

**A systematic revision of the Afrotropical members of  
the dung beetle genus *Catharsius* Hope, 1837  
(Coleoptera: Scarabaeidae)**



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St Peter's College  
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A thesis submitted for the degree of  
*Doctor of Philosophy*  
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**Abstract**

The Afrotropical members of the dung beetle genus *Catharsius* Hope, 1837 (Coleoptera: Scarabaeidae) are investigated and systematically revised. Morphological phylogenetic analyses of 138 taxa and molecular phylogenetic analyses of a subset of 15 taxa are conducted. The results indicate the paraphyly of the genus with regard the monotypic genus *Copridaspidus* Boucomont, 1920 and *Catharsius* is split into five species-groups. Biogeographical ancestral state reconstruction indicates that the woodlands to the south of the Congo Basin are the location of origin of the genus, with several independent colonisations of Asia. Dispersal-vicariance analysis shows that many dispersal events rather than vicariance events are responsible for the current geographical distribution of this genus. A new tribe, *Catharsiini*, is erected to include the genera *Catharsius* and *Metacatharsius*. Two genera, *Copridaspidus* and *Catharsiocopris* Balthasar, 1967, are synonymised with *Catharsius*. In total, 128 African species are recognised, of which 39 species are new to science. Name-bearing type specimens of 98 of 106 described taxa were studied with four neotypes and 48 lectotypes designated. Six taxa are raised from synonymy, eleven new synonymies are established and one species is placed as *incertae sedis*. The *C. molossus* species group of 29 species is fully revised with the re-description of 25 species and description of four new species. For each species of the *C. molossus* species group, images of both sexes and of the male genitalia are figured, along with distribution maps. A key to the five species-groups as well as a key to species of the *C. molossus* group are provided and a gazetteer of all African localities of *Catharsius* is compiled.



*“forsan et haec olim meminisse iuvabit”*

(Virgil, Aeneid I. 203)

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## Chapter 1: General Introduction

As natural habitats worldwide undergo transformations under human influences at an alarming rate in this Anthropocene era, the need for taxonomic research is more urgent than ever. Taxonomy and the classifying of the world's biodiversity underpin the success of other biological enterprises such as ecology and evolutionary biology. Yet, the recent demise of taxonomy has been well-documented (Godfray, 2007; Wheeler, 2014; Higgs, 2016). With the advent of DNA sequencing, traditional descriptive taxonomy is losing ground with biodiversity being classified increasingly and sometimes solely in sequence space. In this study, a mega-diverse genus is revised through the application of modern taxonomic and systematic tools culminating in a user-friendly output. This holistic approach not only utilises both morphological and molecular data in a phylogenetic framework, but also provides descriptions, images and keys to facilitate identification.

The order Coleoptera is the most species-rich group of organisms on this planet displaying a plethora of morphological diversity (Bouchard et al., 2011). Around 360,000 species are described (Bouchard et al., 2009) but the true number is unknown and relatively undescribed (Gaston, 1991; Leather, 2009). Worryingly, the number of amateur entomologists and taxonomists is in decline (Hopkins & Freeman, 2002). Insects provide important socioeconomic and ecosystem services from pollination to waste disposal (Losey & Vaughan, 2006). In this study a genus of dung beetle, *Catharsius* is studied in detail. Dung beetles are one of the most studied groups of insects in ecological assessments owing to their strong affiliations with habitat, animal dung and are a model group for studying the effects of global warming and habitat destruction (Hanski & Cambefort, 1991). Although a vast library of literature exists for dung beetle taxonomy, their identification can still be difficult. Dung beetles exhibit allometric growth, during which males of similar sizes can exhibit different secondary sexual characteristics such as the length and shape of the horn (Emlen et al., 2007; Pokorný et al., 2009). The strong sexual dimorphism shown by the species in this genus have confounded the issue, with females being incorrectly associated to the males. *Catharsius* are a large-bodied dung beetle genus with 106 taxa distributed in Africa and Asia and despite their large size and charismatic nature, their taxonomy is poorly understood and outdated (Davis et al., 2008). The most recent revision of the genus was undertaken by Ferreira in a series of works in the early 1960's and this has since been the go-to reference for identifying these beetles (Ferreira, 1960b; 1960; 1972). These works are however difficult to use with the descriptions and keys in Portuguese and moreover, were not based on the study of all relevant type material. *Catharsius* have often been trapped as part of ecological dung beetle assessments (Davis et al., 1999; 2002; 2003; 2005). The taxonomic impediment has led to the inability to correctly identify the species caught in the samples, which is paramount when these studies aim to understand relationships of dung beetle assemblages (Davis & Philips, 2005; Davis et

al. 2010) and the relationship of species to habitat, soil type, elevation and temperature (Tshikae et al., 2008; Davis & Phillips 2009).

Dung beetles are found on all continents except Antarctica and are most diverse in Africa. Although there have been a number of recent taxonomic revisions of other African genera (Josso & Prévost, 2000; Barbero et al., 2003; Genier & Moretto, 2017), these genera each comprise a small number of taxa (all less than 30 species). The largest revision of a dung beetle genus was that of Nguyen-Phung & Cambefort who partially revised over a series of publications (1986a; 1986b; 1987) the Afrotropical members of the worldwide genus *Copris*. The most species-rich dung beetle genera to have been recently revised were two South American genera: *Ontherus* (58 species) by Genier (1996) and *Eurysternus* (53 species) also by Genier (2009). This revision of *Catharsius* is not only the largest revision of an African dung beetle genus but of any other group of dung beetle in the world. A large scale systematic revision is challenging not only in the difficulties of gathering the material and literature but also in the careful examination of both external and internal characters. In order to hypothesize the relationships between the taxa, a wide set of techniques is needed to improve the prospects of successfully revising the group. All of the currently described taxa of the genus are included in the phylogenetic analyses but only the Afrotropical taxa will be fully revised<sup>1</sup>. The aim of this study is to take an integrative approach to combine a wide range of methods, tools and theories to provide the most comprehensive revision deliverable in the time available.

In this chapter, I present the aims of this thesis, and introduce the techniques employed, and discuss the place of this work with respect to the current schools of taxonomic and systematic thought and philosophy.

## Systematics

Systematics can be summarised as the study of the evolutionary origin and relationships of taxa, whilst taxonomy is usually considered a branch of biological systematics that is concerned with the nomenclature and classification of taxa. These two terms are not mutually exclusive and may reasonably be considered synonymous. Most systematists would agree that the hierarchical system of names in biology should be governed by phylogenetic hypotheses rather than by intuitive or overall (phenetic) similarity (Page & Holmes, 1998). Historically, organisms have been grouped together that were phenotypically similar essentially splitting taxa into groups on the basis of the presence or absence of some character, mostly irrespective of how variable or homoplasious that character may be. These features weigh upon the utility of the character for phylogenetic inference.

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<sup>1</sup>The Asian *Catharsius* species are currently being revised by D.J. Mann, Oxford University Museum of Natural History.

Phylogenetic definitions are relevant to several issues in the philosophy of taxonomy, which include the general methods for defining the name and classification of composite wholes. Phylogenetic systematics provides an objective framework for evaluating characters according to their meaning for the evolution of a taxon. Although a classification based on overall similarity might be an important step in biological systematics it should be perceived as more of an approximation to a classification based on phylogenetic hypotheses since the hierarchical structure of groups of organisms in the natural world is the result of continuous evolution. Phylogenetic analyses have not been undertaken for many groups of organisms whilst large numbers of new taxa are being described based purely on morphological characters (Godfray, 2002). The isolated description of a new species is in itself important as in the process of description, those taxa which are most closely allied will naturally be compared and contrasted to it. It is important to note that only through these descriptions of new taxa can subsequent phylogenetic, behavioural and ecological work be undertaken.

In this study, phylogenetic analyses are conducted utilising both morphological and molecular datasets. The morphological phylogenetic analyses are the more comprehensive of the two, including all species in the genus and thus allowing for maximum taxon coverage in phylogeny reconstruction. Ancestral state reconstructions will benefit from this extensive and relatively unusual taxon coverage, as it has been shown that estimation at the base of small clades show in particular strong sensitivity to tree topology and number of terminal taxa (Salisbury & Kim, 2005). The taxon sampling for the molecular studies is considerably smaller than in the morphological analyses. From initial investigations, not a great deal of modern material exists of this group of beetles in museum collections and sequences of only a very few species exist in the public repository GenBank (three African taxa). Moreover, there are a number of taxa only known from holotype specimens collected in the 19<sup>th</sup> century making even the task of sequencing museum specimens complicated. Notwithstanding that DNA can be extracted from historic specimens, it is generally accepted that extraction and sequencing of DNA is most successful from fresh material. For this reason, a number of fieldtrips to Africa have been undertaken to sample fresh material specifically for this purpose.

There are a number of methods of phylogenetic inference which can be used in both morphological and molecular analyses but the major ones that have been used heavily in systematic studies are those based on simple parsimony and the parametric, model-based methods employing maximum likelihood and Bayesian approaches (San Mauro & Agoretta, 2010). Maximum parsimony analyses select the trees requiring the fewest number of character changes or steps and hence minimizing homoplasy (Fitch, 1971). Maximum likelihood analyses select those trees that maximise the probability of observing the data (i.e. the probability of the observed states at each site of the alignment) given the tree and the selected evolutionary model (Edwards, 1972), expressed as log likelihoods. Bayesian inference is similar to the maximum likelihood approach but where the aim is to capture uncertainty

by inferring a distribution of trees based on their posterior probabilities (Huelsenbeck et al., 2001). Thus, in likelihood analyses, a single optimal tree is usually generated whilst Bayesian analyses search for a set of ‘good’ trees. The reliability of a phylogeny depends upon the quality and quantity of the data which involves numerous methodological aspects (Cavalli-Sforza & Edwards, 1967). The completeness, in terms of taxon sampling is considered to be an important contributor to the reliability of an inferred phylogeny (Nabhan & Sarkar, 2011).

### Morphological phylogenetic analyses

The ability to accurately code characters depends upon mastering specialist knowledge of each group. An entomologist with specialist knowledge coding characters for insects is naturally going to create a more informative dataset than if they were to code characters from a bird or plant. There have been a number of detractors of the use of morphological characters in the resolution of phylogenies with the morphological characters mapped instead *a posteriori* onto molecular phylogenies (Scotland et al., 2003; Brusca & Brusca, 2003). The subjectivity of character coding and homology assessment as well as low character to taxon ratio in morphological datasets when compared to a matrix of nucleotide sequences are often cited as drawbacks to morphological phylogenetics (e.g. Hillis et al, 1996; Hillis et al., 2000). The character-to-taxon ratio particularly affects the support values for groups but there have been many recent morphological studies where strong support values have been obtained (Legg et al., 2013; Tarasov & Genier, 2015). It is important to remember however that there is no evidence to suggest that morphological analyses perform any worse than molecules in estimating phylogenetic relationship in general (Baker & Gatesy, 2002; Tarasov & Dimitrov, 2016) and molecular and morphological phylogenies very rarely produce results that are remarkably incongruent. In some cases morphology and molecular data provide complementary evidence, where morphology can contribute unique phylogenetic signals where there is no signal from the molecules (Van Velzen et al., 2016).

There are difficulties in defining, delimiting and ordering morphological characters (e.g. Wilkinson, 1995) with different approaches to coding leading to differing tree topologies, resolution and support (Brazeau, 2011). The presence/absence approach to character analysis has been strongly criticised because it introduces redundancy into the matrix and less compellingly, that since characters are likely to evolve several times, they should be coded as multistate (Hauser & Presch, 1991). Pleijel (1995) countered that presence or absence of a character avoids assumptions regarding character transformations and that this homology statement can be examined for congruence within a single analysis. Seemingly none of these arguments have proven compelling to all practitioners and a diversity of approaches to character construction remain current. Wiens (2001) suggests a method of coding quantitative traits as continuous variables as a solution to the problems of character analysis

and it has been demonstrated that continuously-scaled characters leads to better resolution of the phylogeny (Worthington, 2017).

With the recent advance in techniques such as electron microscopy, the ability to study morphological characters in greater detail has never been better (Souza et al., 2014); for any given character, there may well be many more synapomorphic codable characters that are not visible when viewed through a stereo microscope. Although molecular data may be readily available from freshly collected samples, in many cases there are specimens from which DNA cannot readily be extracted. For example, many vertebrate specimens were traditionally killed or preserved in formaldehyde (Down, 1989), limiting their use for DNA studies. When molecular data is not readily available, being able to accurately include taxa within the framework of a phylogeny is important. Moreover, fossils can only be utilised by coding morphological characters. The integration of fossils in phylogenies has enabled better estimates on divergence times as well as mitigate long branch articles in resolving incongruence between morphological and molecular datasets (Thuy & Stöhr, 2016). The comprehensive understanding of evolution requires the integration of both morphological and molecular data from extant and extinct taxa (Lee & Palci, 2015).

#### Implied weighting

Differential weighting of characters has often been dismissed as being highly subjective for use in practical phylogenetic analyses (e.g. Kluge, 1998; Vogt, 2002), although the idea that certain characters are phylogenetically more informative than others seems obvious given that it is implied by the results of most analyses (Farris, 1982). Within dung beetles, recent studies have shown that the sclerites of the internal sac of the genitalia are particularly informative (Tarasov & Solodovnikov, 2011; Roggero et al., 2016; Tarasov & Génier, 2016; Génier & Moretto, 2017). Differential weighting is unnecessary if all characters were delimited correctly and the dataset contains no homoplasy. In practise however, this is rarely the case. A number of studies have shown that weighting characters against homoplasy improves phylogenetic analyses in large morphological datasets (Goloboff et al. 2008). Differential character weighting require an assumption of the importance of a given character or a reference to a current topology. This however is a circular argument if weighting was based on a topology that was in turn based on weighting (Legg et al., 2013). Implied weighting (Goloboff, 1993) has been suggested as a solution to counter this argument as characters are weighted during tree searches and compared to the resultant MPT's to determine the fit. This fit is based on those characters that are most homoplasious having a lower fit and vice versa, the MPT being the one with the best fit. The character fit can be adjusted by the concavity factor ( $k$ ), where the factor determines to what extent a character is down-weighted (Goloboff, 1999).

In Chapter 2, phylogenetic analyses are conducted on morphological characters coded and scored for every taxon in the genus using both differentially and equally weighted characters to establish hypotheses of relationships. Homoplasy of the characters and the robustness of the inferences are investigated. The evolutionary history of the taxa is explored and the biogeographical ancestral state of the genus reconstructed. The list of characters and the matrix together with images of every character described will be provided.

### Molecular phylogenetic analyses

Over the past 30 years, the field of molecular systematics has grown exponentially. The ability to acquire vast amounts of sequence data has allowed for routine reconstructions of phylogenies using thousands of base pairs and whilst the vast amount of data poses computational issues, the resulting phylogenies are often well-resolved with strong support (Mutanen et al., 2010). These tools have given researchers powerful tools to resolve long-standing problems in many areas of biology (San Mauro & Aagaard, 2010). Novel high-throughput sequencing methods are opening up new avenues for studying taxonomy and biodiversity (Reuter et al., 2015) with metagenomic shotgun sequencing allowing the study of entire complex communities from a single environment sample. Metabarcoding approaches are used to characterize complex communities from soil and water or to study gut content of insects or mammals.

However, molecular phylogenetics is not without its flaws. Molecular data, much like morphological data, is also prone to homoplasy caused by functional constraints or by multiple substitutions (resulting in saturation) that are neutral due to the degeneracy of the genetic code (Grechko, 2013). Different genes evolve at different rates and may yield conflicting phylogenetic signals (Patwardhan et al., 2014). Using a molecule that is fast-evolving to analyse the relationships between distantly related taxa may result in a homoplasious dataset. It is for this reason that certain genes are more suited for resolving the different levels of phylogeny (Petersen & Seburg, 1998). Phylogenies reconstructed from single partial gene sequences alone can result in incongruent topologies and since different genes in a single phylogenetic analysis may lead to conflict, the choice of gene regions to be targeted are important (Planet, 2006). Furthermore, different genes are more or less informative in different groups of organisms (Cruickshank, 2002). However, it is important to note that gene trees are not species trees and the correct gene tree may not correspond to the species tree; this is in part due to gene duplication and loss or incomplete lineage sorting (Page & Holmes, 1998). A multi-gene approach is often selected where aligned gene regions are concatenated. Sequences for three partial gene fragments of only three African and one Asian *Catharsius* taxa are currently available on GenBank from the study of Monaghan et al. (2007). The same three gene regions (COI, 16S and 28S) will be sequenced, in part due to the availability of these sequences but because these regions have

been shown to be particularly informative for phylogenetic analyses in beetles (Sole & Scholtz, 2010; Mlambo et al., 2011; 2014; 2015; Tarasov & Dimitrov, 2016). A further problem with sequence data is the ambiguity in their alignment. Although there are a number of computer programs that will apply algorithms for alignment, there is a level of subjectivity with for example, gap-penalties accounting for insertions or deletions in the sequence strongly influencing the final alignment. Molecular results only show similarities of sequence position and there would be no reason why two nucleotides at the same site couldn't have evolved independently (Pearson, 2013).

As molecular techniques continue to improve and be fine-tuned, it is becoming possible to extract DNA from ancient museum specimens. There have been successful extractions of DNA from extinct animals such as the Quagga and from Egyptian mummies (Pääbo et al., 2004). The reliability of these ancient DNA sequences have been questioned as up to a third of the amplification products contain consistent misincorporations. There is also an issue with laboratory contamination by exogenous DNA. The chemical property of DNA restricts the survival of the molecule in the most favourable conditions (low temperatures and dry conditions). The degradation of the DNA in historic specimens varies upon the idiosyncrasies of preservation. There have been several works dealing with extracting ancient DNA from Coleoptera with mixed results. One work (Thomsen et al., 2009) successfully extracted short sequences from pre-1900 specimens whereas in the second, only very recent specimens yielded any sequences. The most likely conclusion as to these results lies in the preservation of the specimens. The target insects in this work are all small bodied beetles in the Carabidae and Curculionidae families which naturally dry quicker slowing down the degradation of the DNA. Larger insects are more problematic, with the results of extraction and sequencing of rhinoceros beetles DNA being very poor for older, pinned museum specimens (Verdugo & Drumont, 2015).

In chapter 3, DNA sequences produced from freshly caught samples stored in ethanol is combined and aligned with the available data from GenBank and molecular phylogenetic analyses conducted of the partial sequences of two mitochondrial and one nuclear gene allowing a molecular test of the phylogenetic hypotheses inferred from the morphological phylogenetic analyses.

### Species concepts

Species are one of the fundamental units of biology (Mayr, 1982), yet there is a great deal of debate as to its definition (see, de Queiroz, 2005). The differing concepts of species delimitation often lead to different conclusions of where species boundaries lie and the actual number of species. Of a number of different concepts (24 different concepts are listed by Mayden (1997)), some of the main concepts are discussed here. The traditional species concept is the biological species concept of an

interbreeding naturally reproductive community that excludes other species (Mayr, 1942). This is however problematic for taxa that reproduce asexually and is seldom applied strictly where there are cases of limited interbreeding. The ecological species concept is defined as those individuals that share the same niche or adaptive zone, i.e. all of the environmental components with which conspecific organisms interact (Van Valen, 1976). The evolutionary species concept states that a single lineage of ancestor-descendent populations that maintains its identity from other such lineages that has its own evolutionary role and tendencies (Simpson, 1951). The phylogenetic concept is defined by an irreducible grouping of organisms diagnosably distinct from other such groupings and within which there is a parental pattern of ancestry and descent (Hennig, 1966). The monophyletic species concept is defined by an ancestor and all of its decedents sharing a pattern of common decent and derived character states (Rosen, 1979). These different concepts are all a variation on a theme, that species are separately evolving metapopulation lineages (de Queiroz, 2007), but have been defined by scientists from different biological enterprises. In this study, the phylogenetic species concept of Wheeler & Platnick (2000) is used, defined as the smallest aggregation of populations diagnosable by a unique combination of character states.

#### Nomenclature and classification

The naming of species is an integral part of taxonomy and within the formal naming process, there is a need for the preservation of alpha taxonomic skills to correctly identify and describe species. The rules of nomenclature in zoology are governed by the International Code on Zoological Nomenclature (ICZN). Formal taxon descriptions require the designation of a holotype specimen, the single name-bearing specimen for that taxon. Historically, species have often been described without the clear designation of a single specimen as holotype with a number of specimens constituting the type series. In this case, a lectotype can be designated to fix the name to a single specimen. For specimens that have been destroyed, a neotype can be designated. Although the rules of the ICZN are complex only some are mandatory and must normally be strictly adhered to, whereas others are recommendations that are not set in stone. Even with mandatory rules, cases can be put forward to petition the commission to put aside some rule in order to increase nomenclatural stability. For example, in instances such as “Prevailing Usage” (Article 23.9.3.), frequently used taxon names can be maintained despite the presence of an older available name. Furthermore, the code takes into account the likelihood of taxonomic errors made by individuals as a consequence of misidentifications; the validity of a taxon does not change for example, even when it is erroneously synonymised. Despite the success of the binomial nomenclatural system for over 250 years, in the modern era of phylogenetics, a new naming system has been proposed. The PhyloCode provides a new set of nomenclatural rules for the naming of clades through explicit reference to phylogeny where names must strictly reflect clades not morphological distinctiveness, thus replacing the Linnaean system with

rank-free taxa. There have been a number of technical objections to this Code as “unnecessary” (Carpenter 2003) and “change for the sake of change” (Godfray & Knapp, 2004). In this study, all nomenclatural decisions will be made in accordance with the traditional binomial system as governed by the ICZN.

In the world of impact factor driven publications, taxonomic works languish near the bottom but knowledge generated from a large-scale taxonomic body of work will not only immediately benefit those researching the group but will likely provide data or evidence towards future work in other biological and socioeconomic disciplines. Although taxonomy is not an end-user orientated science, taxonomy finds itself poorly funded in comparison to other areas of biology and in order to garner the vital funding it needs, taxonomy needs to provide a sellable output and to generate further funding in the field (Godfray et al., 2008). This end-user is often not only a curator in a museum or an ecologist identifying their samples, but an amateur naturalist or an individual with a passing interest keen on identifying something they have found in their garden. Moreover, the amateur naturalist community have always and still provide an important role in taxonomy, through providing observations and locality data as well as discovering new species.

The taxonomic monograph should in essence be a tool for bringing together, disambiguating and disseminating all the information about the group of organisms in question, especially to those who do not have the luxury of being able to compare specimens side by side in a museum or private collection. This includes everything from the literature to the diagnostic characters that will identify a species from its closest relative. Many old publications often consisted of either very short (one or two sentences) or very long descriptions with terminologies which were only understandable to specialist taxonomists working on those groups. Some publications may have included a key to the species and occasionally figures of the habitus and/or genitalia of the species.

With the vast quantity of data in a monograph, there are suggestions that these works could largely become internet-based, doing away with long descriptions and replaced instead with interactive photographic keys, barcodes as well as information on its natural history and distribution creating a central focal point for anyone wanting to identify a species in a particular group without the access to museum collections. Websites such as the Sphingidae Taxonomic Inventory (<http://sphingidae.myspecies.info>) and Dominique Bernaud’s *Acraea* (<http://acraea.com>) are good example of how taxonomic information is disseminated to the end-user online. Although there is no key in the former, there are images of the upperside, underside and genitalia as well as all the literature associated with most of the world’s hawkmoths and African species of *Acraea*. The two-dimensional Lepidoptera with many of the characters clearly visible on the wings are conducive to this form of “e-taxonomy” (Godfray et al., 2008). However, whether a “unitary-taxonomy” (Godfray,

2007) of all the information gathered together in one place on the internet is the solution to turning the fortunes of taxonomy around are uncertain. Even with internet being more and more accessible even in the remotest parts of the world a hard copy or electronic reprint is still the best option for the fieldworker to identify what they have collected in situ. Images and keys facilitate identification but what happens when a species cannot be identified from an image or does not key out? This is where the good descriptive taxonomy is important, especially when direct comparison with other specimens of closely allied species is not readily possible.

In Chapter 4, all described taxa and previous treatments of the genus are fully investigated and the historical literature compiled and collated. The natural history and ecology of the genus is discussed, a checklist of all species provided together with a key to the related genera and putative species groups. All type specimens studied are imaged together with their labels and this is provided in Appendix V.

In Chapter 5, one species group is fully revised, with exhaustive re-descriptions and descriptions of both male and females of each species. Due to word limit constraints, only one species group is revised in this thesis and the new taxa from only this species group is described in any detail. Diagnoses for easy identification are provided together with figures of adults from varying angles (habitus, frontal and lateral), genitalia (aedeagus and internal sac sclerites), distribution maps and a key to the species to facilitate identification. Despite many entomological taxonomic works not vouchering the specimens examined as part of their study (Packer et al., 2018) all material examined and their depositories will be provided ensuring the data can be fully corroborated and verified or otherwise re-evaluated.

