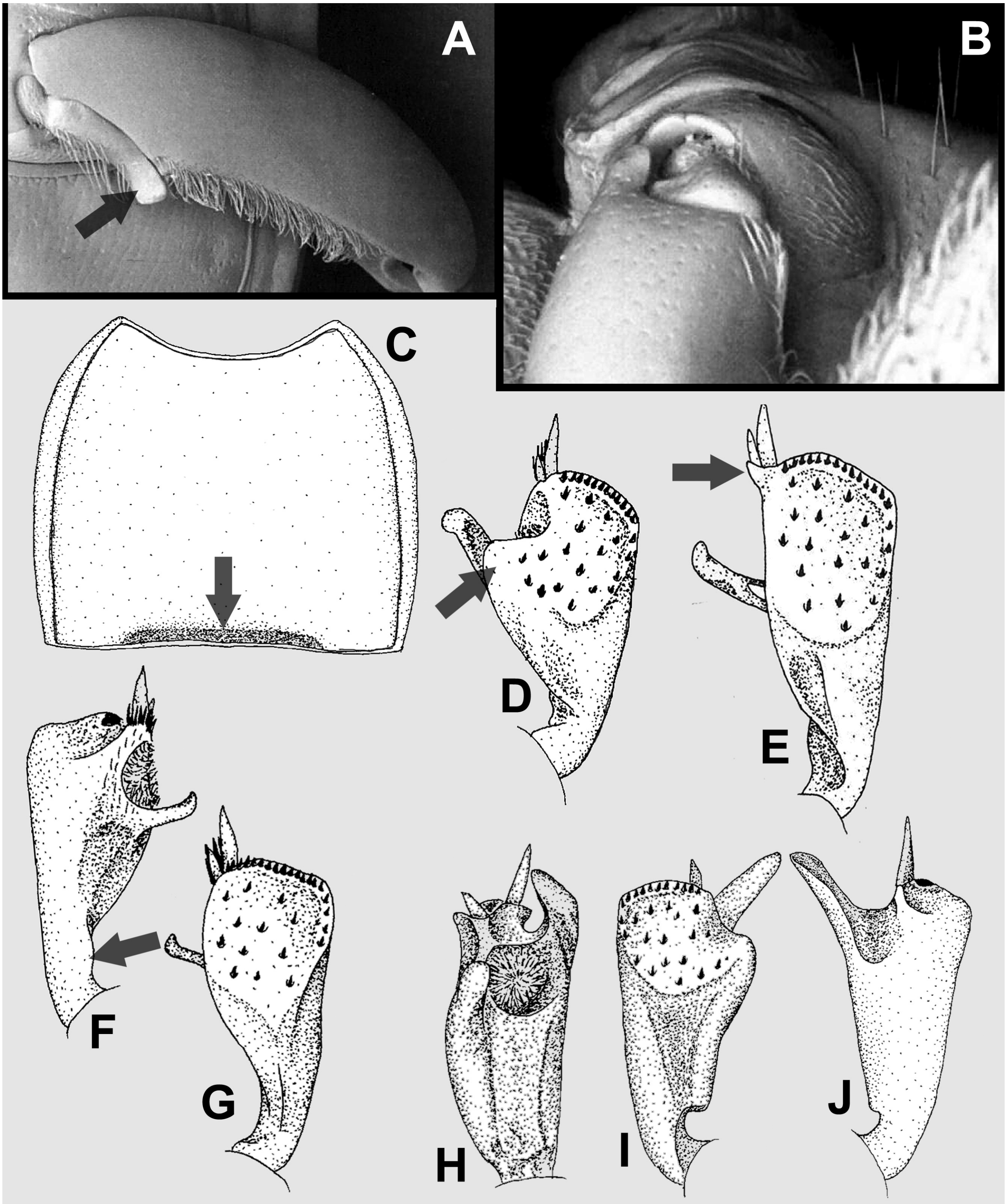

Figure 2. Diagnostic characters of different *Bantodemus* species. Elongated denticle on metatrochanter (A); sloping prosternal process (B); ronotal disc with deeply emarginate base (C); male protibiae (D–J). B. *lucidus* (A, B, F, G); *B. mocambiqueus* (C, D); *B. rectimanus* (E); *B. furcatus* (H–J).