The great museum collections of the world are a repository of the planet's biodiversity and have at their foundation specimens collected by the early explorers and naturalists of the 18<sup>th</sup> and 19<sup>th</sup> century. The natural habitats at many of the localities have undergone great change as the areas have built up from small settlements into large cities. The data from these specimens provide an important insight into the historic distribution of species and how the changing world has impacted upon its extent. There is often a problem with the accuracy of historic label data, with some specimens labelled with a country name or even worse a continent. These specimens aside, there are further issues with the names of certain locations which cannot be located on any modern map. As data from a large number of museum specimens are extracted for the distribution maps in this study, a gazetteer of all African *Catharsius* specimens has been compiled and is provided in Appendix VI. This will be an important document as it is likely the early collectors who collected dung beetle specimens would not only have collected insects but other flora and fauna. The gazetteer therefore will be of interest to not only entomologists but a wider scientific community.

In conclusion, Wheeler (2014: 371) sums up well the identity of a taxonomist and the major aims of this study:

*“[If] the focus of your work is to make as many species of a clade known as possible, to carefully interpret and analyse the transformational history of as many of its homologous characters as possible, to study and master all taxonomic literature of a group since 1753, to apply informative names, and to ultimately build a phylogenetic classification summarising all that is known of a taxon, then you are unquestionably a taxonomist.”*



## Chapter 2: Morphological Phylogenetic Analyses

### Introduction

The mega-diverse dung beetle genus *Catharsius* is currently represented by 89 taxa in Africa and 12 in Asia. These large nocturnal tunnelers provide important ecosystem services mainly utilizing mammalian dung (some species having evolved necrophagic tastes) and are an important model group in ecology, biogeography and climate change. In a recent text on the African dung beetle genera, Davis et al. (2008) state in their chapter on this genus that it is need of a revision and that there is neither a phylogeny nor any formal species groupings for this large group.

Although there have recently been a number of phylogenetic analyses concentrating on the subfamily Scarabaeinae at a broader generic level, there have only been a few phylogenetic analyses at species level as part of a taxonomic revision. Most of the species-level phylogenies have involved genera with a small number of species (Roggero, 2015; Genier & Moretto, 2017). The most recent phylogenetic study of a large genus of dung beetle was the work of Cambefort & Nguyen-Phung (1996) on the genus *Copris*. This genus contains over 200 species which are widely distributed from the Americas, across Europe and Africa into Asia but the phylogenetic analysis included 48 putative and pre-ordained species groups of only the African species.

The lack of a phylogeny and key to the species of *Catharsius* has been a taxonomic impediment to ecologists and this study will form the basis for an upcoming revision of the Afrotropical members of this genus. In this study, phylogenetic relationships of both the Afrotropical and Asian members of the genus *Catharsius* are reconstructed using morphological characters. This is the first work to reconstruct a comprehensive phylogeny of a Scarabaeine genus containing over 100 species as well as a biogeographical ancestral state reconstruction to infer where the ancestor of this genus originated.

### Identification of the genus *Catharsius*

The genus currently contains 101 taxa and is distinguished by the combination of a pseudoepipleural carina, mesepisternal carina and the presence of striae on the ventral surface of the protibia (Ferreira, 1960b). The genus *Metacatharsius*, originally established as a subgenus of *Catharsius*, shares the first two characters but lacks the striae on the ventral surface of the protibia (Paulian, 1939). Until recently, *Catharsius* was included in the tribe Coprini but was placed as *incertae sedis* together with other genera including *Metacatharsius*, due to the absence of several synapomorphic characters in the internal sac of the aedeagus and the structure of the wing (Tarasov & Dimitrov, 2016). In the only

complete revisional works published on the genus, Ferreira partially split the genus into two by revising the “*C. adamastor*” group (1960b) of 21 species and then the rest of the species of the genus in a subsequent paper (1960c). The “*C. adamastor*” group was defined primarily on the shape of the clypeus and the presence of a pronotal carina. The traditional classification approach of grouping species together based mainly on variable secondary sexual characteristics such as the cephalic horn and external shape of the aedeagus has been shown to be problematic in other dung beetle groups such as *Onthophagus* (Tarasov & Solodovnikov, 2011). Ferreira’s revisionary works were based wholly on external characters and the genitalia were not examined. A more recent work (Moretto, 2008) has informally grouped together four species from Ferreira’s “*C. adamastor*” group into a sub-group. Aside from the initial split by Ferreira into two groups, there have been no further formal attempts to establish subdivisions within this large genus.

#### Previous phylogenetic analyses involving the genus *Catharsius*

Over the last quarter of a century, there have been a number of morphological phylogenetic analyses of the subfamily Scarabaeinae of which four studies have included *Catharsius* (Montreuil, 1998; Vaz de Mello, 2007; Bai et al., 2011; Tarasov & Genier, 2015). All these phylogenies included *Catharsius* as part of a study into broader generic level relationships within the subfamily. Owing to the nature of these works, the sample sizes were small with the first three studies utilising only the type species of the genus, *C. molossus* (Linnaeus, 1758) for the purpose of character coding and the most recent work coding a single African species. The placement of *Catharsius* and the relationships with its sister groups were largely congruent in all four studies, the general consensus being that *Catharsius* is sister to *Metacatharsius*. Two large scale molecular phylogenies of the Scarabaeinae also recovered the two genera as sister groups (Monaghan et al., 2007; Tarasov & Dimitrov, 2016). More detail of other molecular phylogenies that have included the genus will be discussed in the molecular phylogeny chapter (chapter 3). In the analysis of Bai et al. (2008) that reconstructed a phylogeny of the Chinese dung beetles, *Catharsius* was recovered as sister to *Copris* (the genus *Metacatharsius* is not represented in China). The only phylogenetic study using either morphological characters or molecules to have included the genus *Copridaspidus* was Montreuil (1998) with the clade *Catharsius* + *Copridaspidus* being recovered as sister to *Metacatharsius*.

#### Fossil records

The integration of fossil records in the reconstruction of phylogenies has enabled estimations of divergence times and early evolutionary history of lineages, as well as mitigating long branch artefacts and resolving incongruence between morphological and molecular phylogenies (Legg et al., 2013; Thuy & Stöhr, 2016; Yamamoto & Maruyama, 2017). There are 35 fossil Scarabaeinae known

(Tarasov et al., 2016), none of which currently belong in the genus *Catharsius*. The generic placement of *Metacatharsius rusingae* Paulian, 1976, a species described from the Early Miocene deposits of Rusinga Island in Lake Victoria, is however uncertain due to the poor preservation of the type specimen with the diagnostic characters being obscured. From the original description, Paulian mentions a prosternal carina and a curved meso-metasternal suture as the main reasons for placing this species in the genus *Metacatharsius* although both these characters are present in *Metacatharsius* and *Catharsius*. Further investigation, including the study of the type specimen is required to ascertain the exact generic placement which is beyond the scope of this study. No fossils are included as part of these phylogenetic analyses.

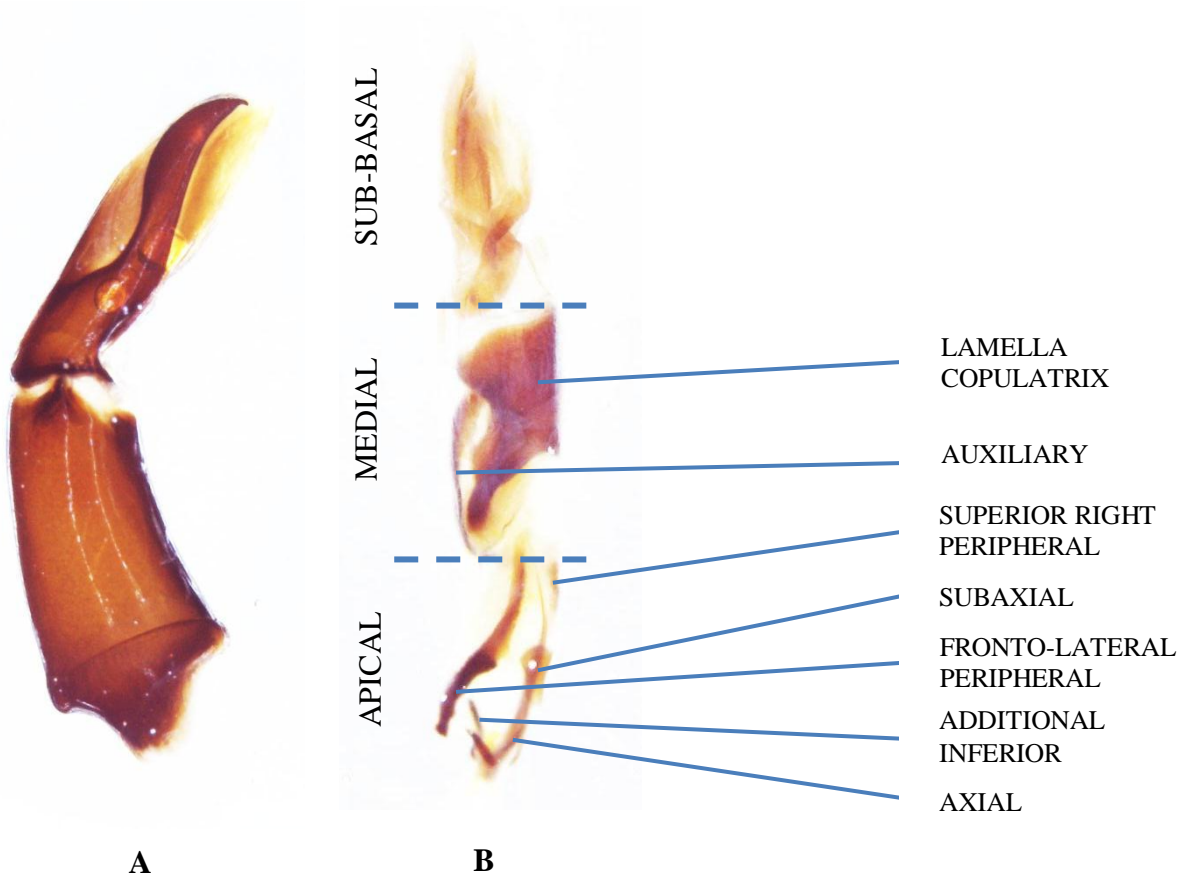
## **Materials and methods**

### Material examined

Specimens belonging to 142 taxa in total were examined in this study. The specimens studied for the current analysis are housed mainly in the Natural History Museum, London (BMNH) and the Oxford University Museum of Natural History (OUMNH), but other specimens from the following institutions were also studied as part of this analysis: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB), Jean-François Josso private collection, Muzillac, France (JFJC), Michaël Dierkens private collection, Lyon, France (MDCL), Muséum national d'Histoire Naturelle, Paris, France (MNHN), Musée Royal de l'Afrique Centrale, Brussels, Belgium (MRAC), Naturhistorisches Museum, Basel, Switzerland (NMB), National Museum of Kenya, Nairobi, Kenya (NMK), Philippe Moretto private collection, Toulon, France (PMOC), Naturalis Natuurhistorisch Museum, Leiden, Netherlands (RMNH) and Museum für Naturkunde, Berlin, Germany (ZMHB).

### Examination of specimens

All specimens that were examined were dry-pinned museum specimens. Specimens were cleaned for detailed morphological study using a warm solution of distilled water and a few drops of *Decon 90*. The aedeagus was prepared further in order to extract the internal sac by soaking in 10% Potassium hydroxide solution and warming at 70°C for around 10 minutes. Once extracted, both the aedeagus and endophallus were soaked in glacial acetic acid for a further 10 minutes before being cleaned and prepared in ethanol. They were stored in glycerol within small capsules which were pinned to the specimens. Recently collected specimens were preferred when available as the internal sac sclerites of the endophallus can be cleared much quicker than for historic specimens. With certain species being known solely from holotype specimens, only non-destructive examinations of the specimens were utilised, i.e. the specimens were not disarticulated. When possible, a maximum of ten specimens were



**Figure 1.** Aedeagus (A) and the three regions of the internal sac with sclerites (B) of *Catharsius eteocles* (Castelnau, 1840)

dissected in order to study the aedeagus and internal sac. Specimens were photographed using a Canon EOS 5D SR with Macro 100mm or MP-E 65mm lenses. The aedeagus and internal sac were photographed through a Leica MS5 stereo microscope. Images were stacked using Helicon Focus 6.0. Images were processed and edited using Adobe Photoshop Elements 10.

#### Morphological terminology

Terminology used for external beetle morphology follows Edmonds (1972), whilst the sclerites of the internal sac follow Medina et al. (2013) and Tarasov & Génier (2015). The endophallus of certain genera such as *Digitonthophagus* (Génier & Moretto, 2017) has been investigated thoroughly but due to the wildly differing sclerites of the internal sac within the Scarabaeinae, the terminology of the *Catharsius* endophallus is here outlined. The internal sac of the aedeagus is known to provide taxonomically useful characters for differentiating between taxa at both the generic and specific levels, although the precise functioning of these structures is poorly understood (Medina et al., 2013). The internal sac of all *Catharsius* species contains several sclerites in the apical and medial regions of the internal sac (Figure 1). The apical region contains the *axial* (A) and *subaxial* (SA) sclerites, the *additional inferior* (AIS) sclerite, the *fronto-lateral peripheral* (FLP) sclerite and the *superior right peripheral* (SRP) sclerite. The medial region contains two sclerites, the large *lamella copulatrix* (LC)

and a smaller *auxiliary sclerite* (AS). In some species, one or two *raspulae* are present in the sub-basal region of the internal sac.

#### Character coding and outgroup taxa

The extreme morphological similarity of the closely allied species led to difficulty in coding for characters. In general, absent/present coding was applied assuming an independent origin of each character state. Without knowing how the different structural configurations of a given character were related to each other, this form of coding was considered as the most parsimonious assumption. This was especially the case with the shape (groundplan) of the phylogenetically informative LC. The coding of these internal sac sclerites follows several morphological dung beetle phylogenetic studies of Tarasov & Solodovnikov, 2011, Tarasov & Génier, 2015 and Génier & Moretto, 2017. Despite arguments for and against this form of coding (e.g. Meier, 1994; Pleijel, 1995, Hawkins et al., 1997; Forey & Kitching, 2000; Brazeau, 2011), one of the advantages of absent/present coding is the simplicity of transforming observations into a character matrix whilst avoiding statements regarding the homology of states within a given character. Variable secondary sexual characters such as the shape of the anterior margin of the clypeus and cephalic horn were coded as multistate characters. Missing characters, such as those for the females in taxa where only males are known were coded as “?” and inapplicable characters were coded as “-”.

The character matrix was constructed in Mesquite version 3.10 (Maddison & Maddison, 2009) and included 130 characters (118 binary and 12 multistate) scored from both sexes (characters and matrix in Appendix II and III respectively). 95 characters were coded from external morphology, with the head and pronotum of the male providing most of the characters (17 and 31 respectively). The phylogenetically informative regions of the genitalia and endophallus provided 35 characters (see Appendix I for the complete character matrix). Much like other genera within the Scarabaeinae, these beetles are sexually dimorphic and the female characters were also coded. Studies of female characters in other groups of beetles have been shown to be phylogenetically informative (Gaiger & Vanin, 2013). In the process of coding characters for the morphological dataset, it has become apparent that a large number of the Afrotropical species are undescribed. Around a third of the total number of species are yet undescribed and these will be described in the forthcoming revision. The species are here denoted as “sp. nov.” but these names are merely manuscript names and according to the International Code on Zoological Nomenclature (ICZN), the mention of these names are not intended as valid descriptions. Although there are also many undescribed Asian species (D. Mann, 2015, pers. comm.), this is beyond the scope of this work and only topotypical specimens pertaining to each species were used in this study. To allow future studies to utilise the matrix, every character coded has been imaged (Appendix IV).

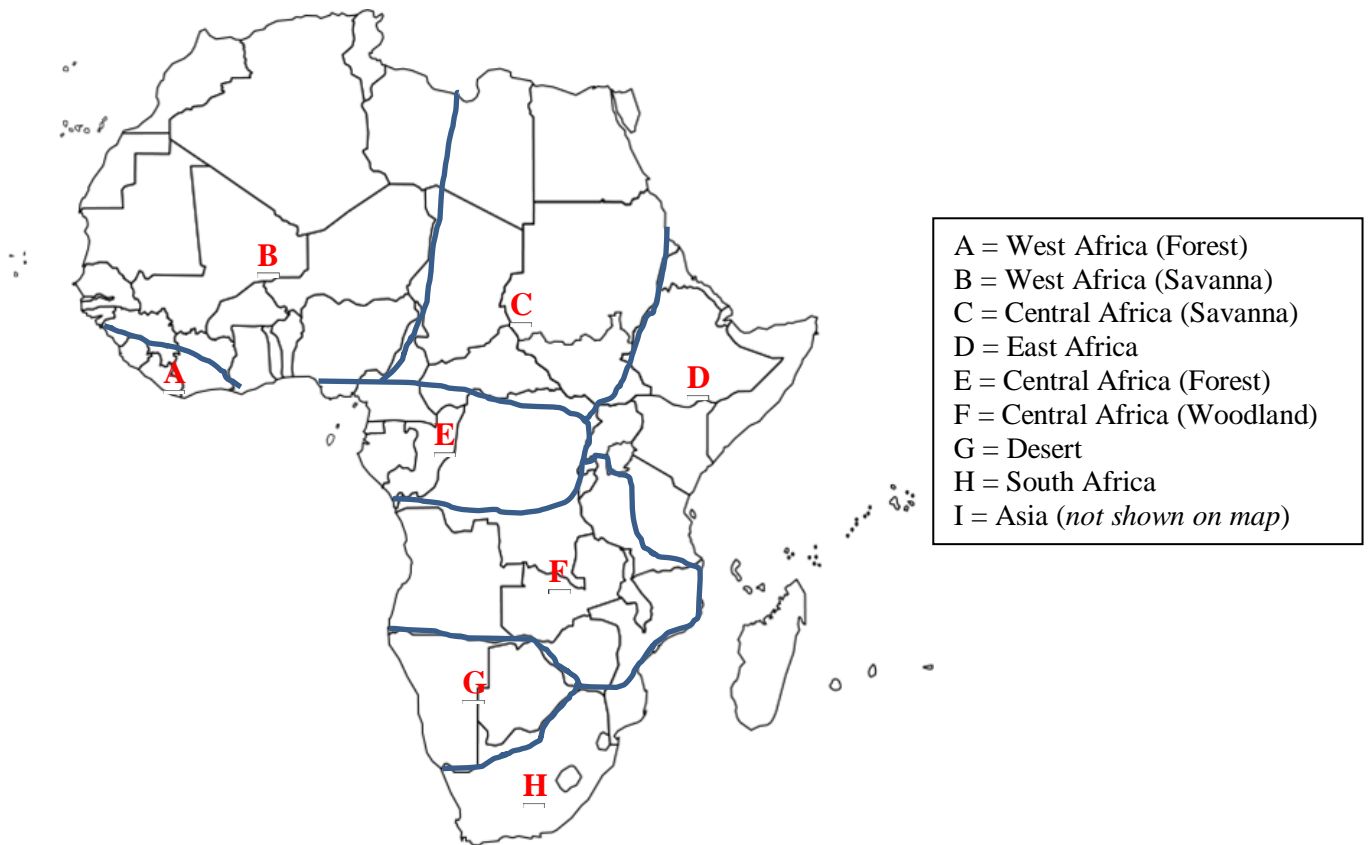
The ingroup for the analysis consisted of every species of *Catharsius* (138 taxa, including undescribed taxa) and the three genera recovered as sister to *Catharsius* in previous phylogenetic works (discussed above), namely *Metacatharsius*, *Copridaspidus* and *Copris* were chosen as outgroups.

### Phylogenetic analysis

The phylogenetic analysis was run in TNT version 1.1 (Goloboff et al., 2003) using the “traditional search” options to find the most parsimonious trees (MPT) under the following parameters: memory set to hold 15000 trees, 1000 tree bisection-reconnection (TBR) replicates, saving 1000 trees per replicate, zero-length braches collapsed. All character states were treated as unordered. In the first analysis (analysis #1), the full character matrix was used. To test the strength of the character matrix, a second analysis (analysis #2) was run using the same matrix excluding all the cephalic horn and pronotal form characters (1-15) using the same parameters as the initial analysis. The shape and position of the cephalic horn as well as the structural form of the pronotum are well known to be homoplasious (Emlen et al., 2007) but were coded as they were one of the very few characters to distinguish between very closely allied species. A third analysis (analysis #3) was run excluding two taxa, *C. calaharicus* and *C. mirabilis*, which each have very different LC ground plans (character 126 and 129 respectively) as well as many unique external morphological traits, to see how the topology of the trees would be affected. A fourth analysis (analysis #4) was run using only the characters from the genitalia which have been phylogenetically highly informative in previous studies of Scarabaeine dung beetles. A final analysis (analysis #5) was run using the full matrix but under implied weights, with concavity factor  $k$  varying from 1 to 10. Bremer supports were calculated for the strict consensus trees searching for suboptimal trees up to 8 steps longer than the shortest one using TBR swapping on the shortest branches. The resulting trees were drawn using Winclada (Nixon, 2002) and Figtree version 1.3 (Rambaut, 2009).

### Biogeographic and habitat-based ancestral state reconstructions

The geographical data from all specimens studied (10827 specimens) was georeferenced and used to build maps in Simplemappr (Shorthouse, 2010), with dots overlaid onto a terrestrial ecosystem map (Olson et al., 2002) from which geographical regions were assigned based on the distribution of each species. The African continent was separated into eight regions (Figure 2) and Asia was kept as a single region broadly following the dispersal-vicariance analyses of Aduse-Poku et al. (2009). The distribution data and habitat type were entered into two absence/presence matrices which were used together with the full character matrix to carry out two independent historical biogeographical analyses using the S-Diva function of RASP (Yu et al., 2012).



**Figure 2.** The different regions identified for the biogeographical ancestral reconstruction, based on geographical data extracted from 10127 specimens.

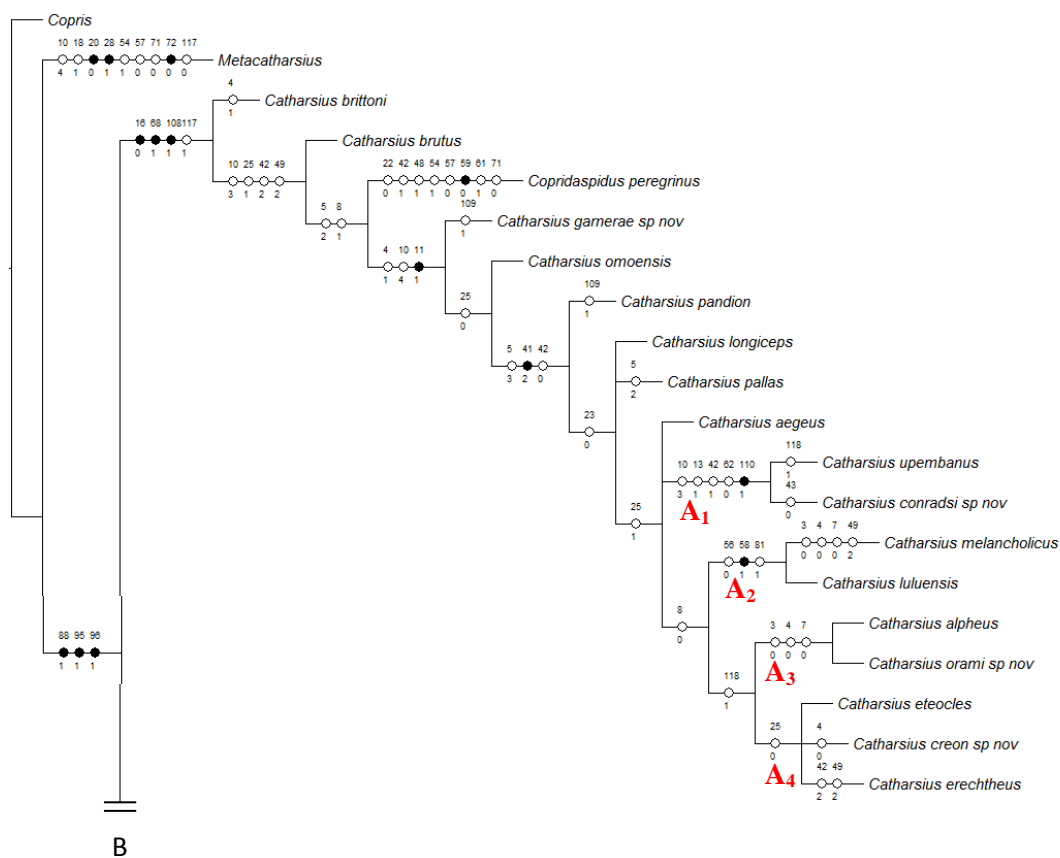
## Results

### Phylogenetic Analysis

Analysis #1 of all characters produced 7000 trees (length: 510; Retention Index (RI): 0.826; Consistency Index (CI): 0.294). Analysis #2 excluding the cephalic horn and pronotal characters produced 2000 trees (length: 340; RI: 0.861; CI: 0.351). Analysis #3 excluding *C. mirabilis* and *C. calaharicus* resulted in 4000 trees (length 492; RI: 0.830; CI: 0.299). Analysis #4 of just the genitalia characters produced 12000 trees (length 61; RI: 0.959; CI: 0.590). Analysis #5 with concavity factor ranging from 1 to 10 yielded consensus trees with the highest resolution. The concavity factor  $k=6$  yielded the fewest trees (45) and the resulting majority rule (50%) tree will be used for the detailed description of the phylogenetic results (strict consensus and majority rule trees for all analyses are found in Appendix I). 22 characters were parsimony-uninformative but were included as they provide trait data. In every analysis, the genus *Catharsius* was recovered as paraphyletic with regard the outgroup *Copridaspides* whilst in Analysis #1 and #3, the genus *Metacatharsius* was additionally recovered as an ingroup. In Analysis #2, #4 and #5, five distinct groups consisting of the same taxa

were recovered with the exception of the placement of *C. calaharicus* which differed in Analysis #2. The *Catharsius* + *Copridaspidus* clade was supported by three non-homoplasious synapomorphies (88:1, 96:1, 97:1). The five groups recovered within this clade suggest the subdivision of the genus into species groups, here named the *Catharsius eteocles* group (Clade A), the *Catharsius sesostris* group (Clade B), the *Catharsius molossus* group (Clade C), the *C. pithecius* group (Clade D) and the *C. tricornutus* group (Clade E), each species group taking the name of the oldest available species name in its group. Each species group is discussed in detail below.