Bantodemus lajumaiensis sp. nov.

urn:lsid:zoobank.org:pub:394CAB8F-B2EE-4078-8BB2-3C5E5854AAFA

(Figs 1A, 3)

Type data. Specimens deposited in the Ditsong Museum (Pretoria, South Africa): **Holotype**, male: “7-11.2.2017; E-Y: 3997 / on forest roads / leg. Ruth Müller”, “S. Afr.: Limpopo Prov. / Lajuma, Soutpansberg / 23.02 S - 29.25 E”. **Paratypes**, male and female: same data as holotype; male: “9S1/A3 (1) shrubland / Lajuma Research Station / Soutpansberg, Limpopo / -23.06S, 29.49E pitfall / 25/09/2015 / C.MUNYAI”; male “S.Afr: Limpopo. / Lajuma Research / Station, Soutpansberg / Short Forest”, “23°4’2.1’’S / 29°29’ 37.824’’E / C. Munyai, P. Tshililo / 13/01/2015 / 12S2,4/A1”; male “S.Afr: Limpopo. / Lajuma Research / Station, Soutpansberg / Tall Forest”, “23°2’18.78’’S / 29°28’ 36.516’’E / C. Munyai, P. Tshililo / 13/01/2015 12S4/A5”

Specimens deposited in the Museum and Institute of Zoology (Warsaw, Poland): **Paratypes**, male: “12S2.4|B3 (1) thicket / Lajuma Research Station / Soutpansberg, Lajuma / -23.04S, 29.45E pitfall / 25/09/2015 C.MUNYAI”; male: “7-11.2. 2017; E-Y: 3997 / on forest roads / leg. Ruth Müller”, “S. Afr.: Limpopo Prov. / Lajuma, Soutpansberg / 23.02 S - 29.25 E”; male: “S.Afr: Limpopo. / Sedgeland / Lajuma Research / Station, Soutpansberg / Short Forest”, “23°2’39.696’’S / 29°27’ 52.128’’E / C. Munyai, P. Tshililo / 13/01/2015, 12S2,1/A3”.

Etymology. The name refers to the type locality, surrounding of the Lajuma Research Centre (Limpopo, South Africa).

Diagnosis. On account of having sloping prosternal process, elongated denticle on metatrochantes in males and enlarged additional sac in bursa copulatrix related to other representatives of the *lucidus* species-group. Diagnostic characters of the *Bantodemus lajumaiensis* sp. nov. are presented above in the identification key.

Description. Measurements. Body — length = 9.0–10.0 mm; breadth ratio elytra / pronotum ca. 1.0; length