### 1. The *Catharsius eteocles* species group (Clade A: Figure 3)

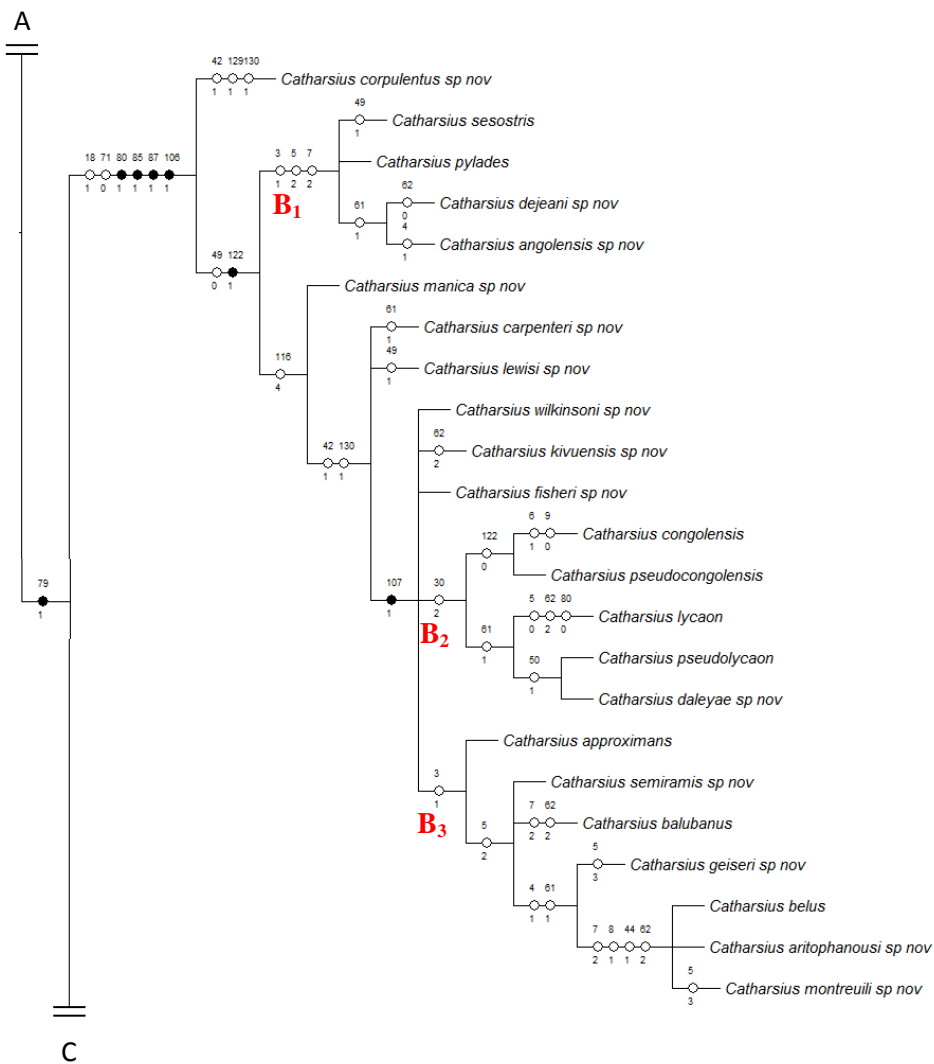


**Figure 3.** Phylogeny of the *C. eteocles* group obtained from parsimony analysis #5 under implied weighting ( $k=6$ ) with mapped synapomorphies.

This species group is represented by 18 taxa (Figure 3) and supported by three non-homoplasious synapomorphies: the pointed ventral clypeal tooth (16:0), the presence of the scutellum (68:1), a character which is also present in some other dung beetle genera (e.g. *Cheritonitis*) and the unique shape of the LC (108:1). This clade was recovered in every analysis with Bremer support of 3 in each of the analyses. The outgroup genus *Copridaspidus* was always recovered in this clade. Although this group was not completely resolved, two distinct clades were recovered in every study. Clade A<sub>1</sub> consists of *C. upembanus* + *C. conradi* sp. nov. and is supported by a single non-homoplasious

synapomorphy: the undulating base of the LC (110:1). Clade A<sub>2</sub> consists of *C. melancholicus* + *C. luluensis* and supported by a single non-homoplasious synapomorphy: the projection on the prosternum (58:1). Two further clades were recovered in analysis #5 consisting of *C. alpheus* + *C. orami* sp. nov. (Clade A<sub>3</sub>) and *C. eteocles* + *C. creon* sp. nov. + *C. erchtheus* (Clade A<sub>4</sub>). In analysis #1 and #3, a clade consisting of *C. brutus* + *Copridaspidus* + *C. omoensis* + *C. garnerae* sp. nov. was recovered with Bremer support of 2, but this clade was recovered as a polytomy in analysis #5. *C. brittoni* was recovered as the most basal of this group. This species group comprises only African taxa and many species in this group are known to feed on carrion (Genier, 2017). They are distributed widely through the drier woodland and savannah habitats with the majority of the species being found in eastern, central and southern Africa with only one species, *C. eteocles*, being found in West Africa.

## 2. The *Catharsius sesostris* species group (Clade B: Figure 4)

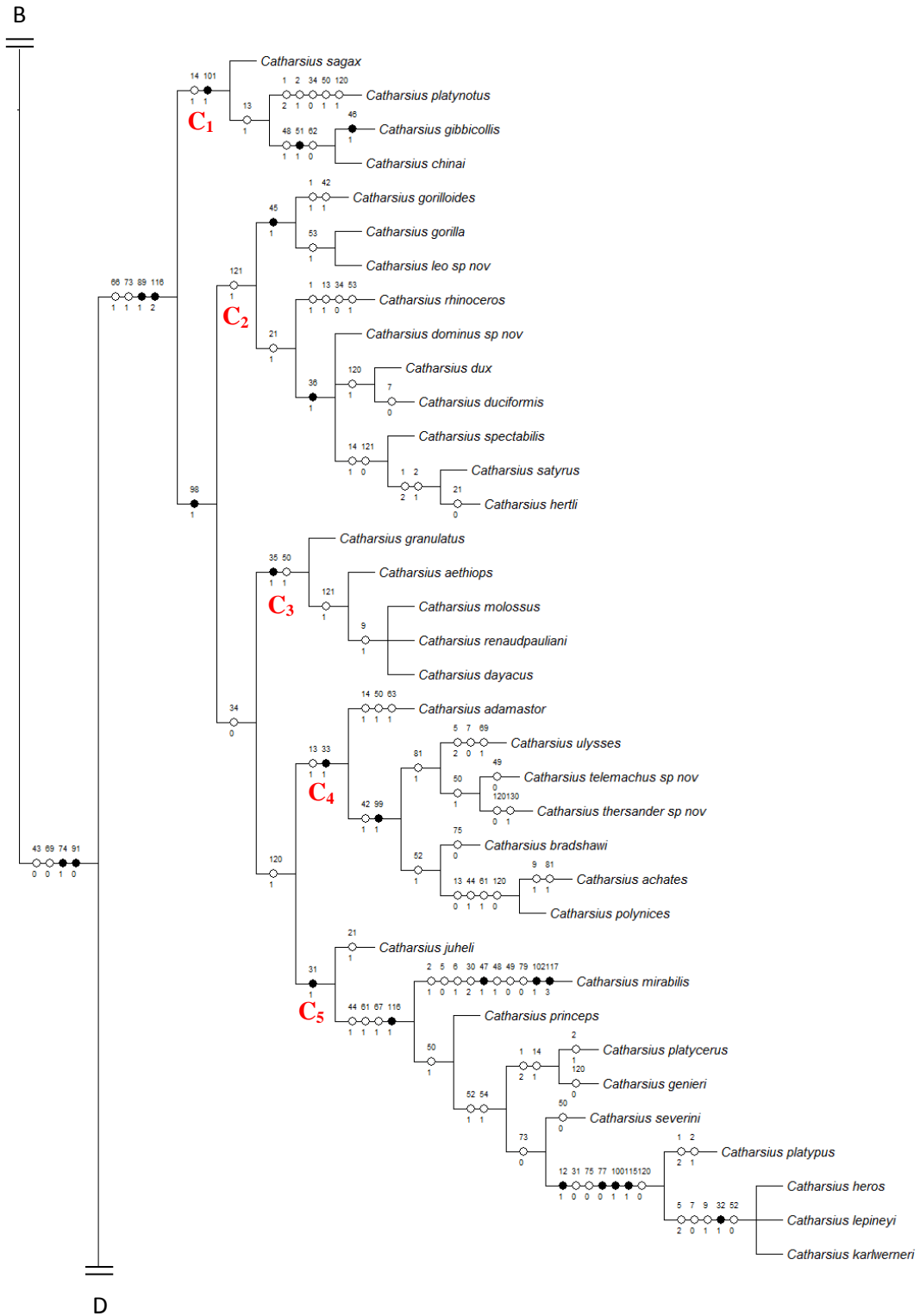


**Figure 4.** Phylogeny of the *C. sesostris* group obtained from parsimony analysis #5 under implied weighting ( $k=6$ ) with mapped synapomorphies.

This species group is represented by 23 species and supported by four non-homoplasious synapomorphies: a rounded apex of the parameres (80:1), large lateral excavation along the length of the parameres (85:1), the AS fuse to the LC (87:1) and the unique shape of the LC (106:1). This clade was recovered with Bremer support of 4 in analysis #4. All members of this group have the presence of an internal apical spur on the protibia of male specimens, a character which is also present in the genus *Metacatharsius*. *C. corpulentus* sp. nov. is recovered as most basal in this group. Again, although not fully resolved, four clades were consistently recovered in this clade. Clade B<sub>1</sub> consists of a polytomy of *C. sesostris* + *C. pylades* + *C. dejeani* sp. nov. + *C. angolensis* sp. nov. recovered in analyses #3 (with Bremer support of 1) and #5. Clade B<sub>2</sub> consists of *C. congolensis* + *C. pseudocongolensis* (recovered in every analysis with Bremer support of 1) and *C. lycaon* + *C. pseudolycaon* + *C. daleyae* sp. nov. (also recovered in every analysis with Bremer support of 1). Clade B<sub>3</sub> consists of *C. approximans* + *C. semiramis* sp. nov. + *C. balubanus* + *C. geiseri* sp. nov. and a polytomy of *C. belus* + *C. aristophanousi* sp. nov. + *C. montreuili* sp. nov. (this polytomy is also recovered in every analysis with Bremer support of 1). This species-group contains solely African species that feed on a wide range of dung and is found throughout forested and open habitats.

### 3. The *Catharsius molossus* species group (Clade C: Figure 5)

This species group is represented by 36 species supported by two non-homoplasious synapomorphies: the sclerotised region of the FLP fused only medially (89:1) and the tridentate clypeal carina of the female (116:2). The mixed African/Asian Clade C<sub>1</sub> supported by a single non-homoplasious synapomorphy (102:1) consists of *C. sagax* + *C. platynotus* + *C. gibbicollis* + *C. chinai* and was recovered as the most basal group in analysis #5. The clade was recovered with Bremer support of 1 in analyses #1 and #3, whilst *C. gibbicollis* + *C. chinai* was recovered in every analysis with Bremer supports of 3 in analyses #1 and #2 and 2 in analysis #3. The African Clade C<sub>2</sub> consists of *C. gorilloides* + *C. gorilla* + *C. leo* sp. nov. (recovered in every analysis with Bremer support of 1), *C. rhinoceros*, *C. dominus* sp. nov. + *C. dux* + *C. duciformis* and *C. spectabilis* + *C. satyrus* + *C. hertli* (recovered in analysis #1 with Bremer support of 1). The Asian Clade C<sub>3</sub> consists of *C. granulatus* + *C. aethiops* + *C. molossus* + *C. renaudpauliani* + *C. dayacus* recovered with Bremer support of 1 in analyses #1 and #3. The African Clade C<sub>4</sub> consists of *C. adamastor*, *C. ulysses* + *C. telemachus* sp. nov. + *C. thersander* sp. nov. and *C. bradshawi* + *C. achates* + *C. polynices*. The clade *C. achates* + *C. polynices* was recovered with Bremer supports of 1 in analysis #2 and 2 in analysis #3. The mixed African/Asian Clade C<sub>5</sub> consists of *C. mirabilis*, *C. princeps*, *C. platycerus* + *C. genieri*, *C. severini* and *C. platypus* + *C. heros* + *C. lepineyi* + *C. karlwernerii*. This clade is recovered with Bremer support of 2 in analysis #2.



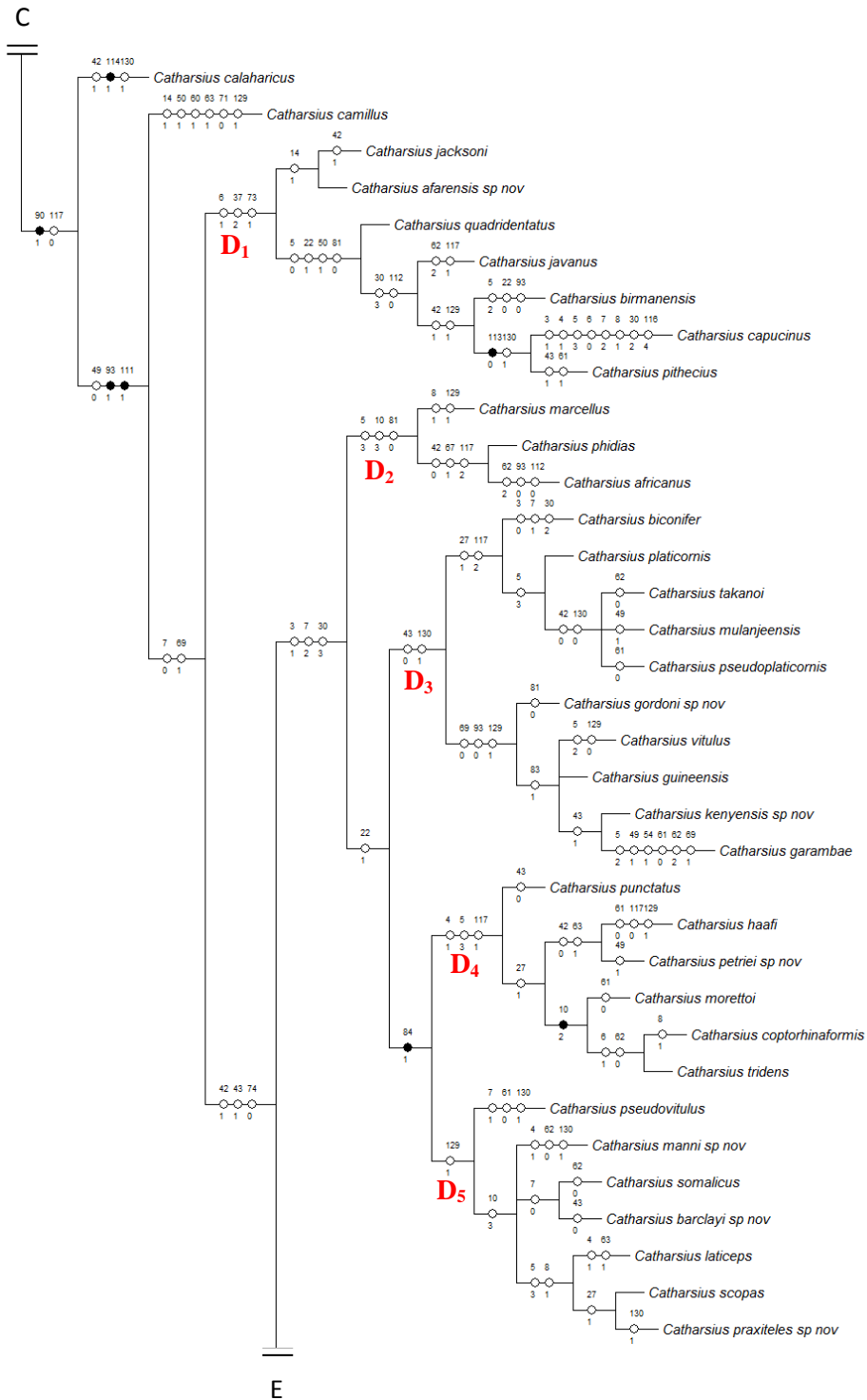
**Figure 5.** Phylogeny of the *C. molossus* group obtained from parsimony analysis #5 under implied weighting ( $k=6$ ) with mapped synapomorphies.

When *C. mirabilis* is excluded (analysis #3), the Bremer support for the other members of the clade is 4. The clade *C. platypus* + *C. heros* + *C. lepineyi* + *C. karlwerneri* is supported by four unambiguous synapomorphies: the lateral clypeal margin with upward pointing tooth (12:1), the broad and expanded first metatarsal segment (77:1), the bilobed and emarginate LC (100:1) and the presence of

the raised angled clypeal shield in the female (115:1). The clade was recovered in every analysis with strong Bremer supports (5 in analysis #1, 6 in analysis #2 and 7 in analysis #3). *C. juheli*, is recovered most basally in Clade C<sub>5</sub>. This species-group contains both African and Asian species including the type species of the genus, *C. molossus*. In general, all of the species in this group are large bodied and with the exception of *C. mirabilis* and the Asian species, this group contains all of the species delimited by Ferreira as the “*C. adamastor*” group. The species in clade C<sub>1</sub> and C<sub>5</sub> appear to feed solely on large monogastric herbivore dung and especially elephant dung. The majority of species are found in woodland and dry open habitats but a few species are found in forested habitats. Species within this group are powerful fliers and a number of species are very widely distributed.

#### 4. The *Catharsius pithecius* species group (Clade D: Figure 6)

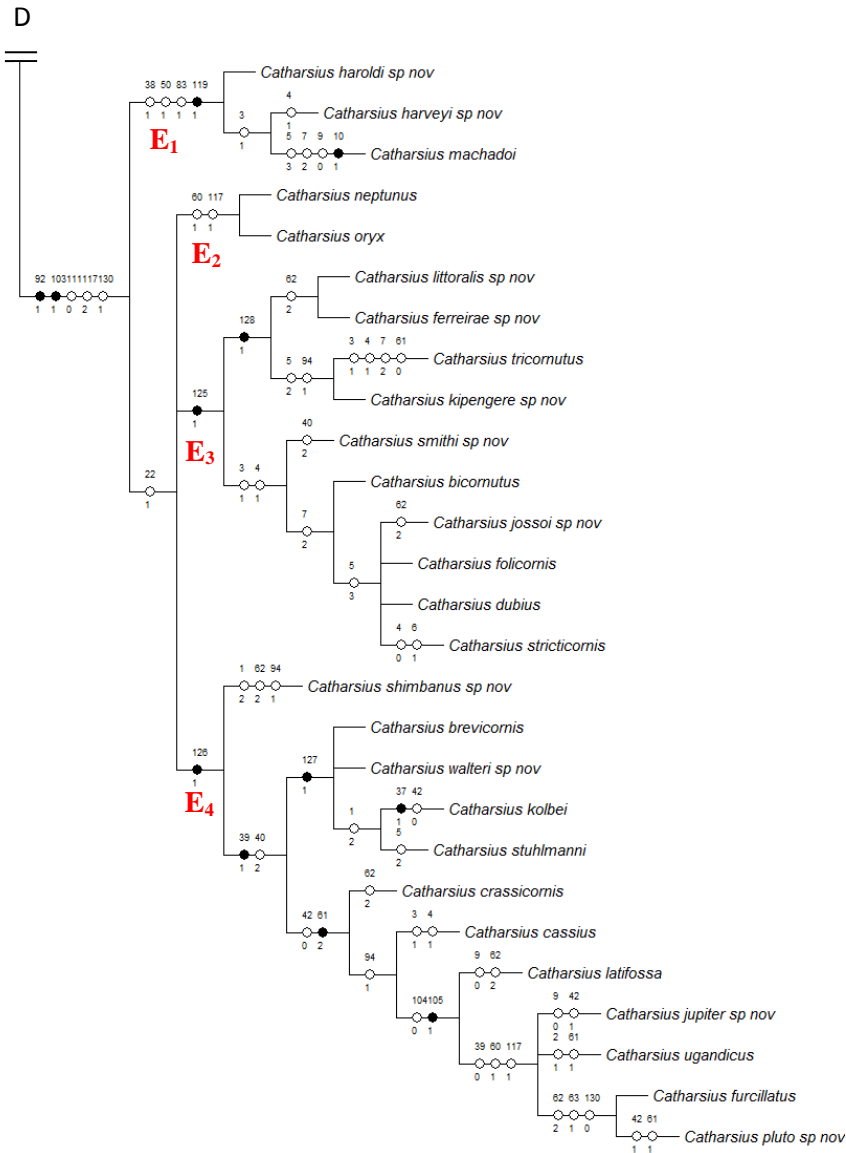
This species group is represented by 42 species and supported by one non-homoplasious synapomorphy: the sclerotised region of the FLP fused along its whole length (90:1). *C. calaharicus* is recovered as the most basal in this group. This taxon was recovered as basal to the *Catharsius molossus* group in Analysis #2 but basal to the *Catharsius pithecius* group in Analysis #4 and #5. The following six clades are supported by two non-homoplasious synapomorphies: the presence of the left raspula (93:1) and the unique shape of the LC (111:1). The Clade D<sub>1</sub> consists of the African *C. jacksoni* + *C. afarensis* sp. nov. and the Asian *C. quadridentatus* + *C. javanus* + *C. birmanensis* + *C. capucinus* + *C. pithecius*. This clade is recovered with Bremer support of 1 in analyses #1, whilst the Asian clade is recovered with Bremer supports of 1 in analyses #1 and #3 and 2 in analysis #2. Clade D<sub>2</sub> consists of *C. marcellus* and *C. phidias* + *C. africanus* (the latter two taxa recovered in every analysis with Bremer supports of 1 in analyses #1 and #3 and 2 in analysis #2). Clade D<sub>3</sub> consists of *C. biconifer* + *C. platicornis* + *C. takanoi* + *C. mulanjeensis* + *C. pseudoplaticornis* which is recovered in analysis #2 with Bremer support of 1. Clade D<sub>4</sub> consists of *C. gordonii* sp. nov. + *C. vitulus* + *C. fastidiosus* + *C. kenyensis* sp. nov. + *C. garambae*. Clade D<sub>5</sub> consists of *C. punctatus*, *C. haafi* + *C. petriei* sp. nov. and *C. morettoii* + *C. coptorhinaformis* + *C. tridens* (the latter two taxa recovered in every analysis with Bremer support of 1). Clade D<sub>6</sub> consists of *C. pseudovitulus*, *C. manni* sp. nov., *C. somalicus* + *C. barclayi* sp. nov. and *C. laticeps* + *C. scopas* + *C. praxiteles* sp. nov.. *C. camillus* is recovered basally to these six groups. All of the African taxa are found in open woodland and grassland habitats with the majority of species distributed in eastern, central and southern Africa.



**Figure 6.** Phylogeny of the *C. pithecius* group obtained from parsimony analysis #5 under implied weighting ( $k=6$ ) with mapped synapomorphies.

### 5. The *Catharsius tricornutus* species group (Clade E: Figure 7)

This species group is represented by 27 species supported by two non-homoplasious synapomorphies: the notch on the lateral margin of the FLP (92:1) and the unique shape of the LC (103:1). This clade was recovered in every analysis with Bremer support of 1. Four further distinct clades were recovered.



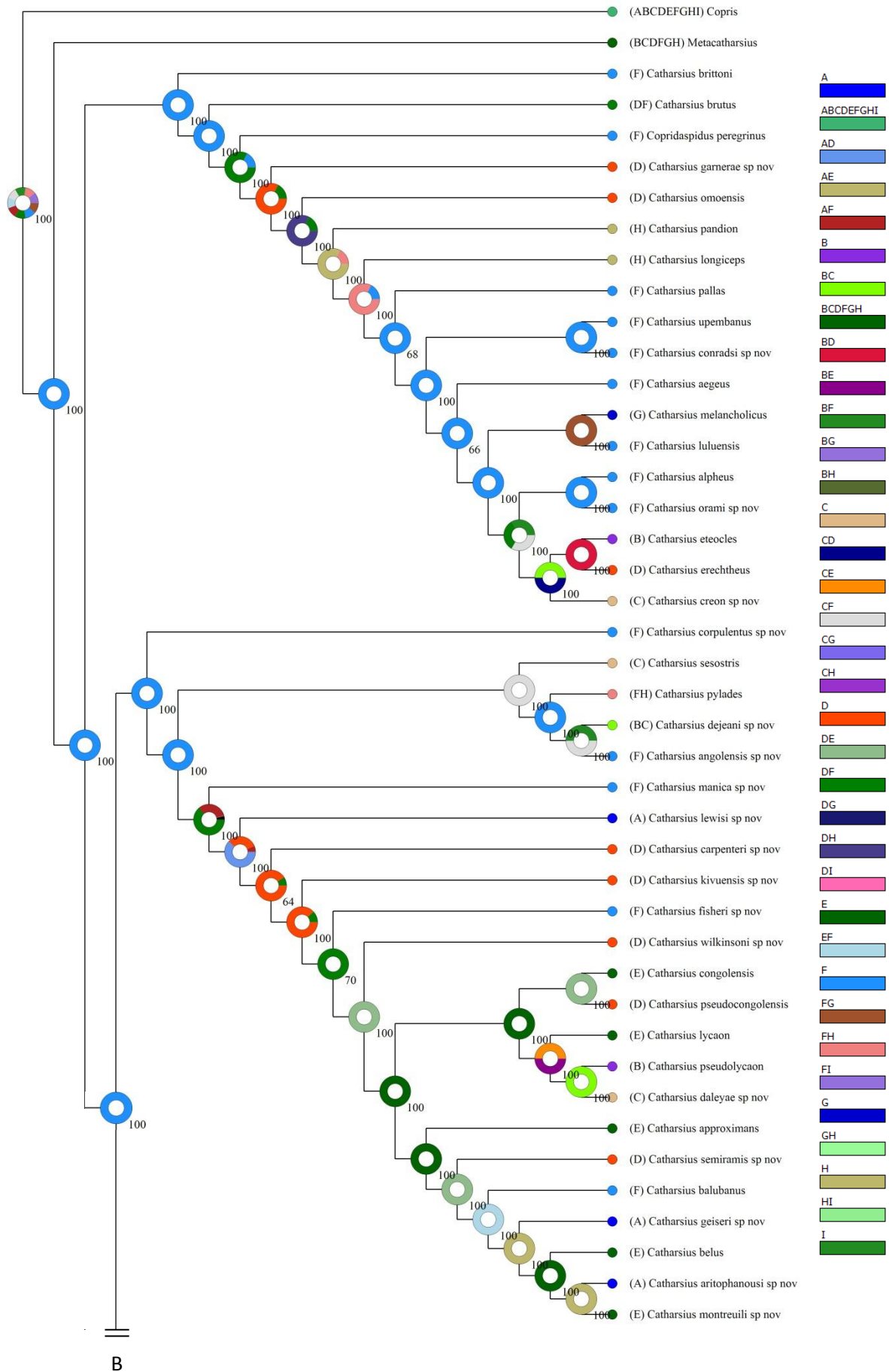
**Figure 7.** Phylogeny of the *C. tricornutus* group obtained from parsimony analysis #5 under implied weighting ( $k=6$ ) with mapped synapomorphies.

The most basal Clade E<sub>1</sub> which consists of *C. haroldi* sp. nov. + *C. harveyi* sp. nov. + *C. machadoi* was recovered in every analysis with Bremer support of 4 in analyses #1 and #3 and 3 in analysis #2. Clade E<sub>2</sub> consists of *C. neptunus* + *C. oryx* which was recovered in analysis #2 with Bremer support of 1. Clade E<sub>3</sub> consists of *C. littoralis* sp. nov. + *C. ferreirae* sp. nov. + *C. tricornutus* + *C. kipengere* sp. nov. and *C. smithi* sp. nov. + *C. bicornutus* + *C. jossoi* sp. nov. + *C. folicornis* + *C. dubius* + *C. stricticornis*. *C. littoralis* sp. nov. + *C. ferreirae* sp. nov. was recovered with Bremer supports of 1 in analyses #1 and #3, whilst *C. tricornutus* + *C. kipengere* sp. nov. was recovered with Bremer support of 1 in analysis #2. Clade E<sub>4</sub> consists of *C. shimbanus* sp. nov. basally, *C. walteri* sp. nov. + *C. kolbei* + *C. stuhlmanni*, *C. crassicornis* + *C. cassius* + *C. latifossa* and *C. jupiter* sp. nov. + *C. ugandicus* + *C. furcillatus* + *C. pluto* sp. nov.. This clade is recovered with Bremer support of 1 in analysis #2. *C.*

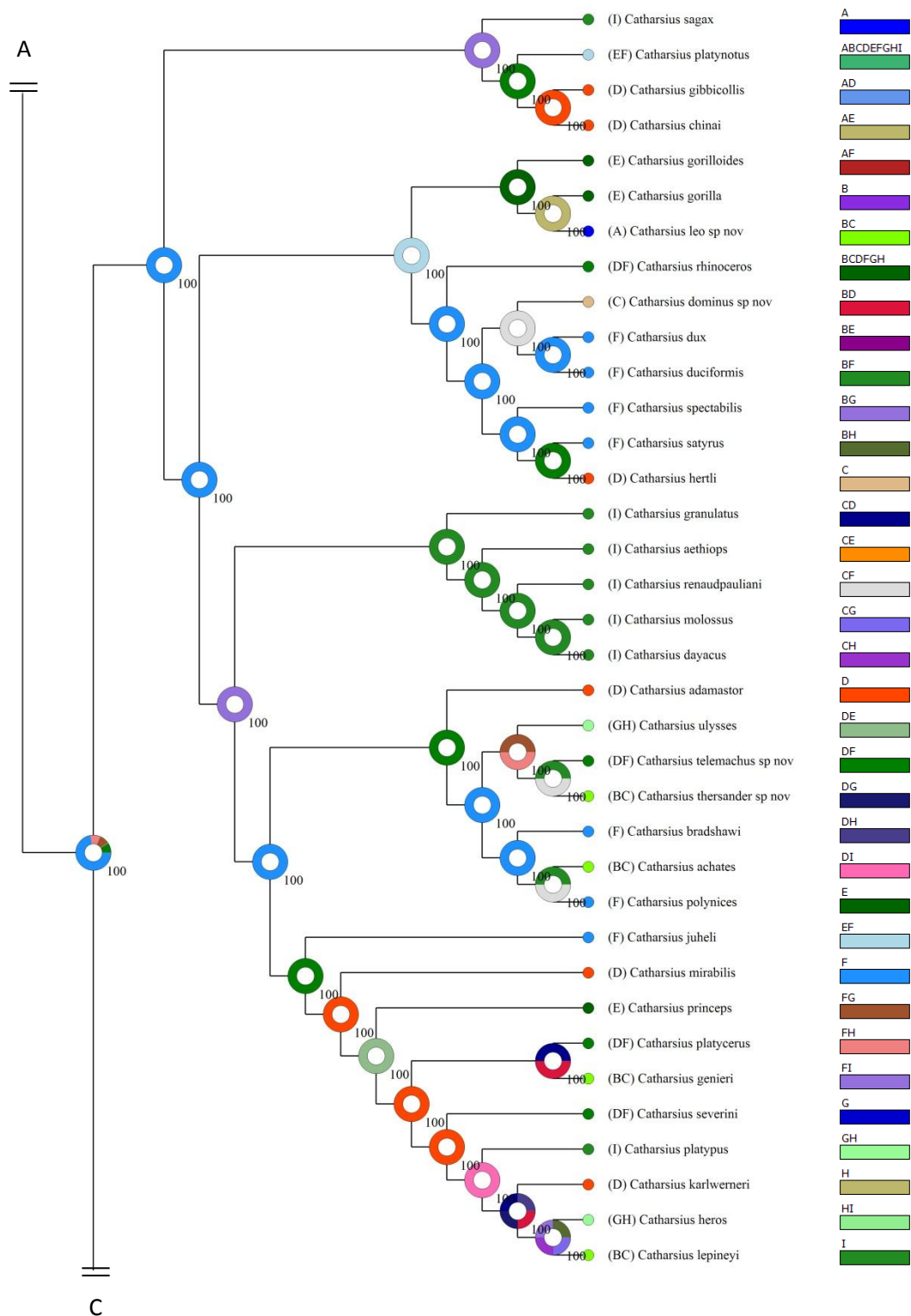
*jupiter* sp. nov. + *C. ugandicus* + *C. furcillatus* + *C. pluto* sp. nov. is recovered in all analyses with Bremer support of 2. This species group contains solely African species that are distributed throughout woodland and grassland habitats. The majority of the species are found in eastern, central and southern Africa with just one species, *C. crassicornis*, being found in West Africa.

#### Biogeographic and habitat-based analyses

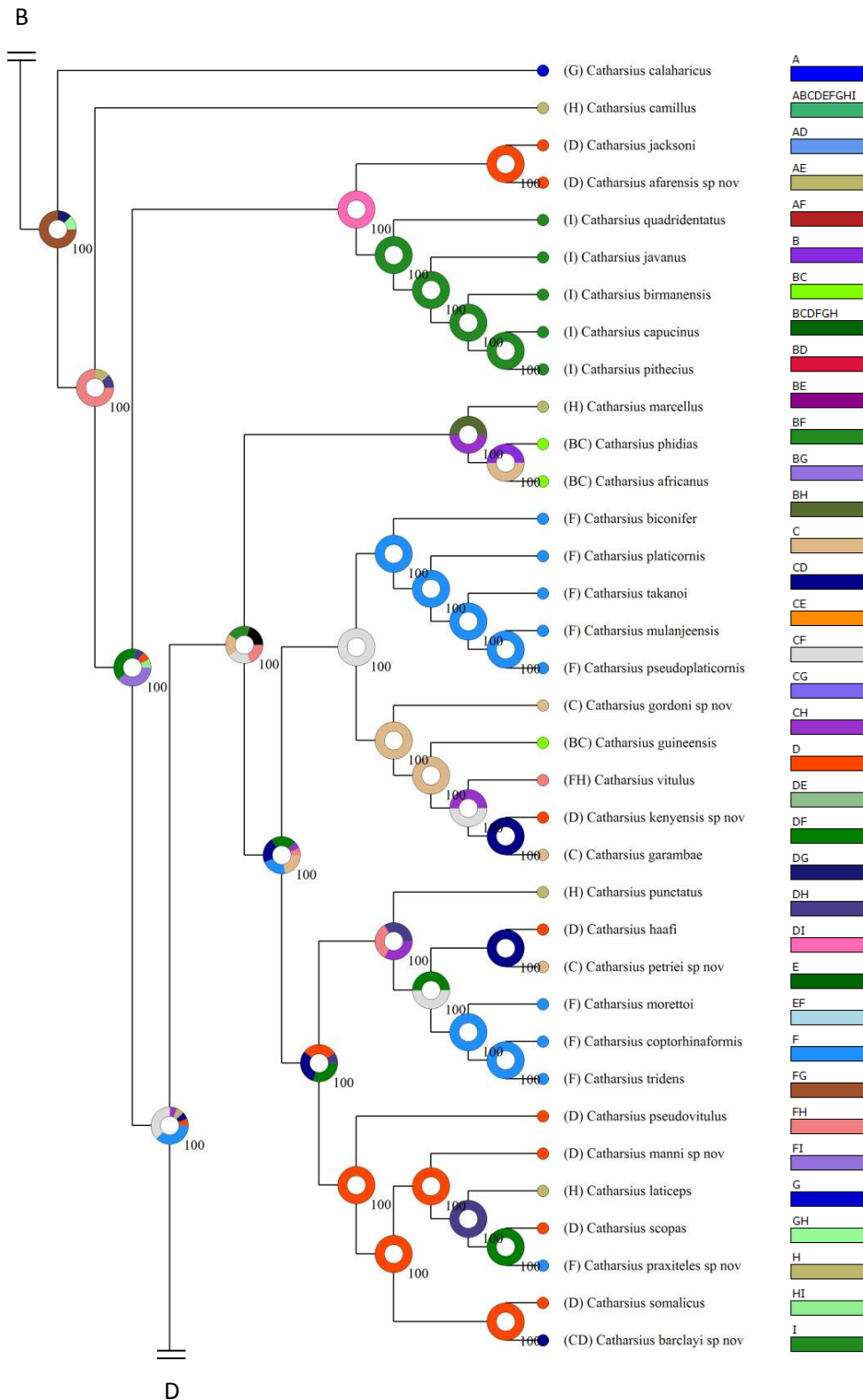
The ancestral state reconstruction suggests that the genus *Catharsius* has an African origin. Most species were found to be distributed in only one region although 20 taxa were found across two regions. No taxa are found in both Africa and Asia. The optimal distribution at most of the nodes gave a probability (p) value scaled to 100.00. There were however 35 nodes which gave equally probable alternative hypotheses. From this analysis, it is hypothesized that the woodlands of central-south Africa (Region F) was the origin of *Catharsius*. Based on data from museum specimens, this area is one of the most diverse in terms of the number of species and major lineages found there. The analysis has shown that many dispersal (100) rather than vicariance (62) events are responsible for the current distribution of *Catharsius* (Figures 8-11). Furthermore, the highest number of dispersal events appears to have occurred from Region F into Region D (15), whilst 43 and 21 speciation events occurred within Region F and Region D respectively. It appears Asia has been colonised independently four times, once by the ancestor of *C. sagax*, *C. granulatus*, *C. platypus* (Figure 9) and *C. quadridentatus* (Figure 10). Only species from two of the five groups (the *C. molossus* and *C. pithecius* groups) have successfully colonised Asia. The ancestral state reconstruction of the habitat preference suggests that the small proportion of species found in tropical forest environments (22 taxa) colonised from open savanna and woodland habitats into forested habitats. Only species from three out of the five species groups (the *C. sesostris*, *C. molossus* and *C. pithecius* groups), have successfully colonised forested habitats (Figure 12).



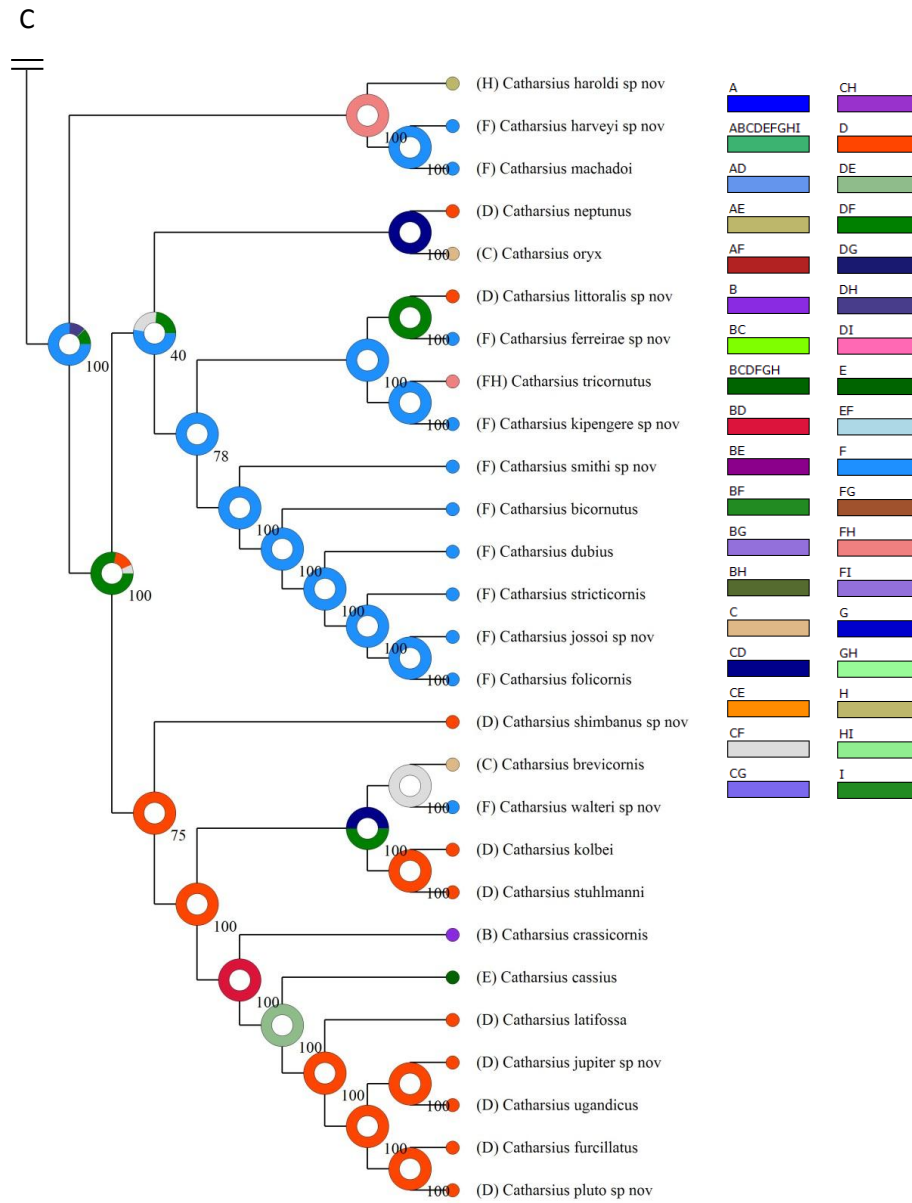
**Figure 8.** A biogeographical ancestral state reconstruction of the genus *Catharsius*. The inferred ancestral distributions (colour key on right) shown in pie chart form, at each node. The probability (p) of ancestral ranges is also shown at each node. The *C. eteocles* and *C. sesostris* groups are figured here. The ancestor of *Catharsius* originated in Region F (Node A). Refer back to Figure 2 for geographical areas.



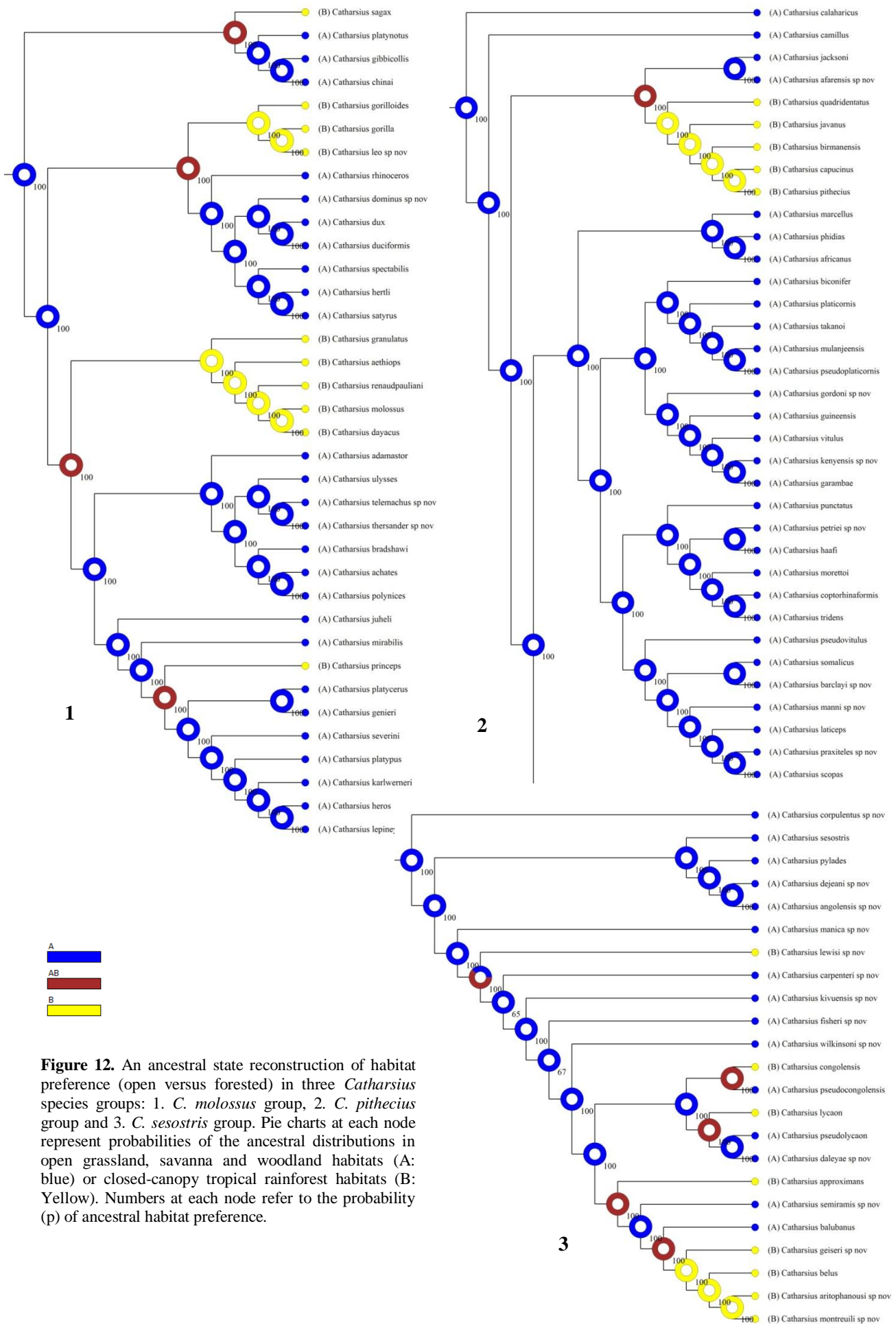
**Figure 9.** A biogeographical ancestral state reconstruction of the genus *Catharsius*. The inferred ancestral distributions (colour key on right) shown in pie chart form, at each node. The probability (p) of ancestral ranges is also shown at each node. The *C. molossus* group is figured here. Refer back to Figure 2 for geographical areas.



**Figure 10.** A biogeographical ancestral state reconstruction of the genus *Catharsius*. The inferred ancestral distributions (colour key on right) shown in pie chart form, at each node. The probability (p) of ancestral ranges is also shown at each node. The *C. pithecius* group is figured here. Refer back to Figure 2 for geographical areas.



**Figure 11.** A biogeographical ancestral state reconstruction of the genus *Catharsius*. The inferred ancestral distributions (colour key on right) shown in pie chart form, at each node. The probability (p) of ancestral ranges is also shown at each node. The *C. tricornutus* group is figured here. Refer back to Figure 2 for geographical areas.



**Figure 12.** An ancestral state reconstruction of habitat preference (open versus forested) in three *Catharsius* species groups: 1. *C. molossus* group, 2. *C. pithecius* group and 3. *C. sesostris* group. Pie charts at each node represent probabilities of the ancestral distributions in open grassland, savanna and woodland habitats (A: blue) or closed-canopy tropical rainforest habitats (B: Yellow). Numbers at each node refer to the probability (p) of ancestral habitat preference.

## Discussion and taxonomic implications

This study presents the first attempt to establish the phylogenetic relationships within the genus *Catharsius* and in so doing, reconstruct a phylogeny for a mega-diverse genus of Scarabaeinae containing nearly 140 species. The genus *Catharsius* has been shown to be paraphyletic with regard to the genus *Copridaspidus* in every analysis which raises questions over the validity of *Copridaspidus*. This will be investigated further in the subsequent chapter. The phylogenetic analysis suggests the genus can be confidently split into five distinct species groups. The strict consensus of the MPT's for each analysis were poorly resolved whilst the resolution of the Majority Rule (50%) consensus trees were better. The low CI as well as the differing topology in all analyses is likely down to the inclusion of conflicting characters as well as unstable taxa in the matrix causing instability. The slightly improved CI score in analysis #2 which excluded characters of the cephalic and pronotal armature suggests that these characters introduce homoplasy. The strict consensus of analysis #3 excluding two taxa was better resolved than the other analyses but this was contrary to the aims of the study which is to reconstruct a phylogeny for all the taxa. The phylogeny was well resolved although a number of polytomies were recovered in each group which is likely owing to the limited codable external characters and the low taxa to character ratio. The generally weak Bremer Supports may also be owing to the low character to taxa ratio with very few synapomorphies supporting each clade.