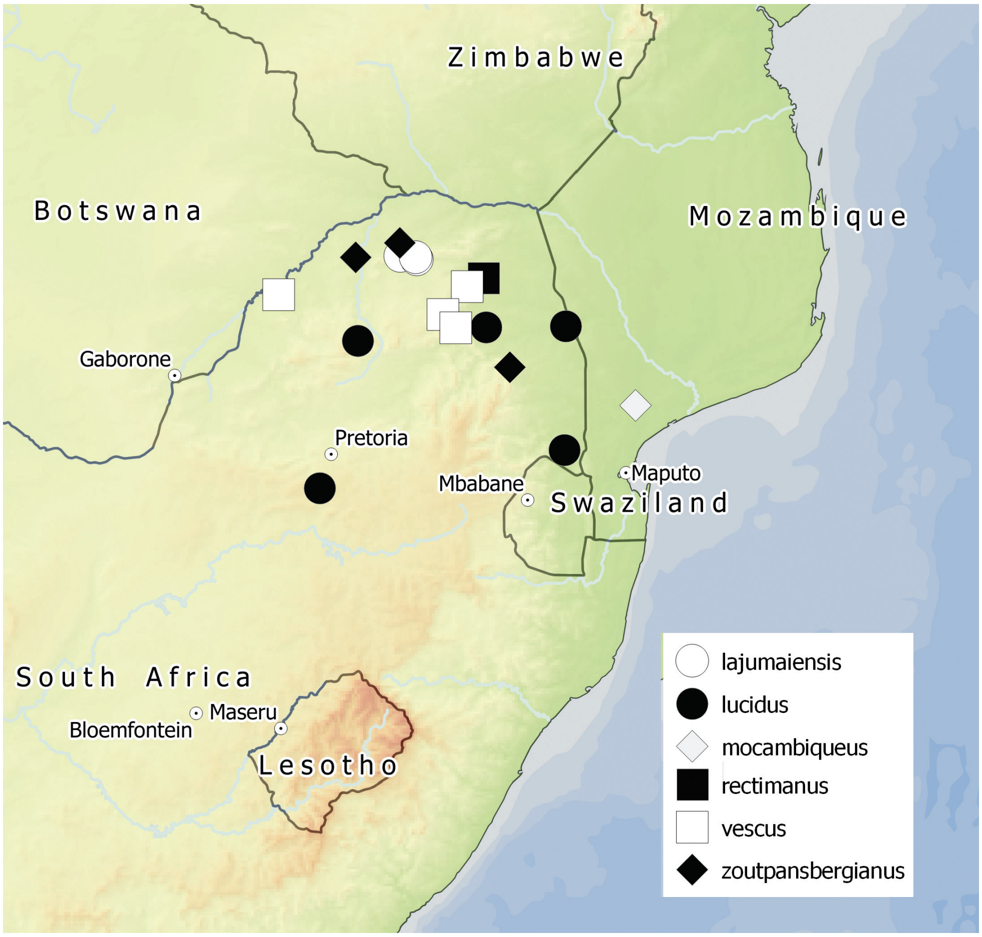

Figure 3. Distribution of the species representing *lucidus* species group.

ratio elytra / pronotum ca. 1.5. Clypeus — clypeal emargination width/depth ratio ca. 6.0. Antennae — length ratio antenna / pronotum ca. 0.9; ratio length of antenna / width of 3rd antennomere ca. 17.0; length ratio of antennomere 3rd/2nd ca. 2.0; ratio length / width of 5th antennomere ca. 1.3. Maxillary palp — ratio width of maxillary palp / length of 3rd antennomere ca. 1.6. Pronotum — pronotum length / breadth ratio ca. 0.86-0.88; length ratio pronotum (measured in the middle) / side of pronotum (measured at the level of anterior angle) ca. 0.9. Elytra — elytra length / breadth ratio = 1.3-1.4. Scutellum — width ratio anterior margin of elytra / scutellum at base ca. 2.2. Metaventrite — length ratio cavity of hind coxa / metaventrite between the insertions of mid and hind coxae ca. 5.0. Abdomen — width ratio process of 1st abdominal ventrite / process of metaventrite = 1.0. Legs — protibia length / width ratio ca. 2.7; profemur length / width ratio ca. 2.6. Tarsi — length ratio metatarsomere 1st / 2nd ca. 3.3. Male genitalia — length of parameres / basal part of aedeagus ca. 0.4; length of clavae / paramers ca. 0.6. Female genitalia — length of paraproct/all coxites ca. 1.0; length of body/ovipositor ca. 5.72.

Body surface bare and dull (Fig. 1A). Head with fine punctures, 2-3 diameters apart. Clypeus scarcely emarginated. Mentum widest at the middle; narrowing towards apex. Submentum pentagonal. Middle of proventrite covered with long but sparse setae. Hypomeron glabrous. Pronotum covered with fine punctures, 4-5 diameters apart. Basal border of pronotum complete (anterior interrupted in the middle). Lateral border of pronotum narrowed basally; broad (its width is four times greater than the width of the submarginal depression). Lateral sides of pronotum rounded. Intercoxal process of prosternum obtuse in lateral view. Scutellum triangular, with fine punctures. Elytral rows punctate-sulcate; punctures fine, 1–2 diameters apart. Intervals dull; with visible microsculpture (magnification 50x); punctures scarcely visible, 6–7 diameters apart. Elytral strongly humeri protruding outwards. Last abdominal ventrite without submarginal sulcus; with fine punctures, 1-2 diameters apart. Male protarsi widened. Protibiae as in Fig. 1A. Mesotibiae straight. Metatibiae slightly widende towards apex. All femorae with a longitudinal fringle of setae. Female legs without modifications. Parameres evenly narrowing towards apex; not fused basally. Ovipositor with coxites almost the same length as paraproct. Valvifers short and wide, other lobes longitudinal. Gonostyli situated on the dorsal part of the apical lobe of coxities.

Distribution (Fig. 3). This species has been collected in the surroundings of the Lajuma Research Centre.