The highest CI score obtained was in analysis #5 based just on the genitalia characters supporting the results of many of the most recent works dealing with dung beetle phylogenetics that the aedeagus and internal sac sclerites are phylogenetically informative. This was also the case in this study with several characters of the internal sac of the aedeagus, namely the FLP and LC being phylogenetically informative within this genus. Both the monophyly of the genus and all species groups were supported by these sclerites and in some cases were the only unambiguous synapomorphy supporting the group. In order to take a more robust approach to the analysis of the shapes of the sclerites the use of geometric morphometric analyses may be a better way of coding shapes such as the LC. A combined approach using geometric morphometrics as part of a phylogenetic reconstruction has yielded informative results in other dung beetle genera (Roggero et al. 2016; 2017). Further examination of the mouthparts, epipharynx and the wings may provide additional characters but with certain taxa known from only a single holotype specimen and the need for destructive sampling to view these characters, these were not included in this present study.

The results from the biogeographical ancestral state reconstruction suggest that *Catharsius* has an African origin and more specifically the woodlands to the south of the Congo basin. Just under half

of the world's Scarabaeine fauna is found in Africa (Davis et al., 2008) and a number of old world dung beetle genera have a similar distribution to that of *Catharsius*, i.e. with the major lineages in Africa and a limited number of taxa in Asia (e.g. *Heliocopris*, *Onitis*, *Liatongus*, *Digitonthophagus*). The woodlands and grasslands south of the Congo have a rich Scarabaeine fauna (Walter, 1978) and like *Catharsius*, another dung beetle genus, *Diastellopalpus* also has its origins in this region (Josso, MS in prep.). A number of previous studies have suggested that dung beetles originated in the grasslands of Africa (Halfter & Matthews, 1966; Sole & Scholtz, 2010) and this also appears to be the case in *Catharsius*. Just over 15% of *Catharsius* species are forest specialists, the majority of these being Asian taxa. Only a very small proportion of dung beetle species have colonised tropical forest habitats in Africa, a pattern that is contrary to that of dung beetle distribution in other tropical regions (Cambefort & Walter, 1991). None of the forest specialist *Catharsius* species have necrophagic feeding habits unlike the large-bodied South American forest species such as *Coprophanæus* and *Deltochilum* which are predominantly or exclusively necrophagic (Gill, 1991; Edmonds & Zidek, 2009).

In chapter 3, a phylogeny of a smaller subset of species using molecular data is reconstructed. The level of congruence in the topology of the trees between the morphological and molecular analyses as well as the species groupings and taxonomic implications will be discussed.



## Chapter 3: Molecular Phylogenetic Analyses

### Introduction

There have been a number of studies that have utilised molecular data to resolve taxonomic issues at the genus level in the family Scarabaeidae. A recent phylogeny of the charismatic rhinoceros beetle genus *Dynastes* (subfamily Scarabaeinae) revealed that many of the taxa synonymised as island forms were in fact good species (Huang, 2017). A study of the chafer genus *Dicronocephalus* (subfamily Cetoniinae) on the other hand revealed that too many taxa, based on variable secondary characteristics such as colour, had been described and a number of new synonymies were proposed (Lee et al., 2015).

Only a handful of molecular phylogenies of Scarabaeine dung beetle genera exist, targeting between two and four gene regions (Mlambo et al., 2011; Sebastian et al., 2014; Roggero et al., 2017; Maldaner et al., 2018). All of the genera dealt with in these works contain only a small number of species and in spite of this, complete taxon sampling was not possible owing most likely to the unavailability of fresh material for sequencing. DNA extraction and sequencing of older, pinned scarab beetles has been shown to be problematic (Verdugo & Drumont, 2015) and in order to obtain fresh *Catharsius* specimens for this study, fieldwork was undertaken in Zambia and Sierra Leone.

In this chapter, molecular data are used to reconstruct a phylogeny of a small subset of the genus *Catharsius* to test the relationships recovered in the morphological phylogeny in the previous chapter.

Previous molecular phylogenetic analyses involving the genus *Catharsius*

Two molecular phylogenies of the subfamily Scarabaeinae have included the genus *Catharsius* as part of a broader study into the tribal and generic relationships within the subfamily. In both phylogenies, the results were identical. The earliest work was that of Monaghan et al. (2007) targeting one nuclear (28SD3) and two mitochondrial (COI and 16S) gene regions of worldwide dung beetles where *Catharsius* (4 species sampled) was recovered as sister to *Metacatharsius* (2 species sampled). The most recent and comprehensive work to date by Tarasov and Dimitrov (2016) targeted eight gene regions where *Catharsius* was again recovered as sister to *Metacatharsius* in a strongly-supported clade. Mlambo et al. (2015) also included *Catharsius* in their phylogeny of Afrotropical dung beetle genera but on searching the GenBank accession numbers given in their publication, all of the taxa identified as *Catharsius* in the phylogeny have since been re-identified as *Coprins* species and therefore no *Catharsius* sequences were actually included in their analyses. The results from the

morphological phylogeny in chapter 2 suggest that *Catharsius* is paraphyletic with regard *Copridaspidus* and the latter genus is here sequenced for the first time.

## Materials and methods

### Taxon sampling

Previous sequencing efforts of Afrotropical *Catharsius* is limited to the work of Monaghan et al. (2007) who provided cytochrome oxidase subunit I (COI), 16S rRNA and 28S domain 3 rRNA sequences for three Afrotropical species and one Asian species (Table 1). A total of 44 ingroup taxa were sent away for extraction and sequencing together with the same three outgroup taxa used in the morphological phylogeny (*Copris*, *Copridaspidus* and *Metacatharsius*). However this current study has added only four COI, five 16S and ten 28SD3 sequences of Afrotropical *Catharsius*. The genus *Copridaspidus* was here successfully sequenced for the first time (Table 2). All specimens used in this study were preserved in 95-100% ethanol and the most recently collected individuals were selected. Voucher specimens were pinned and dried, labelled with voucher designation and stored in the collections of the Natural History Museum, London (BMNH) and Oxford University Museum of Natural History, Oxford (OUMNH). The voucher specimens from the Monaghan et al. study could not be located in the BMNH and although the nomenclature for two of the taxa is now different, the identifications of these species are likely to be correct.

### DNA extraction, amplification and sequencing

Leg samples from each specimen were sent to a commercial laboratory for DNA extraction, amplification and sequencing. The samples were extracted using a hybrid CTAB/Qiagen protocol to remove as many potential PCR inhibitors as possible. The femurs were removed from the samples provided, bisected with a clean scalpel blade, and digested for a minimum of 3 days before processing. For the PCRs, an initial pass was made using 16S primers and a Promega GoTaq PCR mix, then a subset of samples used to optimise the PCRs, looking at various combinations of commercial chemistry (Promega GoTaq / Bioline BioTaq / Qiagen Taq DNA Polymerase), annealing temperature and MgCl<sub>2</sub> concentration, in an attempt to find the best variant for each primer set. Partial gene sequences were amplified following Monaghan et al. (2007) using primers “Pat” and “Jerry” for COI (Simon et al., 1994), 16Sar/16Sbr for 16S (Simon et al., 1994) and D3a/D3b for 28Sd3 (Nunn et al., 1996). Any successful amplifications were sequenced and analysed using the Sequencher program, with any readable results put through a BLAST search to check their identity against GenBank. All of the samples went through at least one round of PCR for each of the primer sets, with some additionally tested using alternate primer variations.

Species	Voucher	COI	16S	28SD3	Country
<i>Copris amyntor</i> Klug, 1855	BMNH679777	AY131858	AY131491	AY131683	South Africa
<i>Catharsius calaharicus</i> Kolbe, 1893	BMNH679771	AY131852	AY131485	AY131677	South Africa
<i>Catharsius molossus</i> (Linnaeus, 1758)	BMNH679772	AY131853	AY131486	AY131678	Indonesia
<i>Catharsius pylades</i> Péringuey, 1901	BMNH679774	AY131855	AY131488	AY131680	South Africa
<i>Catharsius vitulus</i> Boheman, 1857	BMNH 679773	AY131854	AY131487	AY131679	South Africa

**Table 1.** Partial gene sequences of all known African species of *Catharsius* used in this study together with one Asian taxon and an outgroup taxon together with their voucher numbers, GenBank accession numbers and country of origin. All sequences in this table refer to the work of Monaghan et al. 2007. *Catharsius pylades* is accessioned in GenBank as *C. sesostris* and *C. vitulus* as *C. philus*.

Species	Voucher	Country	Coll. date	Coll. technique	COI	16S	28S
<b><i>Copridaspis peregrinus</i> (Harold, 1878)</b>	BMHT003	Zambia	Dec 2017	General collection	X	X	X
<b><i>Metacatharsius troglodytes</i> (Boheman, 1857)</b>	BMHT004	Mozambique	Jan 2018	Dung pitfall trap	X	X	X
<b><i>Catharsius heros</i> Boheman, 1860</b>	BMHT005	Mozambique	Nov 2017	At light			X
<i>Catharsius obtusicornis</i> Boheman, 1857	BMHT006	Zambia	Dec 2013	General collection			
<i>Catharsius achates</i> (Olivier, 1789)	BMHT007	Senegal	Jul 2009	Dung pitfall trap			
<i>Catharsius bradshawi</i> Lansberge, 1887	BMHT008	Zambia	Nov 2013	Dung pitfall trap			
<i>Catharsius gibbicollis</i> Gerstaecker, 1884	BMHT009	Tanzania	Apr 2012	At light			
<i>Catharsius gorilla</i> (Thomson, 1858)	BMHT010	Gabon	Jun 2016	Dung pitfall trap			
<b><i>Catharsius leo</i> sp. nov.</b>	BMHT011	Ivory Coast	May 2017	At light	X		X
<i>Catharsius rhinoceros</i> (Klug, 1855)	BMHT012	Tanzania	Dec 2012	General collection			
<i>Catharsius juheli</i> Josso, 2011	BMHT013	Zambia	May 2015	Dung pitfall trap			
<i>Catharsius dux</i> Harold, 1878	BMHT014	Zambia	Nov 2013	Dung pitfall trap			
<i>Catharsius duciformis</i> Ferreira, 1959	BMHT015	Zambia	Nov 2016	Dung pitfall trap			
<i>Catharsius satyrus</i> Kolbe, 1893	BMHT016	Zambia	Dec 2013	Dung pitfall trap			
<b><i>Catharsius takanoi</i> Josso 2018</b>	BMHT017	Zambia	Nov 2016	At light			X
<i>Catharsius biconifer</i> Felsche, 1907	BMHT018	Zambia	May 2015	Dung pitfall trap			
<i>Catharsius laticeps</i> Boheman, 1857	BMHT019	Zambia	Dec 2016	Dung pitfall trap			
<i>Catharsius phidias</i> (Olivier, 1789)	BMHT020	Senegal	Jul 2009	Dung pitfall trap			
<b><i>Catharsius stricticornis</i> Josso 2018</b>	BMHT021	Zambia	Jan 2017	Dung pitfall trap		X	X
<b><i>Catharsius smithi</i> sp. nov.</b>	BMHT022	Zambia	Dec 2017	At light	X	X	X
<i>Catharsius crassicornis</i> Gillet, 1911	BMHT023	Ivory Coast	Jul 2015	Dung pitfall trap			
<i>Catharsius dubius</i> Péringuey, 1901	BMHT024	Zambia	Apr 2014	Dung pitfall trap			
<b><i>Catharsius tricorutus</i> (De Geer, 1778)</b>	BMHT025	Mozambique	Jun 2017	At light		X	X
<i>Catharsius haroldi</i> sp. nov.	BMHT026	Mozambique	Dec 2016	Dung pitfall trap			
<i>Catharsius harveyi</i> sp. nov.	BMHT027	Zambia	Nov 2013	At light			
<i>Catharsius machadoi</i> Ferreira, 1960	BMHT028	Zambia	Dec 2014	At light			
<i>Catharsius geiseri</i> sp. nov.	BMHT029	Ivory Coast	Dec 2017	Dung pitfall trap			
<i>Catharsius pseudolycaon</i> Ferreira, 1960	BMHT030	Ivory Coast	Jul 2015	Dung pitfall trap			
<i>Catharsius aristophanousi</i> sp. nov.	BMHT031	Ivory Coast	Apr 2017	Dung pitfall trap			
<i>Catharsius pylades</i> Péringuey, 1901	BMHT032	Zambia	Oct 2012	At light			
<i>Catharsius corpulentus</i> sp. nov.	BMHT033	Zambia	Dec 2013	General collection			
<i>Catharsius fisheri</i> sp. nov.	BMHT034	Zambia	Oct 2013	Dung pitfall trap			
<b><i>Catharsius balubanus</i> Kolbe, 1893</b>	BMHT035	Zambia	Nov 2017	Dung pitfall trap	X	X	X
<i>Catharsius lewisi</i> sp. nov.	BMHT036	Sierra Leone	June 2016	Dung pitfall trap			
<b><i>Catharsius lycaon</i> Kolbe, 1893</b>	BMHT037	Cameroon	Mar 2018	Dung pitfall trap			X
<i>Catharsius upembanus</i> Ferreira, 1962	BMHT038	Zambia	Dec 2013	Dung pitfall trap			
<i>Catharsius brutus</i> Harold, 1880	BMHT039	Kenya	Oct 2012	General collection			
<b><i>Catharsius pandion</i> Harold, 1870</b>	BMHT040	Mozambique	Dec 2017	General collection	X		X
<i>Catharsius luluensis</i> Ferreira, 1960	BMHT041	Zambia	Nov 2013	Dung pitfall trap			
<b><i>Catharsius eteocles</i> (Castelnau, 1840)</b>	BMHT042	Ivory Coast	Jun 2016	General collection			X
<i>Catharsius aegeus</i> Génier, 2017	BMHT043	Zambia	Oct 2013	At light			
<i>Catharsius pallas</i> Génier, 2017	BMHT044	Zambia	Oct 2013	Dung pitfall trap			
<i>Catharsius orami</i> sp. nov.	BMHT045	Zambia	Oct 2013	General collection			
<i>Catharsius renaudpauliani</i> Ochi & Kon, 1996	OUHT001	Borneo	Oct 2013	Dung pitfall trap			
<i>Catharsius dayacus</i> Lansberge, 1886	OUHT002	Borneo	Mar 2011	Dung pitfall trap			
<i>Catharsius birmanensis</i> Lansberge, 1874	OUHT003	Thailand	Oct 1999	General collection			

**Table 2.** The two outgroup and 44 ingroup taxa sampled in this study, together with voucher numbers, country of origin, date of collection and collection technique. Taxa where DNA was successfully extracted and sequenced are highlighted in blue.

## Phylogenetic analyses

The verified sequences were aligned using MUSCLE in MEGA version X (Kumar et al., 2018) and genetic distances were calculated using Kimura's two-parameter model (Kimura, 1980). Phylogenetic tree searches were performed using Bayesian Inference (BI), Maximum Likelihood (ML) and Parsimony analysis (PA). Due to the incomplete species sampling for the three gene regions, four different datasets were analysed:

1. COI sequences only (~820bp) representing 7 African and 1 Asian *Catharsius* and three outgroup taxa.
2. 16S sequences only (~450bp) representing 7 African and 1 Asian *Catharsius* and three outgroup taxa.
3. 28SD3 sequences only (~660bp) from 13 African and 1 Asian *Catharsius* and three outgroup taxa.
4. concatenated COI, 16S and 28SD3 sequences (~1930bp) representing 5 African and 1 Asian *Catharsius* and three outgroup taxa.

BI analyses were performed using MrBayes version 3.2.5 (Ronquist et al., 2012). Metropolis-coupled Markov chain Monte Carlo (MCMC) analyses were run with four chains (one cold and three heated) for 5,000,000 generations sampling every 100 generations, discarding the first 25% as burn-in. The two runs converged with the standard deviation of split frequencies below 0.01. ML analyses were performed using MEGA version X, the model parameters independently optimized for each dataset using the Bayesian Information Criterion (Dataset 1: LG+G+I; Dataset 2: T92+G; Dataset 3: JC+G+I; Dataset 4: GTR+G+I). Initial trees for the heuristic search were obtained by applying Neighbor-Join and BioNJ algorithms. PA analyses were performed using TNT version 1.1 (Goloboff et al., 2003) using the "traditional search" options to find the most parsimonious trees (MPT) under the following parameters: memory set to hold 10000 trees, 1000 tree bisection-reconnection (TBR) replicates, saving 1000 trees per replicate, zero-length branches collapsed. Support for clades was evaluated for BI using posterior probabilities, ML using non-parametric bootstrapping with 1000 replicates and PA using Bremer supports searching for suboptimal trees up to 10 steps longer than the shortest one using TBR swapping on the shortest branches. Pairwise genetic distances were calculated for each of the gene regions. Trees were visualised in Figtree version 1.4.3 (Rambaut, 2012).

## Results

### Analysis 1: COI only

The dataset consisted of 257 variable sites of which 164 were parsimony informative. The phylogenetic inferences based on BI, ML and PA recovered similar topologies (Fig. 1 for ML tree). The PA analysis retained 1 tree (length: 553; Consistency Index (CI): 0.602; Retention Index (RI):

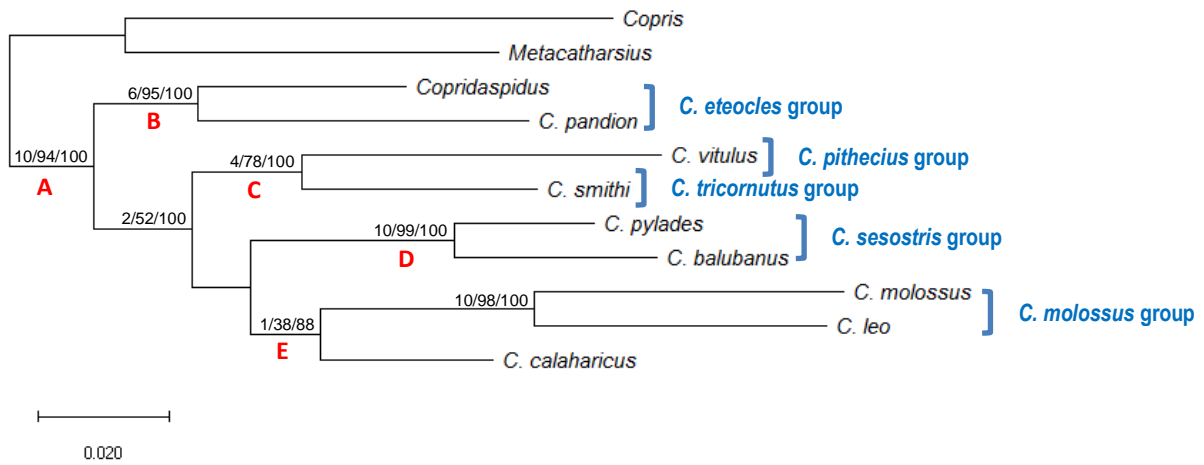
0.404). *Catharsius* is recovered as paraphyletic with regard the putative outgroup *Copridaspidus* (Clade A) with strong Bremer, bootstrap and posterior probability values (10/94/100). This monophyletic group consisted of four clades, *Copridaspidus* + *C. pandion* (Clade B) recovered basally to *C. vitulus* + *C. smithi* (Clade C), *C. pylades* + *C. balubanus* (Clade D) and *C. calaharicus* + *C. molossus* + *C. leo* (Clade E). All of the groups were recovered with strong posterior probability (>88). The interspecific divergences of taxa within Clade A were variable ranging from 8.6%–12.9%. The distances between the Clade A taxa and the two outgroup taxa ranged from 11.4%–16.1% (Table 3).

#### Analysis 2: 16S only

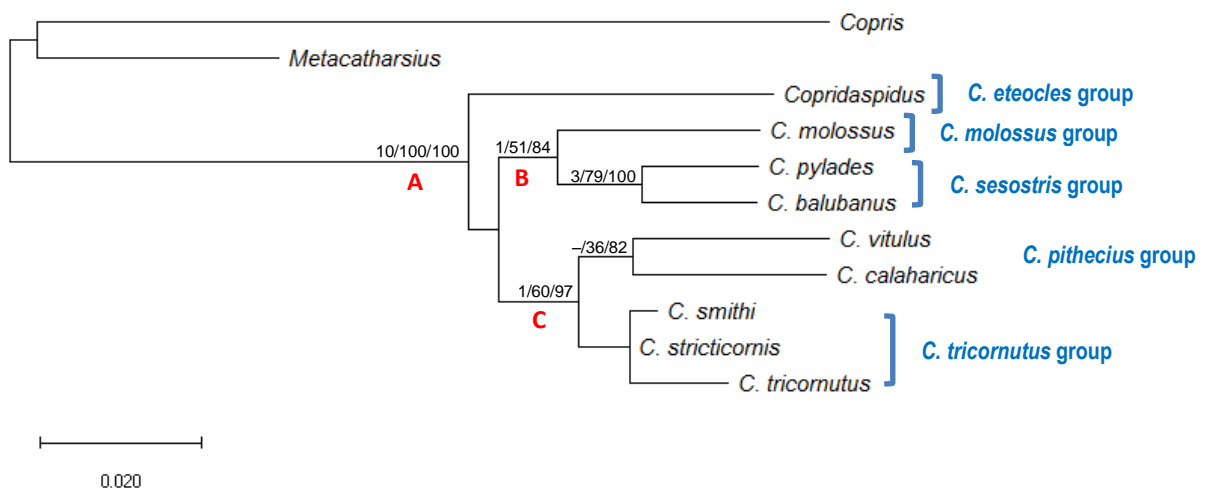
The dataset consisted of 102 variable sites of which 53 were parsimony informative. The phylogenetic inferences based on BI, ML and PA recovered similar topologies (Fig. 2 for ML tree). The PA analysis retained 3 trees (length: 156; CI: 0.782; RI: 0.605). *Copridaspidus* is recovered as sister to *Catharsius* (Clade A) with strong Bremer, bootstrap and posterior probability values (10/100/100). *Copridaspidus* is recovered basally to two clades, Clade B consisting of *C. molossus* and *C. pylades* + *C. balubanus* and Clade C consisting of *C. vitulus* + *C. calaharicus* and *C. smithi* + *C. stricticornis* + *C. tricornutus*. Both Clade B and C have strong posterior probability values (84 and 97 respectively) as well as moderately strong bootstrap values (51 and 60). The interspecific divergences of taxa within Clade A ranged from 0.2%–7.4%. The distances between the Clade A taxa and the two outgroup taxa ranged from 10.3%–18.5% (Table 4).

#### Analysis 3: 28SD3 only

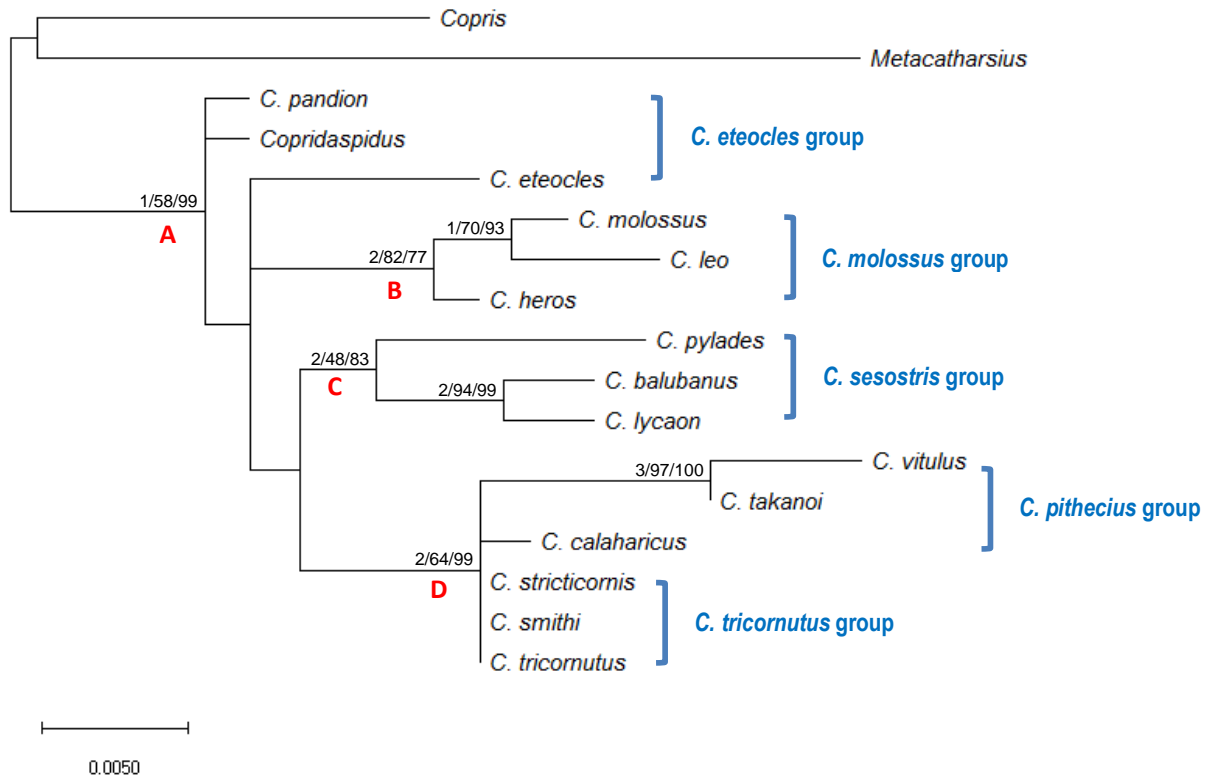
The dataset consisted of 46 variable sites of which 22 were parsimony informative. The phylogenetic inferences based on BI, ML and PA recovered similar topologies (Fig. 3 for ML tree). The PA analysis retained 1 tree (length: 76; CI: 0.750; RI: 0.694). *Catharsius* is recovered as paraphyletic with regard the outgroup *Copridaspidus* (Clade A) with strong posterior probability values (99). The polytomy of *Copridaspidus* + *C. pandion* and *C. eteocles* are recovered basally, to three well supported clades, Clade B consisting of *C. heros* and *C. molossus* + *C. leo* (1/70/90), Clade C of *C. pylades* and *C. balubanus* + *C. lycaon* (2/48/83) and Clade D of *C. vitulus* + *C. takanoi* and a polytomy of *C. calaharicus*, *C. stricticornis*, *C. smithi* and *C. tricornutus* (2/64/99). The interspecific divergences of taxa within Clade A ranged from 0%–2.6%. The distances between the Clade A taxa and the two outgroup taxa ranged from 2.0%–4.9% (Table 5).



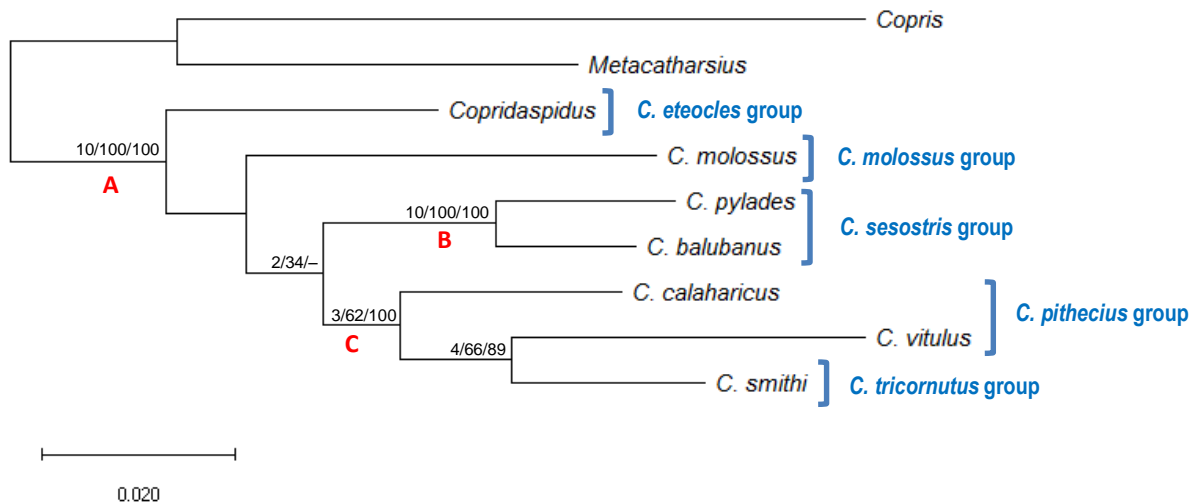
**Figure 1.** Maximum Likelihood tree of *Catharsius* based on dataset 1: COI sequences only. Numbers above branches indicate Bremer support, bootstrap values and posterior probabilities. Putative species groups as recovered in the morphological phylogeny are highlighted in blue.



**Figure 2.** Maximum Likelihood tree of *Catharsius* based on dataset 2: 16S sequences only. Numbers above branches indicate Bremer support, bootstrap values and posterior probabilities. Putative species groups as recovered in the morphological phylogeny are highlighted in blue.



**Figure 3.** Maximum Likelihood tree of *Catharsius* based on dataset 3: 28SD3 sequences only. Numbers above branches indicate Bremer support, bootstrap values and posterior probabilities. Putative species groups as recovered in the morphological phylogeny are highlighted in blue.



**Figure 4.** Maximum Likelihood tree of *Catharsius* based on dataset 4: concatenated COI, 16S and 28SD3 sequences. Numbers above branches indicate Bremer support, bootstrap values and posterior probabilities. Putative species groups as recovered in the morphological phylogeny are highlighted in blue.

	<i>Copris</i>	<i>Metacatharsius</i>	<i>Copridaspidus</i>	<i>C. pandion</i>	<i>C. vitulus</i>	<i>C. smithi</i>	<i>C. pylades</i>	<i>C. balubanus</i>	<i>C. molossus</i>	<i>C. leo</i>	<i>C. calaharicus</i>
<i>Copris</i>											
<i>Metacatharsius</i>	0.133										
<i>Copridaspidus</i>	0.145	0.116									
<i>C. pandion</i>	0.151	0.134	0.086								
<i>C. vitulus</i>	0.149	0.135	0.109	0.125							
<i>C. smithi</i>	0.134	0.134	0.106	0.118	0.092						
<i>C. pylades</i>	0.138	0.138	0.104	0.118	0.118	0.097					
<i>C. balubanus</i>	0.153	0.142	0.107	0.123	0.122	0.110	0.055				
<i>C. molossus</i>	0.161	0.132	0.115	0.129	0.118	0.117	0.122	0.130			
<i>C. leo</i>	0.156	0.138	0.124	0.123	0.120	0.121	0.114	0.127	0.094		
<i>C. calaharicus</i>	0.144	0.114	0.086	0.112	0.099	0.088	0.093	0.093	0.104	0.094	

**Table 3.** Pairwise distances of COI between the *Catharsius* species and outgroup taxa.

	<i>Copris</i>	<i>Metacatharsius</i>	<i>Copridaspidus</i>	<i>C. molossus</i>	<i>C. pylades</i>	<i>C. balubanus</i>	<i>C. vitulus</i>	<i>C. calaharicus</i>	<i>C. smithi</i>	<i>C. striticornis</i>	<i>C. tricornutus</i>
<i>Copris</i>											
<i>Metacatharsius</i>	0.128										
<i>Copridaspidus</i>	0.185	0.119									
<i>C. molossus</i>	0.168	0.120	0.060								
<i>C. pylades</i>	0.179	0.119	0.069	0.045							
<i>C. balubanus</i>	0.179	0.116	0.054	0.045	0.028						
<i>C. vitulus</i>	0.159	0.116	0.074	0.057	0.061	0.067					
<i>C. calaharicus</i>	0.173	0.108	0.067	0.060	0.056	0.059	0.047				
<i>C. smithi</i>	0.159	0.106	0.057	0.040	0.047	0.047	0.037	0.035			
<i>C. striticornis</i>	0.156	0.103	0.054	0.038	0.045	0.045	0.035	0.033	0.002		
<i>C. tricornutus</i>	0.164	0.114	0.064	0.040	0.047	0.057	0.042	0.038	0.014	0.012	

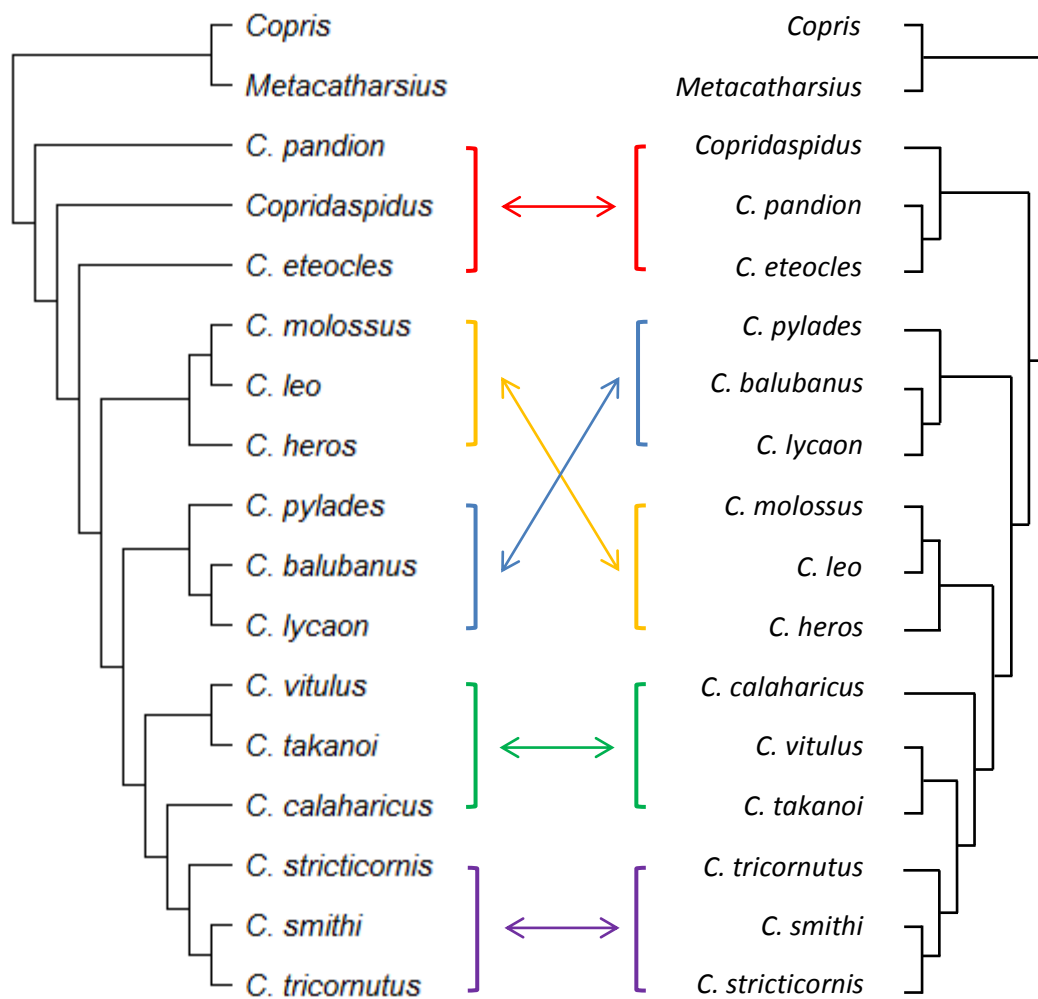
**Table 4.** Pairwise distances of 16S between the *Catharsius* species and outgroup taxa.

	<i>Copris</i>	<i>Metacatharsius</i>	<i>C. pandion</i>	<i>Copridaspidus</i>	<i>C. eteocles</i>	<i>C. molossus</i>	<i>C. leo</i>	<i>C. heros</i>	<i>C. pylades</i>	<i>C. balubanus</i>	<i>C. lycaon</i>	<i>C. vitulus</i>	<i>C. takanoi</i>	<i>C. calaharicus</i>	<i>C. striticornis</i>	<i>C. smithi</i>	<i>C. tricornutus</i>
<i>Copris</i>																	
<i>Metacatharsius</i>	0.040																
<i>C. pandion</i>	0.022	0.037															
<i>Copridaspidus</i>	0.020	0.035	0.003														
<i>C. eteocles</i>	0.027	0.035	0.011	0.011													
<i>C. molossus</i>	0.028	0.042	0.013	0.015	0.021												
<i>C. leo</i>	0.030	0.040	0.017	0.014	0.022	0.006											
<i>C. heros</i>	0.025	0.035	0.011	0.011	0.016	0.006	0.009										
<i>C. pylades</i>	0.029	0.041	0.015	0.015	0.020	0.017	0.018	0.018									
<i>C. balubanus</i>	0.025	0.040	0.014	0.013	0.019	0.015	0.021	0.016	0.015								
<i>C. lycaon</i>	0.025	0.040	0.013	0.011	0.019	0.015	0.019	0.017	0.013	0.006							
<i>C. vitulus</i>	0.035	0.049	0.017	0.019	0.022	0.019	0.024	0.019	0.022	0.026	0.026						
<i>C. takanoi</i>	0.028	0.043	0.017	0.016	0.020	0.017	0.020	0.016	0.020	0.022	0.024	0.005					
<i>C. calaharicus</i>	0.023	0.041	0.012	0.012	0.017	0.017	0.018	0.015	0.013	0.015	0.015	0.012	0.010				
<i>C. striticornis</i>	0.024	0.038	0.011	0.009	0.014	0.017	0.017	0.013	0.015	0.014	0.016	0.010	0.008	0.002			
<i>C. smithi</i>	0.024	0.038	0.011	0.009	0.014	0.017	0.017	0.013	0.015	0.014	0.016	0.010	0.008	0.002	0.000		
<i>C. tricornutus</i>	0.024	0.038	0.011	0.009	0.014	0.017	0.017	0.013	0.015	0.014	0.016	0.010	0.008	0.002	0.000	0.000	

**Table 5.** Pairwise distances of 28S between the *Catharsius* species and outgroup taxa.

#### Analysis 4: concatenated COI, 16S and 28S

The phylogenetic inferences based on BI, ML and PA recovered similar topologies (Fig. 4 for ML tree). The PA analysis retained 2 trees (length: 679; CI: 0.691; RI: 0.413). *Copridaspidus* is recovered as sister to *Catharsius* (Clade A) with strong Bremer, bootstrap and posterior probability values (10/100/100). Within Clade A, two well supported clades are recovered; bootstrap and Clade B consisting of *C. pylades* + *C. balubanus* (10/100/100) and Clade C consisting of *C. calaharicus* and *C. vitulus* + *C. smithi* (3/62/100).



**Figure 5.** Maximum Likelihood tree of *Catharsius* based on dataset 3: 28SD3 sequences only (left) compared to a tree of the same taxa as recovered in the phylogeny reconstructed from morphological characters (right). The different coloured brackets denote the five putative species groups: *C. eteocles* group (red), *C. sesostris* group (blue), *C. molossus* group (yellow), *C. pithecius* group (green) and *C. tricornutus* group (purple).

#### Discussion

The genus *Catharsius* was recovered as paraphyletic with regard *Copridaspidus* in two analyses (Analyses 1 and 3), where *Copridaspidus* was recovered within the *C. eteocles* group. In the other two

analyses (Analyses 2 and 4), *Copridaspidus* was recovered as sister to the other *Catharsius* species. However, in these two analyses, no other *C. eteocles* group species were sampled. The results of these analyses provides support for the synonymy of *Copridaspidus* with *Catharsius* as suggested in Chapter 2. Although the flattened habitus of *Copridaspidus* species is unique, it shares all of the generic characters of *Catharsius*. The resulting topology of analyses 2, 3 and 4 were similar but differed from analysis 1. In every analyses, the *C. eteocles* group was always recovered as the most basal group and the *C. pithecius* and *C. tricornutus* groups were always recovered as sister groups. The placement of *C. calaharicus* differed in analysis 1, where it was recovered basally to the *C. molossus* group whilst in all the other analyses, *C. calaharicus* was recovered with the *C. pithecius* and *C. tricornutus* groups. The incongruence between the analyses may be owing to the natural variation found in genes, the incomplete lineage sorting or the taxon poor taxon sampling. Different gene regions give differing topologies due in part to factors such as the stochastic nature of gene mutation as well as computational phylogenetic reconstruction artefacts (Jeoffroy et al., 2006; Rokas & Carroll, 2006). The impact of taxon sampling in phylogenetic inference has been well-documented (Pollock et al., 2002; Heath et al., 2008; Havird & Miyamoto, 2010), with even the topology of large phylogenies being affected by the inclusion of additional taxa (Torres-Pérez et al., 2017; Cox et al., 2018).

#### Congruence with morphological phylogeny and re-examination of characters

The overall impression is that there is considerable congruence between the morphological and molecular trees and far more than would be expected by chance (Figure 5). The *C. molossus*, *C. pithecius*, *C. tricornutus* and *C. sesostris* group species as delimited in the morphological phylogeny were all recovered as monophyletic clades whilst the *C. eteocles* group was recovered as monophyletic in the COI analyses but a polytomy in the 28S analyses. The *C. eteocles* group was recovered as the most basal in both studies. The *C. pithecius* and *C. tricornutus* groups were always recovered as sister groups and these two groups were supported by a single unambiguous synapomorphy in the morphological analyses (the FLP fused along its entire length). The majority of the taxa in these two groups have raspulae present in the internal sac of the aedeagus. Only the topology within the *C. molossus* and *C. sesostris* groups were congruent between the two studies. The placement of *C. calaharicus* was problematic in the morphological phylogeny and this was also the case in the molecular phylogeny. Although this taxon has a number of autapomorphic traits including the lateral depressions of the pronotal disc and the shape of the LC, the shape of the FLP is almost identical to that of the *C. tricornutus* and *C. pithecius* groups.

The ancestral state reconstruction of the genus based on the morphological tree suggested an African origin to the genus with the Asian species recovered in two groups, the *C. molossus* and *C. pithecius*

groups. This theory is supported by the molecular phylogenetic analyses with the solely African *C. eteocles* group species being recovered as the most basal group. However, a wider sampling of taxa would be required to critically test this hypothesis.

#### Specimen storage and DNA degradation

The samples sent for DNA extraction and sequencing yielded very poor results. Out of the 44 ingroup taxa, only 10 were successfully sequenced for at least one gene region and only two taxa were successfully sequenced for the three target genes regions (Table 2). With the exception of *C. birmanensis*, all of the specimens were recently collected (<10 years), stored in 95-100% ethanol and at -20°C. Standard dung beetle trapping protocol involves a ball of dung suspended over a receptacle sunk into the ground with a solution of water and soap (Krell, 2007). The dung beetles are then collected after a given exposure period, sieved from the solution and stored in ethanol. Not unsurprisingly, well over half of the taxa used in this study were caught using this method. This form of sampling is effective for ecological assessments but DNA degradation is inevitable as the beetles are left suspended in the solution at an ambient tropical African temperature for at least 12 hours. Other samples used in this study were collected from under dung pats or at light and these specimens were preferred as they would have been killed directly in ethanol. A recent work on a small bodied scarab genus *Calicnemis* Laporte, 1832 successfully sequenced partial COI sequences from 10-year old specimens (Verdugo & Drumont, 2015) whereas the taxa successfully sequenced for at least one gene region in this current study were all collected within the last two years.

There may be several explanations for the poor results. Firstly, these large beetles probably fix very poorly in ethanol with the ethanol unable to penetrate the exoskeleton. Secondly, the mammalian dung in the gut will start to decompose and adult beetles are often clearly distended when emptying the pitfall traps (personal observation). The purity and concentration of the ethanol available to the fieldworker is likely to vary from country to country especially with restrictions in place on transporting this flammable liquid by air. It has been suggested that crytopreservation by immersion of beetles in liquid nitrogen is the best method for long term storage of DNA (Reiss et al., 1995) but this would involve specialised equipment to be taken into the field, which in most cases would not be possible.

It may be pertinent that unless samples are to be sequenced immediately after capture, target taxa are isolated and clearly labelled in the field, legs are removed and crushed and stored directly in Eppendorf tubes with 100% ethanol. The specimens can then be broken in half at the joint of the pronotum and elytra and stored separately allowing the ethanol to penetrate the abdomen and gut as well as the pronotum and head. Tropical fieldwork conditions are not always conducive to storing

specimens at cool temperatures, but by isolating target taxa in this manner, it may be possible to slow down the degradation process of the DNA allowing the samples to be sequenced at a later stage.

#### Taxonomic implications

The genus *Copridaspidus* was recovered within the ingroup taxa in both the morphological and molecular phylogenetic analyses. A monotypic genus, *Copridaspidus* was described by Boucomont (1920) to include one new species, *C. favareli* Boucomont which is currently a junior synonym of *C. peregrinus* (Harold), a taxon that was originally described in the genus *Catharsius*. Boucomont gives the presence of the scutellum as the key distinguishing feature. Janssens (1949) discusses the presence of a scutellum in other species of *Catharsius* but goes on to state that due to its peculiar external morphology of this species with a flattened body that *Copridaspidus* merited generic status. The presence of the scutellum is in fact a synapomorphic character for all taxa in the *C. eteocles* group and aside from sharing all of the key generic characters, the internal sac sclerites are identical in shape and arrangement to members of this group. For these reasons, the following synonymy is here established:

***Catharsius* Hope, 1835 = *Copridaspidus* Boucomont 1920 (new synonymy)**

The alternative would be to split the genus into several genera based on the species groups recovered, but this level of splitting, considering the similar morphology of the internal sclerites of the endophallus, seems unnecessary.

In conclusion, the results from both the morphological and molecular analyses support the splitting of the genus *Catharsius* into species groups and the monophyly of *Catharsius* sensu novo was well supported. The five species groups as recovered in these analyses will form the backbone to the taxonomic revision of the Afrotropical members of this genus.



## Chapter 4: Literature review, taxonomy and natural history of *Catharsius*

Previous taxonomic treatments of the genus *Catharsius* Hope, 1837

Many of the earliest lamellicorn Coleoptera were described in the genus *Scarabaeus* Linnaeus, 1758 and despite the description of a number of dung beetle genera soon after (Geoffroy, 1762; Latreille, 1802; MacLeay, 1819), it was not until Rev. Frederick Hope's 1837 *Coleopterist's Manual* that the first major systematic work on this group of beetles was published consolidating all of the early names.

In his detailed work, Hope (1837) erected a new genus *Catharsius* to include the "*Copridae which are allied to Copris molossus*" (Hope, 1837: 20). The genus name derives from the Greek term *Catharsius* (καθαρσιος), meaning purifier, to acknowledge "*the benefit derived from these scavengers of warm and tropical regions*". Included in this genus were six species of which only three are still standing today (*Catharsius molossus* (Linnaeus), *Catharsius achates* (Olivier) and *Catharsius sagax* (Schönherr)). Hope (1837: 21) lists only a set of simple characters which he "*deems sufficient, as the type is well known*": a horned, intact or subemarginate clypeus, a dentate, retuse, punctured thorax, large smooth lateral foveae and minutely rugose elytra ("*Clypeus integer, seu subemarginatus, cornutus, thorace retuso dentato punctatissimo, fovea laterali magna laevi nec punctata, elytris que minutissime rugulosis*").

Gemminger and Harold (1869) list all of the known species in their *Catalogus Coleopterorum*. Of the 23 species listed, 19 species belong in the genus today with the remaining species having since been transferred into *Metacatharsius* Paulian, 1939. The first review of this genus was undertaken by Hermann Kolbe in 1893, over fifty years after Hope's original description. Kolbe discusses the morphology of this genus commenting on their strong sexual dimorphism as well as the great size differences between the smallest and largest species ("*Catharsius enthält kleine und grosse Formen, unter diesen solche, bei denen der Sexualdimorphismus ganz bedeutend entwickelt ist*"; Kolbe, 1893: 132), adding that the smallest and least sexually differentiated types of *Catharsius* are now confined to Africa ("*Die kleinsten und sexuell am wenigsten differenzierten Arten von Catharsius sind nun auf Afrika beschränkt*"). Here he is no doubt referring to *Metacatharsius* species. Kolbe goes on to describe 15 new species and states that 55 species of *Catharsius* are known from the African continent with "*12 or 13*" in Asia (Kolbe, 1893: 133).

Within his 1901 *Descriptive Catalogue of the Coleoptera of South Africa*, Louis Péringuey reviewed the Southern African dung beetle fauna and provides the first key for the tribe Coprini. Similar to

Kolbe, Péringuey (1901: 324) splits the genus *Catharsius* into “two divisions”, the first containing 13 species “the anterior tibiae of which are obliquely truncate inwardly, with a non-spinose inner angle” and the second comprising 5 species “in which this inner angle is produced in the male into a very distinct acute tooth or sharply curved spine”. He observes that “among the species included in the second division are two, *C. anderssoni* and *C. opacus*, in which the apical spur is curved inwardly at tip almost at right angles”. The two species he mentions now belong in the genus *Metacatharsius*.