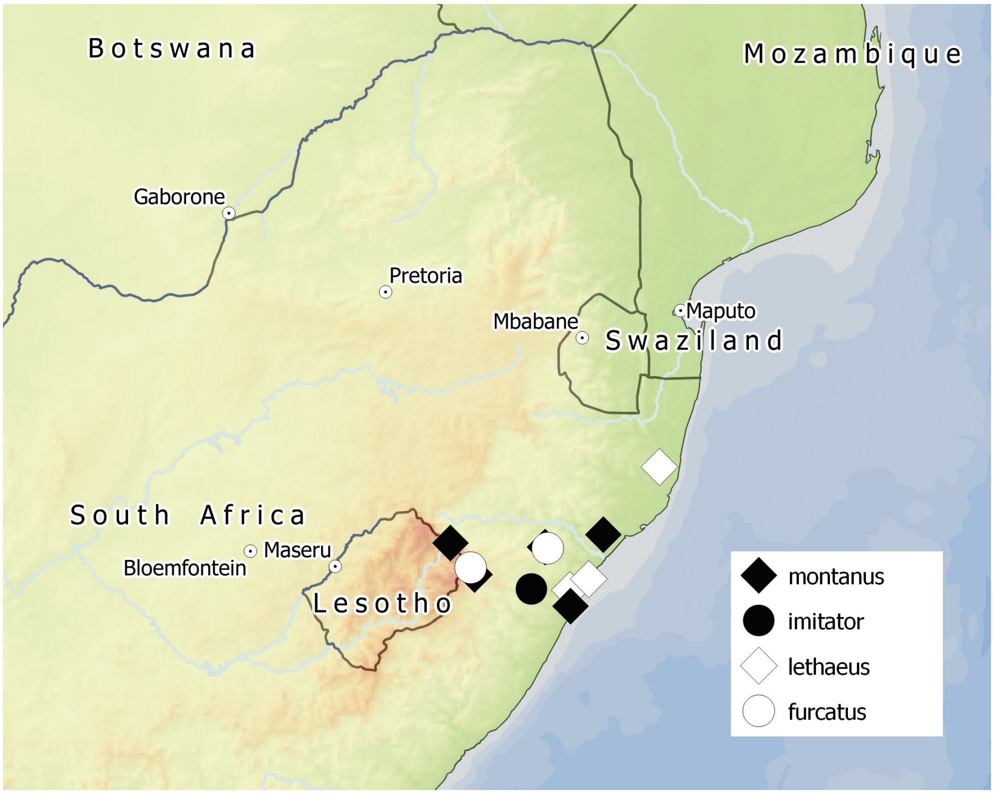

Figure 4. Distribution of the species representing *lethaeus* species group.

lethaeus species-group

Diagnosis. Easily distinguishable by specific structure of female terminalia, *i.e.* presence of ring-like sclerites in bursa copulatrix (see Iwan 2000).

Note. The interpretation of *lethaeus* species-group adapted here is narrower than the ones presented both by Koch (1955) and Iwan (2000, 2001).

Species included (4). *furcatus* Koch, 1955, *imitator* Koch, 1955, *lethaeus* Mulsant & Rey, 1853, *montanus* Iwan, 2001.

Distribution (Fig. 4). Lesotho and Republic of South Africa (KwaZulu-Natal) (see Iwan 2000).

Bantodemus montanus Iwan, 2001
(Figs. 1B–D, 4)

Studied material. **Holotype**, female (Ditsong Museum in Pretoria): "Rep. South Africa: Natal / 75 km WSW Estcourt, Cathedral Peaks For. Sta. / 7-31.XII.79, S.&J. Peck", "Organ Pipes Pass, Lesotho, 3000 m, 30.X1I.79 / alpine grassland, grazed". Male (Ditsong Museum in Pretoria): "29.4219S / 29.5417E / 22/1/18 / Lotheni / South Africa / leg. M. Kamiński & R. Müller ".

Notes. Until now, male morphology of this species remained unknown.

The analysed male specimen indicates a great morphological resemblance between *B. furcatus* and *B. montanus*. Both species shares the same structure of male legs (Figs 1C, D, 2H-J). Therefore, secondary male sexual features are insufficient in order to separate those two species, which can be distinguished by different structure of the elytral base (*B. furcatus*: bordered; *B. montanus*: not bordered) and the fifth abdominal ventrite (*B. furcatus*: without submarginal sulcus; *B. montanus*: with submarginal sulcus.

Distribution (Fig. 4). This species has a relatively wide distributional range in KwaZulu-Natal.

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