*Metacatharsius* was originally established as a subgenus of *Catharsius* by Renaud Paulian, who quotes this “perfectly exact” (1939: 13) observation of Péringuey’s in his description of the genus. The name *Metacatharsius* had been a manuscript name of Joseph Gillet’s but he had died in 1937 before this manuscript was published (Horn et al., 1990). Paulian lists the following characters as characterising the subgenus: the small size, the weakly developed sexual characteristics, the truncate apex of the anterior tibia, the internal apical angle of the tibia stretched into a tooth or hook in the male and the terminal spur of the tibia is curved at right angles towards the interior a little in front of the apex (“la petite taille, le faible développement des caractères sexuels secondaires, le tronçonnement apical des tibias antérieurs droite, l’angle apical interne de ces tibias étiré en dent ou en couchet chez le mâle et l’éperon terminal de ces mêmes tibias courbé à angle droit vers l’intérieure peu avant l’apex.”; Paulian, 1939: 13). Since the description of the subgenus, *Metacatharsius* has been treated both as a subgenus (Ferreira, 1964; Balthasar, 1965) and a genus (Walter, 1976; Cambefort, 1991) and it was not until Montreuil (1998) that a type species was fixed and the genus defined according to Article 13.3 of the International Code on Zoological Nomenclature (ICZN).

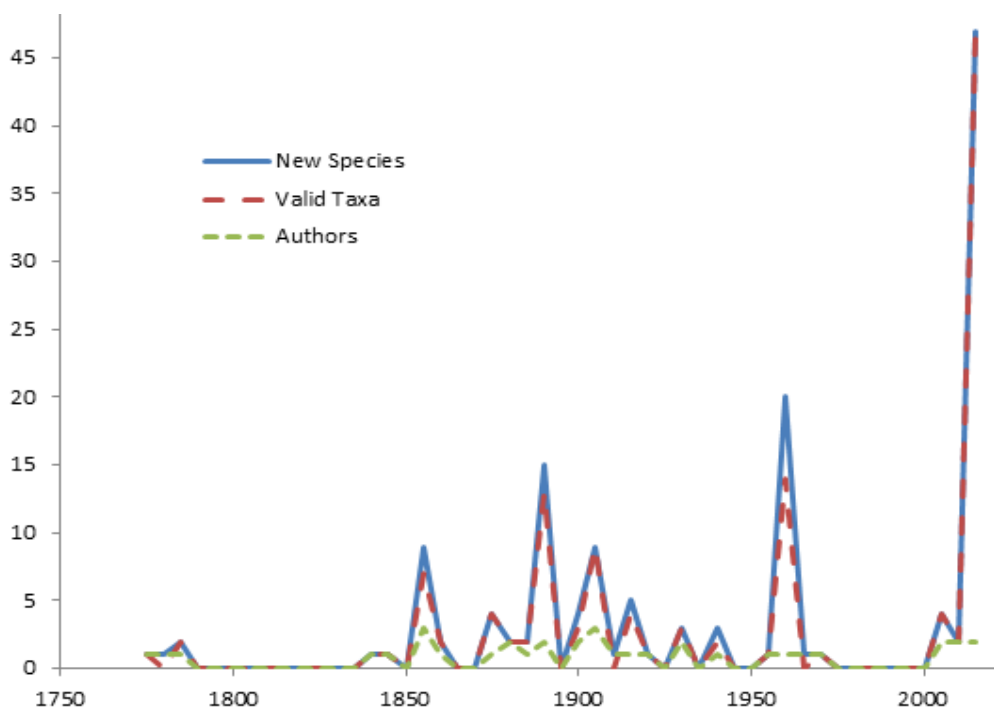
The next overview of this genus was undertaken by Joseph Gillet who lists all known species of *Catharsius* in Junk’s *Coleopterorum Catalogus* (Gillet, 1911). Since the 1893 work of Kolbe, Carl Felsche of Leipzig had described a further 9 species in two works of 1901 and 1907. Gillet’s list contains 82 species of which 59 still belong in this genus (47 Afrotropical and 12 Asian species), 21 in the genus *Metacatharsius* and 1 in *Copridaspilus* Boucomont, 1920. Gillet described a number of species in the following few years but he was the last to have worked on this genus before the Second World War.

The most recent revisional work undertaken on this genus was by Maria Ferreira in the 1960’s and 70’s, in three works on the Scarabaeidae fauna of sub-Saharan Africa (Ferreira, 1960b, 1960c, 1972). In the first of her works (1960b), she reviews the African species of *Catharsius* s. str. of the “adamastor group” and provides a key to genera in good agreement to Péringuey’s key of 1901, using the carina on the seventh and eighth striae as the important character. She goes on to list further characters including the anteriorly angled metasternum, a well carinate mesoepimere and a margined procoxal cavity (1960b: 2) (Fig.2). A series of other characters such as the serrations of the protibia

are given to separate the subgenus *Metacatharsius* but these characters are shared in many species of *Catharsius* sensu Ferreira. Ferreira's "adamastor group" is characterised by the un-toothed, horned clypeus in the male, an anteriorly elevated pronotum with a carina and the tridentate clypeal carina of the female. In the second of her works published later the same year, Ferreira (1960c) revises the other members of the genus without any further grouping. She talks briefly once more about the general characters outlined above as well as providing information on the dimorphism of the secondary sexual characteristics, geographical distribution and their seasonality. In total 71 species are revised between the two publications and in both publications, a key to all the species is provided and many of the species are beautifully and accurately figured. The final work of Ferreira (1972) brings together her many years studying the dung beetles of Africa in a 1000 page monograph on the Scarabs of Africa. This work was "intended for use not only by taxonomists but also by ecologists and economic entomologists" (Ferreira, 1972: 5). Within the *Catharsius* section of her work, she provides a key to all species and provides a checklist of species with references to the original descriptions and type depositories but without any detailed descriptions, concentrating more on "geographical distribution and on collecting localities since these are of importance to ecologists" (Ferreira, 1972: 5). In total, Ferreira (1959; 1960a; 1960b; 1962; 1963; 1964; 1972) described 21 species of *Catharsius* and revised 79 species and one subspecies in her final work of 1972. These monumental works however do have a number of drawbacks including the fact that all descriptions are in Portuguese and the failure to examine type material. Nonetheless, these works are still the go-to references for identifying African *Catharsius* and the errors which occurred in her work have since been propagated in literature over the past forty years. Since Ferreira's work, 17 new species of *Catharsius* have been described (Frey, 1974; Moretto, 2008; Josso & Prévost, 2009; Josso, 2011; Moretto, 2014; Génier, 2017; Josso & Prévost, 2018). Although most of these species were described in isolation without attempting to revise the species groups to which they are associated, Génier (2017) provides a key to the species "possessing acute clypeal teeth" an observation of a character found in the majority of species of the *C. eteocles* group.

It is interesting to note that between the late 18<sup>th</sup> century and the end of the 20<sup>th</sup> century, five individuals working independently at different times have described the majority of taxa in this genus (60 of 89 taxa) - C.H. Boheman (1857) H.J. Kolbe (1893), C. Felsche (1901-1907), J.J Gillet, (1907-1932) and M.C. Ferreira (1959-1964). There is a growing literature which shows that there are more people describing new species than ever before (Costello et al., 2014), and although in this limited data set of a single beetle genus the number of people who have described taxa in a 5-year period since the description of the first species in 1778 is constant (Figure 1), there are a number of observed trends similar to those in other studies. Comparing directly to a study of the description of new species of marine fish over time (Eschmeyer et al., 2010), certain periods of high taxonomic activity are congruent. The period of early discovery post-Linnaeus through the industrial revolution (1760-

1810), where very few taxa were discovered and the period post-Second World War (1950-65) where there was an increased taxonomic focus are similar. Moreover, the first major period of taxonomic activity in marine fish was in the late Regency period (1820's) at the height of marine exploration, whereas the major peak of taxonomic activity of the African beetles (pre-Ferreira in the 1960's) was in the period post the Treaty of Berlin (1885) where European colonization and trade in Africa was regulated (Pakenham, 1991). As a result of this revision, the number of Afrotropical *Catharsius* species has increased by nearly 30%, with the likelihood of 50% increase in the number of species in Asia (D. Mann, pers. comm.). Although the evidence is circumstantial, it is also believed that a number of other dung beetle genera in Africa, such as *Onitis* and *Metacatharsius* will also have a large proportion of new species awaiting description.



**Figure 1.** Number of new *Catharsius* taxa, number of valid taxa and total number of authors per 5-year period.

## Taxonomy

In the most recent and comprehensive molecular phylogeny of the Scarabaeinae, Tarasov & Dimitrov (2016) redefined a number of tribes and provided synapomorphies and diagnostic characters supporting their new concepts for the tribes. One of the redefined tribes was the *Coprini* and as a result, *Catharsius* was treated as *incertae sedis*. Their approach of splitting the phylogeny into groups at shallower nodes producing many monophyletic lineages is sensible due to the strong polyphyly of a number of tribes as recovered in both morphological and molecular phylogenies. This way, it is possible to provide characters that allow unambiguous diagnosis of all included taxa. The tribe *Coprini* now contains five genera: *Copris*, *Litocopris*, *Microcopris*, *Pseudocopris* and *Pseudopedaria*.

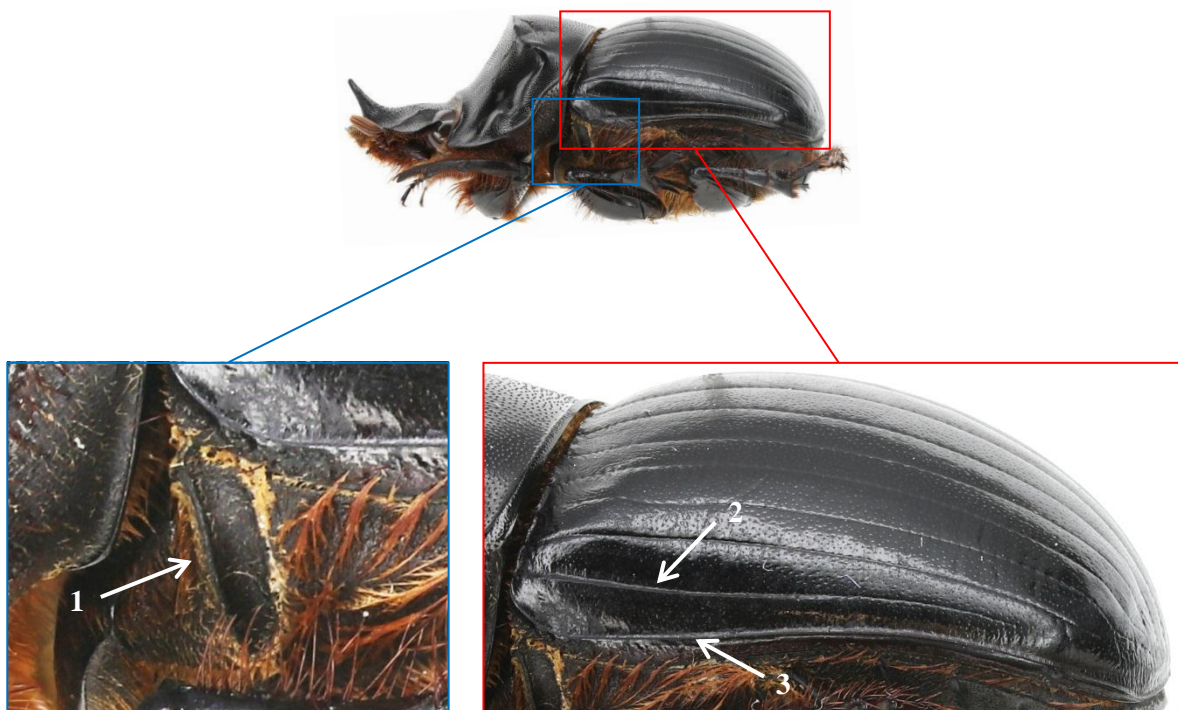
Although *Copris* has a worldwide distribution, the other four genera are restricted to the Afrotropical and Oriental regions. The clade of *Catharsius* + *Metacatharsius* has been recovered in all Scarabaeine dung beetle phylogenies with strong support (Montreuil, 1998; Vaz-de-Mello, 2007; Tarasov & Génier, 2015; Tarasov & Dimitrov, 2016) and after investigating other Coprini genera also placed as *incertae sedis*, such as *Heliocopris* and the Asian *Synapsis*, it has become evident that a new tribal name is required. In order to stabilise dung beetle classification, a new tribe is described to incorporate *Catharsius* and *Metacatharsius*:

### Catharsiini new tribe

**Type genus:** *Catharsius* Hope, 1837

Two genera, *Catharsius* and *Metacatharsius* belong in this new tribe.

The tribe can be unequivocally differentiated by the combination of two external and three internal characters: the presence of both a pseudoepipleural and mesepisternal carina (Figure 2) and the presence of a *lamella copulatrix* (LC), *auxillary sclerite* (AS) and a ring-shaped *superior right peripheral sclerite* (SRP) in the internal sac (see Chapter 2, Figure 1). Both genera are nocturnal paracoprids and have an Old World distribution. The genus *Catharsius* contains 140 species (128 African and 12 Asian) and *Metacatharsius* contains 65 Afrotropical species.



**Figure 2.** lateral view of a male *Catharsius adamastor* showing the mesepisternal carina (1), pseudoepipleural carina (2) and the epipleural carina (3).

A systematic overview of the genus is provided as follows:

Kingdom: **Animalia** Linnaeus, 1758

Phylum: **Arthropoda** Lar, 1904

Class: **Insecta** Linnaeus, 1758

Order: **Coleoptera** Linnaeus, 1758

Suborder: **Polyphaga** Emery, 1886

Infraorder: **Scarabaeiformia** Crowson, 1960

Superfamily: **Scarabaeoidea** Latreille, 1802

Family: **Scarabaeidae** Latreille, 1802

Subfamily: **Scarabaeinae** Latreille, 1802

Tribe: **Catharsiini** trib. nov.

Genus: ***Catharsius*** Hope, 1837

#### Key to genera

In Africa, *Catharsius* can only be confused with *Copris*, *Heliocopris* or *Metacatharsius* species. All four genera can easily be differentiated by external morphology. A key to the genera is provided here:

1. Epipleural carina complete from the base to the apex of elytra.....2  
– Epipleural carina incomplete, starting some way from the base of the elytra.....  
.....***Heliocopris***, Hope, 1837  
[Type species: *Scarabaeus pimal* Fabricius, 1798]
2. absence of both a pseudoepipleural carina and mesepisternal carina.....***Copris*** Müller, 1941  
[Type species: *Scarabaeus lunaris* Linnaeus, 1758]  
– presence of both a pseudoepipleural carina and mesepisternal carina (Fig. 2).....3
3. presence of three diagonal striae on the ventral surface of the protibia (App.IV, Fig. 2B); unique combination of the FLP and A sclerites of the internal sac (App.IV, Fig. 5K).....  
.....***Catharsius*** Hope, 1837  
[Type species: *Scarabeus molossus* Linnaeus, 1758]  
– absence of any striae on the ventral surface of the protibia (App.IV, Fig. 2E); the unique combination of the FLP and A sclerites of the internal sac.....***Metacatharsius*** Paulian, 1939  
[Type species: *Scarabeus ferrugineus* Olivier, 1789]

## ***Catharsius* Hope, 1837**

Type species (by original designation): *Scarabaeus molossus* Linnaeus, 1758

= *Copridaspidus* Boucomont, 1920 **syn. nov.**

Type species (by original designation): *Copridaspidus favareli* Boucomont, 1920

= *Catharsiocopris* Balthasar, 1967 **syn. nov.**

Type species (by original designation): *Catharsiocopris quadrituberculatus* Balthasar, 1967

*Catharsius* Hope, 1837: 21; Burmeister, 1846: 27; Lacordaire, 1856: 98; Kolbe, 1893: 132; Péringuey, 1901: 109; Arrow, 1931: 92; Ferreira, 1960b: 1; Ferreira, 1960c: 158; Balthasar, 1963: 304; Ferreira, 1972: 238.

*Copridaspidus* Boucomont, 1920: 261; Ferreira, 1972: 218.

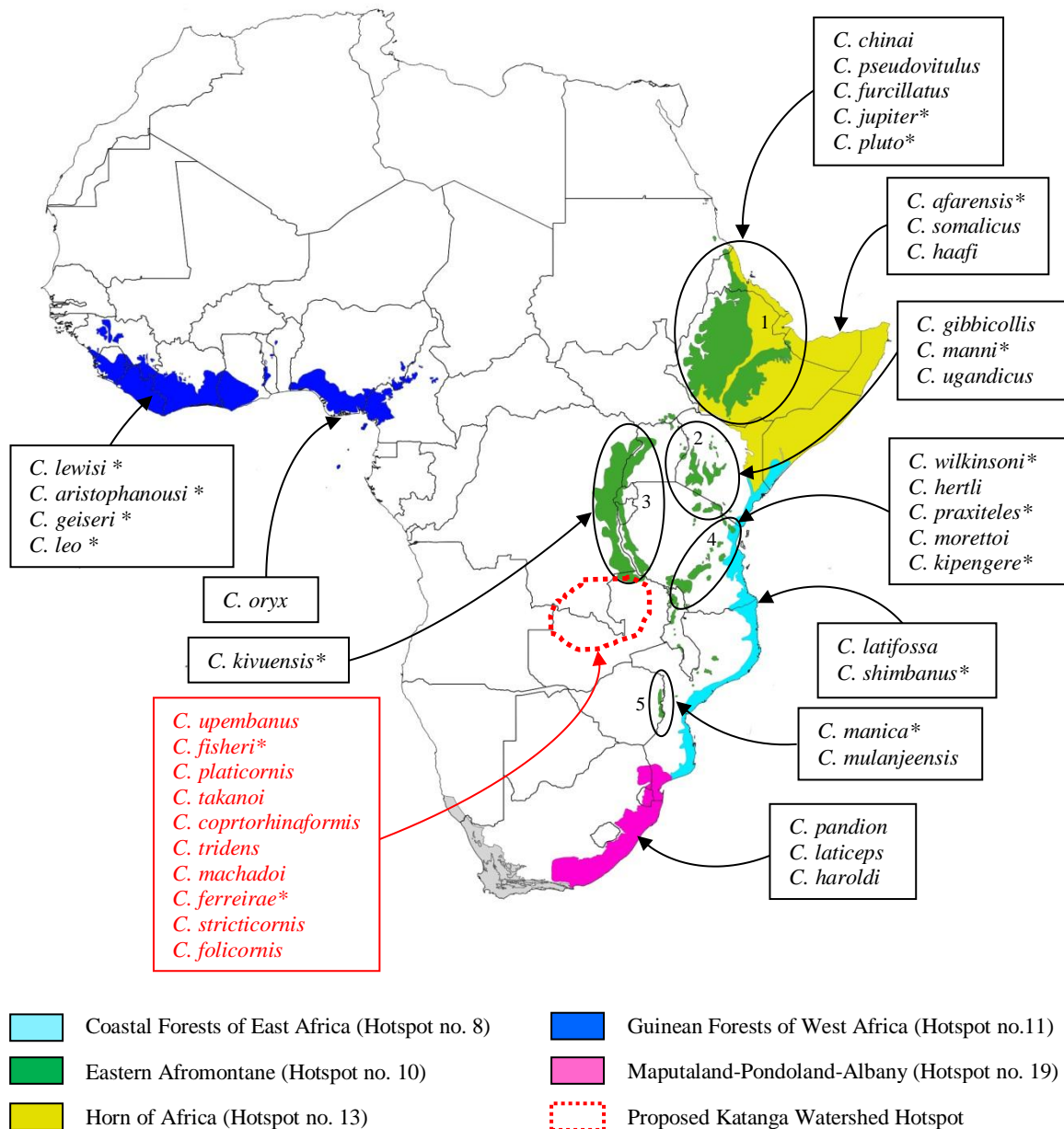
*Catharsiocopris* Balthasar, 1967: 48; Ferreira, 1972: 318.

**Redescription:** **Size:** medium to large (7-42mm). **Colour:** varying from dark slaty grey to black. **Head:** clypeus with cephalic horn or carina; surface with transverse rugulae or granules; clypeogenal suture well developed. **Pronotum:** pronotal disc with carina, tubercles or horns anteriorly; posterior margin complete or incomplete; lateral declivity with fovea; anterior margin of pronotum rounded, emarginate or incomplete, lateroanterior margin rounded or angled, the lateral margin concave or convex. **Elytra:** basally carinate; pseudoepipleural carina always present; triangular or rounded aspect in rear-view. **Pygidium:** transverse, fully margined; surface with punctuations. **Ventrites:** prosternum with longitudinal carina and presence of mesepisternal carina. **Legs:** protibia with moveable apical spur; tridentate or quadridentate; ventral striae always present; meso- and metatibia with serrations basally and bidentate; mesatibia with two apical spurs. **Genitalia:** parameres triangular in lateral view and sinuous anteriorly; internal sac sclerotised with the LC, AS and a ring-shaped SRP always present.

**Diagnosis:** members of the genus *Catharsius* can be identified by the following combination of characters: the elytra with an epipleural carina; the presence of a mesepisternal carina; the presence of ventral striae on the protibia; the unique arrangement of the A and AS sclerites as well as the presence of the LC sclerite in the internal sac. *Catharsius* species can only really be confused with species in the genus *Metacatharsius*, which can easily be separated by the lack of protibial ventral striae.

### Biogeography

*Catharsius* are distributed in the Oriental, Afrotropical and Palearctic regions. The majority of the species are Afrotropical and the ancestral state reconstruction in Chapter 2 suggests that they have an African origin. In Africa, the majority of species are distributed across the open grasslands, savannas and woodlands with only a smaller proportion successfully colonising the tropical rainforests.



**Figure 3.** Strictly endemic species of *Catharsius* occurring in Biodiversity Hotspots of Sub-Saharan Africa as reported in the Critical Ecosystem Partnership Fund ([www.cepf.net](http://www.cepf.net)), with a proposed new hotspot area in southern D.R. Congo and northern Zambia. The Eastern Afromontane (Hotspot no. 10) has been divided into the following five sub-regions: 1. Ethiopian Highlands, 2. Volcanic Highlands of Kenya/Tanzania, 3. Albertine Rift, 4. Eastern Arc Mountains and Southern Rift, 5. Southern Montane (Chimanimani-Nyanga). \* denotes new species.

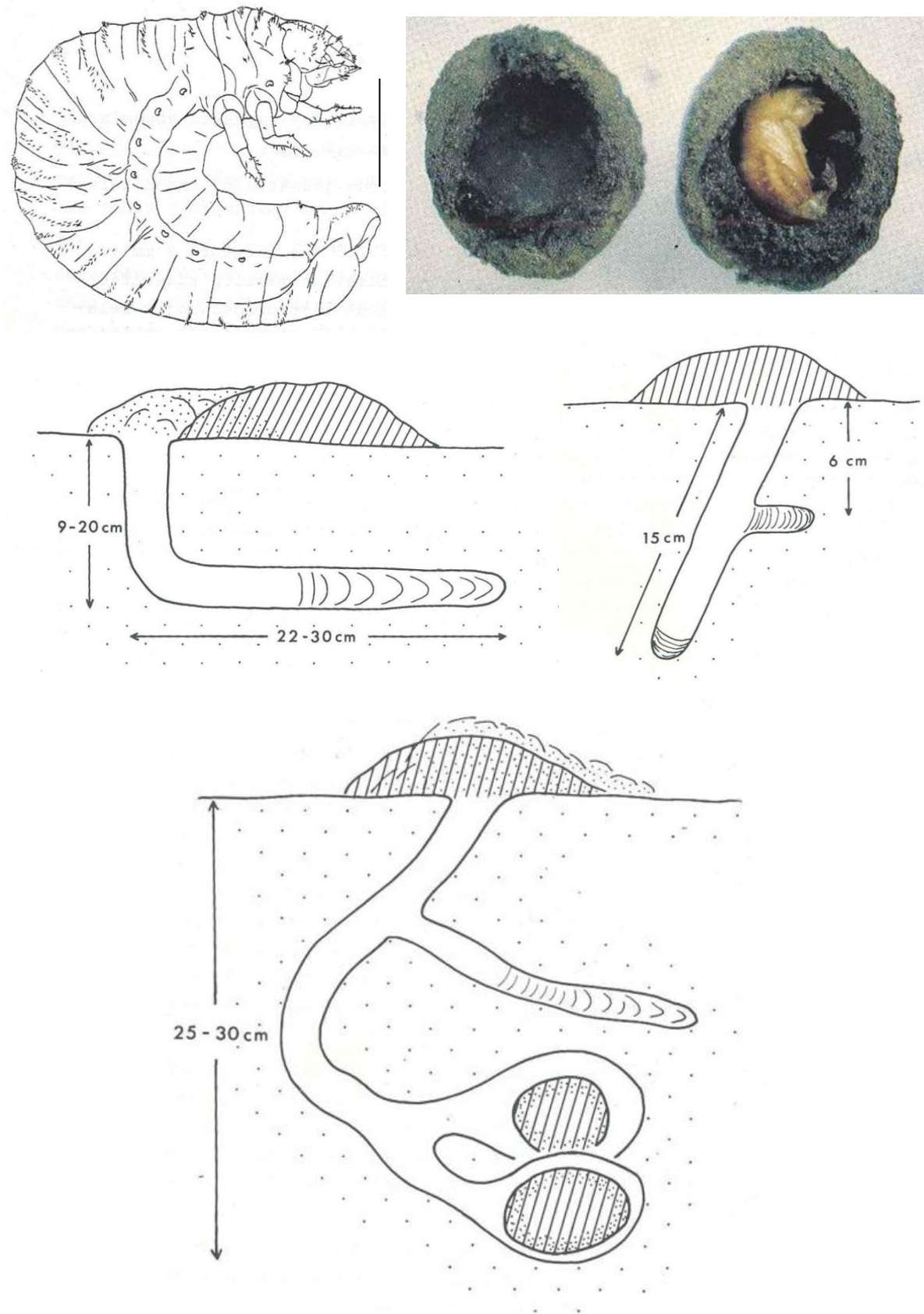
Two species are known from the forested island of Bioko in the Gulf of Guinea, and one species is distributed along the River Nile from its confluence with the Blue Nile at Khartoum in Sudan to Cairo in northern Egypt. The locality data of each *Catharsius* species was plotted onto a map and their distribution was investigated as part of biogeographical ancestral state reconstruction. Superimposing their distribution on the biodiversity hotspots map identified in Sub-Saharan Africa (Critical Ecosystems Partnership Fund (CEPF), 2018) revealed that strictly endemic species occur in five out of the seven hotspots (Figure 3). A further hotspot is here proposed for an area of Central Zambesian Miombo woodland, grassland and swamp mosaic in southern D.R. Congo and northern Zambia. The

high plateaus of this region are criss-crossed with rivers and lakes and the new hotspot is broadly demarcated by Lake Upemba to the north (D.R. Congo), Kalene Hill to the west, the upper Kafue River to the south and the Muchinga Escarpment to the east (all Zambia). There are more strictly endemic species of *Catharsius* in this area (10 species) than in any of the other hotspots. Studies of butterflies (Heath et al., 2002), beetles (Biondi et al., 2015) and reptiles (Broadley & Cotterill, 2004) have also revealed that a high number of endemic and sub-endemic species occur in this area and it has been suggested by Broadley & Cotterill (2004) that undersampling in this region is a possible cause for being overlooked as a hotspot.

The *Catharsius* from this area have been historically undersampled, with six of the ten strictly endemic species having just been described this year or awaiting description. Further patterns have also come to light as a result of the distribution mapping. Although it is important to note that the distributions have not been analysed statistically and that there is likely to be some undersampling for the taxa, there are a number of patterns which are congruent with the distribution of other insect species, and animal species more widely, in Africa. Aside from the better known barriers to speciation such as the Dahomey Gap in West Africa (Booth, 1958) and the Lake Turkana Basin in East Africa (Cohen & Schwartz, 1983), there is some evidence that the formation of rivers has played an important role in the speciation of *Catharsius*. A pair of vicariant species, *C. dux* and *C. duciformis*, are distributed on either side of the Lualaba and Kabompo River System in the D.R. Congo and Zambia, the former species to the west and the latter to the east. Van Daele et al. (2004) found similar distribution patterns in mole rats from the same region in a study of their chromosomal diversity, and hypothesize the river system dynamics have played an important role in speciation.

#### Natural history and ecology

*Catharsius* species are medium to large sized nocturnal paracoprids. Their natural history is poorly known and the research of Walter (1978) in the D.R. Congo provides the only insights into the life history of this group of beetles. Some figures from this unpublished work are here published for the first time with the author's permission (Figure 4). The adults create nests beneath the dung pat with the entrance to the tunnels on the periphery of the dung pat in larger species (such as *C. dux*) and directly underneath the pat in smaller species. It is hypothesized that, similar to other tunnelling dung beetles, the shape of the tunnels and nests of *Catharsius* will be dependent upon the texture and humidity of the soil and the assignment of particular nest types to any given taxon is difficult owing to this variable (Cambefort & Lumaret, 1984; Rougon, 1987). The nests of the three *Catharsius* species figured in figure 3 are referable to Type 6 and Type 7 as outlined by Cambefort & Hanski (1991) and to the nest patterns of the genus *Copris* (Klemperer, 1982). Although the nest structures were not observed, an adult *C. machadoi* was dug up from a depth of over 60cm on sandy soils whilst an adult *C. spectabilis* was discovered at a depth of well over 1m in clay soils (personal observation).



**Figure 3.** Third instar larva (A) and pupa in pupal chamber (B) of *Catharsius walteri* sp. nov.; the nests of *C. dux* (C) and *C. biconifer* (D); the nest and brood balls of *C. walteri* sp. nov.. Reproduced with permission from Walter (1978).

Adult females will lay a single egg in the dung ball providing its offspring with all the food that is required for growth and pupation. Typically, the eclosion will take place in the dung ball before digging its way to the surface (Masumoto, 1973; Klemperer, 1981). Very little literature exists on the larval stages of dung beetle genera, with the possible exception of the genus *Copris* (Lumaret & Paulian, 1977; Edmonds & Halffter, 1978). The third instar larva of *Catharsius* is very similar in appearance to *Copris* (*C. lugubris* and *C. orion*), with the exception of the structure of the mandibles, and chiefly the molars which are more complex in *Copris* (Walter, 1978).

During the process of nesting, paracoprids (and endocoprids) bury a large quantity of dung providing an important ecosystem service in the maintenance of proper ecosystem function (Nichols et al., 2008). One study in Borneo (Slade et al., 2007) demonstrated that the elimination of large-bodied dung beetles and in particular two *Catharsius* species (*C. dayacus* Lansberge and *C. renaudpaulani* Ochi & Kon), from a naturally occurring assemblage reduced dung removal by approximately 75%. Doube & Moola (1988), demonstrated that fly larvae in dung pats were significantly reduced as a direct result of dung burial by a South African species, *C. tricornutus* De Geer. *Catharsius* species are largely coprophagous in habit with the majority of the species feeding on herbivore or omnivore dung. Certain species are known to feed exclusively on monogastric herbivore dung, in particular elephant dung (Davis & Dewhurst, 1993; Moretto, 2014). Some species are also known to supplement their dung diet with carrion (Walter, 1978) and in a few cases are necrophagous (Davis et al, 2008).

## Conservation

There are currently seven species of *Catharsius* listed in the IUCN Red List of Threatened Species. Four species are classed as “Least Concern” and three as “Data Deficient” ([www.iucnredlist.org](http://www.iucnredlist.org)). From all the data compiled for each species in this genus, including locality and habitat data it would appear that there are no immediate extinction risks for any of the African *Catharsius* species. Although there are a number of species known from only a few specimens where clearly the status “Data Deficient” should be applied, this perceived scarcity is most likely down to undersampling rather than from an actual extinction threat. It should be noted however that over the past half a century, the distribution of some species with a reliance upon elephant dung have shrunk (see under *C. platycerus* and *C. platynotus* in Chapter 5). Naturally, the diminishing elephant populations (Chase et al., 2016) will continue to have an impact on the distribution of these species in the future.

## Species groups

The genus has been confidently split into five species groups based on the phylogenies recovered in Chapter 2 and 3. In total, 128 African species are recognized with a further 12 species in Asia. Of the African taxa, one taxon is a junior primary homonym, 15 taxa are junior synonyms (of which 11 are new synonymies) and 39 species are new to science. One taxon is placed in *incertae sedis*. A key to the species groups and a list of the constituent taxa in each group are provided here:

1. scutellum present (App.IV, Fig. 4M); moveable apical spur of metatibia apically pointed (App.IV, Fig. 2C).....***C. eteocles* group**
  - scutellum absent; moveable apical spur of metatibia apically square-ended (App.IV, Fig. 2A) .....2
2. protibia with inner spur in males (App.IV, Fig. 2A).....***C. sesostris* group**
  - protibia without an inner spur (App.IV, Fig. 2D).....3
3. pronotal disc anteriorly carinate (App.IV, Fig. 2I) or with two large, conical, forward-pointing horns (App.IV, Fig. 1F); sclerotised region of FLP fused to unsclerotised region only along the central portion (App.IV, Fig. 5K); basal region always lacking raspulae.....***C. molossus* group**
  - pronotal disc anteriorly tuberculate (App.IV, Fig. 1E) or with two (App.IV, Fig. 2J), three (App.IV, Fig. 3C) or four horns (App.IV, Fig. 3D); sclerotised region of FLP fused to unsclerotised region along its whole length (App.IV, Fig. 5L); basal region with or without raspulae.....4
4. pronotal disc anteriorly tuberculate or with two or four horns; the lateral margin of the FLP between sclerotised and unsclerotised regions straight; basal region with or without one raspula; LC with groundplan 7 (App.IV, Fig. 6M).....***C. pithecius* group**
  - pronotal disc anteriorly with two or three horns; the lateral margin of the FLP between sclerotised and unsclerotised regions notched (App.IV, Fig. 5L [92:1]); basal region always with one or two raspulae (App.IV, Fig. 7A); LC with groundplan 4 (App.IV, Fig. 6O) .....***C. tricornutus* group**

### **C. eteocles group (19 African species)**

1. *Catharsius brittoni* Ferreira, 1963
2. *Catharsius brutus* Harold, 1880
3. *Catharsius peregrinus* Harold, 1878 **stat. res.**
4. *Catharsius favareli* (Boucomont, 1920) **comb. nov.**<sup>1</sup>
5. *Catharsius garnerae* **sp. nov.**
6. *Catharsius omoensis* Müller, 1941
7. *Catharsius pandion* Harold, 1877  
= *Catharsius mossambicanus* Ferreira, 1960
8. *Catharsius longiceps* Gillet, 1907  
= *Catharsius vansoni* Ferreira, 1960 **syn. nov.**
9. *Catharsius pallas* Génier, 2017
10. *Catharsius aegeus* Génier, 2017
11. *Catharsius upembanus* Ferreira, 1962
12. *Catharsius conradi* **sp. nov.**
13. *Catharsius melancholicus* Boheman, 1860
14. *Catharsius luluensis* Ferreira, 1960
15. *Catharsius alpheus* Gillet, 1932
16. *Catharsius orami* **sp. nov.**
17. *Catharsius eteocles* (Castelnau, 1840)
18. *Catharsius creon* **sp. nov.**
19. *Catharsius erechtheus* Felsche, 1907

### **C. sesostris group (23 African species)**

1. *Catharsius corpulentus* **sp. nov.**
2. *Catharsius sesostris* Waterhouse, 1888
3. *Catharsius pylades* Peringuey, 1901 **stat. res.**
4. *Catharsius dejeani* **sp. nov.**
5. *Catharsius angolensis* **sp. nov.**
6. *Catharsius manica* **sp. nov.**
7. *Catharsius carpenteri* **sp. nov.**
8. *Catharsius lewisi* **sp. nov.**
9. *Catharsius wilkinsoni* **sp. nov.**
10. *Catharsius kivuensis* **sp. nov.**
11. *Catharsius fisheri* **sp. nov.**
12. *Catharsius congolensis* Ferreira, 1962  
= *Catharsiocopris quadrituberculatus* Balthasar, 1967 **syn. nov.**
13. *Catharsius pseudocongolensis* Ferreira, 1963
14. *Catharsius lycaon* Kolbe, 1893
15. *Catharsius pseudolycaon* Ferreira, 1960
16. *Catharsius daleyae* **sp. nov.**
17. *Catharsius approximans* Kolbe, 1893  
= *Catharsius ninus* Gillet, 1918 **syn. nov.**
18. *Catharsius semiramis* **sp. nov.**
19. *Catharsius balubanus* Kolbe, 1893
20. *Catharsius geiseri* **sp. nov.**
21. *Catharsius belus* Gillet, 1918
22. *Catharsius aristophanousi* **sp. nov.**
23. *Catharsius montreuili* **sp. nov.**

### **C. molossus group (29 African and 7 Asian species)**

#### **African Species:**

1. *Catharsius platynotus* Felsche, 1907
2. *Catharsius gibbicollis* Gerstaecker, 1884 **stat. res.**
3. *Catharsius chinai* Ferreira, 1960
4. *Catharsius gorilloides* Felsche, 1907
5. *Catharsius gorilla* (Thomson, 1858)
6. *Catharsius leo* **sp. nov.**
7. *Catharsius rhinoceros* (Klug, 1855)
8. *Catharsius dominus* **sp. nov.**
9. *Catharsius dux* Harold, 1878
10. *Catharsius duciformis* Ferreira, 1959

<sup>1</sup> *Catharsius favareli* (Boucomont) was not included in the morphological phylogeny as this taxon was a junior synonym of *Copridaspidus peregrinus* (Harold). The type specimens of both these species were investigated when the genus *Copridaspidus* was recovered as an ingroup in the phylogeny and it has since become apparent that *C. favareli* is a valid species.

11. *Catharsius spectabilis* Gillet, 1918
12. *Catharsius satyrus* Kolbe, 1893
13. *Catharsius hertli* Ferreira, 1964
14. *Catharsius adamastor* Gillet, 1932
15. *Catharsius ulysses* Boheman, 1857
16. *Catharsius telemachus* **sp. nov.**
17. *Catharsius thersander* **sp. nov.**
18. *Catharsius bradshawi* Lansberge, 1887  
= *Catharsius insignis* Péringuey, 1892
19. *Catharsius achates* (Olivier, 1789)
20. *Catharsius polynices* Kolbe, 1893  
= *Catharsius oedipus* Felsche, 1907 **syn. nov.**
- = *Catharsius simillimus* Ferreira, 1960 **syn. nov.**
21. *Catharsius juheli* Josso, 2011
22. *Catharsius mirabilis* Felsche, 1901
23. *Catharsius princeps* Kolbe, 1893 **stat. res.**  
= *Catharsius pseudoedipus* Ferreira, 1960 **syn. nov.**
24. *Catharsius obtusicornis* Boheman, 1857 **stat. res.**  
= *Catharsius platycerus* (Klug, 1855) **jr. prim. hom.**
25. *Catharsius genieri* Moretto, 2014
26. *Catharsius severini* Gillet, 1907
27. *Catharsius heros* Boheman, 1860
28. *Catharsius lepineyi* Boucomont, 1934
29. *Catharsius karlwerneri* Moretto, 2008

### Asian species:

1. *Catharsius sagax* (Quenstedt, 1806)
2. *Catharsius granulatus* Sharp, 1875
3. *Catharsius aethiops* Sharp, 1875
4. *Catharsius molossus* (Linnaeus, 1758)
5. *Catharsius renaudpauliani* Ochi & Kon, 1996
6. *Catharsius dayacus* Lansberge, 1886
7. *Catharsius platypus* Sharp, 1875

### **C. pithecius group (30 African and 5 Asian species)**

#### African species:

1. *Catharsius calaharicus* Kolbe, 1893
2. *Catharsius camillus* Harold, 1877  
= *C. disseptus* Péringuey, 1901 **syn. nov.**
3. *Catharsius jacksoni* Waterhouse, 1891
4. *Catharsius afarensis* **sp. nov.**
5. *Catharsius marcellus* Kolbe, 1893
6. *Catharsius phidias* (Olivier, 1789)
7. *Catharsius africanus* Ferreira, 1960
8. *Catharsius biconifer* Felsche, 1907
9. *Catharsius platicornis* Ferreira, 1960  
= *Catharsius straeleni* Ferreira, 1963 **syn. nov.**
10. *Catharsius takanoi* Josso & Prévost, 2018
11. *Catharsius mulanjeensis* Josso & Prévost, 2018
12. *Catharsius pseudoplaticornis* Josso & Prévost, 2018
13. *Catharsius gordonii* **sp. nov.**
14. *Catharsius vitulus* Boheman, 1857  
= *Catharsius philus* Kolbe, 1893 **syn. nov.**
15. *Catharsius guineensis* Ferreira, 1963
16. *Catharsius kenyensis* **sp. nov.**
17. *Catharsius garambae* Ferreira, 1960  
= *Catharsius saegeri* Ferreira, 1960 **syn. nov.**
18. *Catharsius punctatus* Josso & Prévost, 2018
19. *Catharsius haafi* Ferreira, 1960
20. *Catharsius petriei* **sp. nov.**
21. *Catharsius morettoii* Josso & Prévost, 2009
22. *Catharsius coptorhinaformis* Josso & Prévost, 2009
23. *Catharsius tridens* Josso & Prévost, 2009
24. *Catharsius pseudovitulus* Müller, 1941
25. *Catharsius manni* **sp. nov.**
26. *Catharsius somalicus* Gillet, 1918
27. *Catharsius barclayi* **sp. nov.**
28. *Catharsius laticeps* Boheman, 1857
29. *Catharsius scopas* Felsche, 1907
30. *Catharsius praxiteles* **sp. nov.**

### **Asian species:**

1. *Catharsius quadridentatus* Lansberge, 1885
2. *Catharsius javanus* Lansberge, 1886
3. *Catharsius birmanensis* Lansberge, 1874
4. *Catharsius capucinus* (Fabricius, 1781)
5. *Catharsius pithecius* (Fabricius, 1775)

### ***C. tricornutus* group (27 African species)**

1. *Catharsius haroldi* Takano, 2018
2. *Catharsius harveyi* sp. nov.
3. *Catharsius machadoi* Ferreira, 1960
4. *Catharsius neptunus* Kolbe, 1893
5. *Catharsius oryx* Frey, 1974
6. *Catharsius littoralis* sp. nov.
7. *Catharsius ferreirae* sp. nov.
8. *Catharsius tricornutus* (De Geer, 1778)  
= *Catharsius nemestrinus* (Fabricius, 1781)  
= *Catharsius areolatus* Boheman, 1857
9. *Catharsius kipengere* sp. nov.
10. *Catharsius smithi* sp. nov.
11. *Catharsius bicornutus* Kolbe, 1893
12. *Catharsius jossoi* sp. nov.
13. *Catharsius folicornis* Josso & Prévost, 2018
14. *Catharsius dubius* Peringuey, 1901 **stat. res.**
15. *Catharsius stricticornis* Josso & Prévost, 2018
16. *Catharsius shimbanus* sp. nov.
17. *Catharsius brevicornis* Felsche, 1907
18. *Catharsius walteri* sp. nov.
19. *Catharsius kolbei* Felsche, 1907
20. *Catharsius stuhlmanni* Kolbe, 1893
21. *Catharsius crassicornis* Gillet, 1911
22. *Catharsius cassius* Kolbe, 1893
23. *Catharsius latifossa* Müller, 1941
24. *Catharsius jupiter* sp. nov.
25. *Catharsius ugandicus* Gillet, 1918  
= *Catharsius furcillatus laeviplaga* Müller, 1941 **syn. nov.**
26. *Catharsius furcillatus* (Guérin-Ménéville, 1847)
27. *Catharsius pluto* sp. nov.

### ***incertae sedis* (1 African species)**

1. *Catharsius fastidiosus* (Thomson, 1858)

### Designation of lectotypes and neotypes

A number of lectotypes and neotypes are designated throughout this revision. The ICZN requires that designations of lectotypes after 1999 contain “an express statement of deliberate designation” (Article 74.7.3), to fix the status of the specimen as the sole name-bearing type of that nominal taxon. The designation of neotypes “is validly designated when there is an exceptional need and only when that need is stated expressly” (Article 75.3). Of the 106 described taxa, type specimens of 98 taxa housed in 22 collections were studied (Table 1). Of the eight taxa where the types could not be located, four neotypes were designated (*C. longiceps*, *C. gibbicollis*, *C. spectabilis* and *C. furcillatus*), the identity of three further taxa was not in doubt (*C. eteocles*, *C. pseudocongolensis* and *C. lepineyi*) and one taxon was placed in *incertae sedis* (*C. fastidiosus*). Figures of the habitus and labels of the type specimens are in Appendix V.

The Natural History Museum, London, UK	BMNH	<b>30</b>	(2)
Museum für Naturkunde, Berlin, Germany	ZMHB	<b>24</b>	(2)
Museum für Tierkunde, Dresden, Germany	MTD	<b>13</b>	(1)
Musée Royal de l'Afrique Centrale, Brussels, Belgium	MRAC	<b>12</b>	(3)
Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium	IRSNB	<b>11</b>	(1)
Naturhistoriska riksmuseet, Stockholm, Sweden	NHRS	<b>8</b>	(1)
Jean-François Josso private collection, Muzillac, France	JFJC	<b>7</b>	
Muséum national d'Histoire Naturelle, Paris, France	MNHN	<b>6</b>	
South African National Collection of Insects, Pretoria, South Africa	SANC	<b>4</b>	(1)
Canadian Museum of Nature, Quebec, Canada	CMNC	<b>4</b>	
Museo Civico di Storia Naturale, Trieste, Italy	MCST	<b>3</b>	(1)
Naturhistorisches Museum, Basel, Switzerland	NMB	<b>3</b>	
Transvaal Museum, Pretoria, South Africa	TMSA	<b>2</b>	(2)
South African Museum, Cape Town, South Africa	SAMC	<b>2</b>	(1)
Národní Museum, Prague, Czech Republic	NMPC	<b>2</b>	
Naturalis Natuurhistorisch Museum, Leiden, The Netherlands	RMNH	<b>2</b>	
Philippe Moretto private collection, Toulon, France	PMOC	<b>2</b>	
Oxford University Museum of Natural History, Oxford, UK	OUMNH	<b>2</b>	
National Museum of Kenya, Nairobi, Kenya	NMK	<b>1</b>	
Natural History Museum, Budapest, Hungary	HNHM	<b>1</b>	(1)
Museo Civico di Storia Naturale Giacomo Doria, Genoa, Italy	MCG	<b>1</b>	
Zoologische Staatssammlung München, München, Germany	ZSM	<b>1</b>	

**Table 1.** the collections (and their abbreviations) where the primary name-bearing *Catharsius* type specimens are held. Numbers in bold indicate the total number of taxa and those in brackets indicate invalid taxa.

#### On the identity of *Copris fastidiosus* Thomson, 1858

James Thomson (1858) described *Copris fastidiosus* from a unique male specimen in Count Mniszech's collection. The species was described as part of a large monographic work entitled "Voyage au Gabon" documenting all of the entomological specimens collected by Henri Deyrolle in Gabon during his expedition of 1856-57. Since this expedition was financed by Thomson and Mniszech, it appears the resulting specimens were shared equally between the two collectors. In his description of *C. fastidiosus*, Thomson compares this new species to *Copris pithecius* (Fabricius, 1775) with the only major difference being the angled lateral sides of the cephalic horn. Both these taxa were subsequently placed in the genus *Catharsius* by Gemminger & Harold (1869), and the types of *Catharsius pithecius* are present in the BMNH. Although *C. pithecius* is an Asian species, Olivier (1789) misidentified this species as originating from Senegal and this error was propagated by Dejean in his Catalogue (1833). Thomson, who was based in Paris, followed Olivier and Dejean in identifying *C. pithecius* as an African species rather than an Asian one. This is supported by a single specimen from the Thomson collection in IRSNB that has his unique handwritten circular label attached to what is an undescribed African species, *Catharsius dejeani* sp. nov. [= *C. pithecius* sensu Olivier nec Fabricius], a species of the *C. sesostris* group. With this in mind, the only species of the *C. sesostris* group matching the description found in Gabon is *C. belus* Gillet, which would become a junior synonym.

However, the provenance of specimens from the Mniszech collection described in Thomson's 1858 monograph is in doubt with at least two species of scarab stated as being collected in Gabon (or Guinea) having non-African distributions: *Heliocopris tyrannus* Thomson is an Asian species and *Heterogomphus mniszechi* (Thomson) is a South American species. Mniszech's collection was purchased by Rene Oberthür and the types of these two species are in the MNHN collections. The holotype of *C. fastidiosus* however could not be located. Within the boxes of *Catharsius* in the Oberthür collection, there is a label in one box with the species name *C. fastidiosus* with two specimens sitting under it. Interestingly, neither is the holotype but both are specimens of *C. belus*.

To further add to this confusion, the species identified as *C. fastidiosus* in many collections refers to *C. guineensis* Ferreira. In fact, the holotype of *C. guineensis* has an identification label of *C. fastidiosus* pinned to it. Joseph Gillet also refers to *C. fastidiosus* in his description of *C. somalicus*, and *C. fastidiosus* sensu Gillet, in this instance is clearly *C. guineensis*. This misidentification is down to the similarity of *C. guineensis* with the true *C. pithecius* from Asia. Gillet, who had visited the BMNH collections, is likely to have studied the Fabrician types of *C. pithecius*, and hence *C. pithecius* is correctly identified as an Asian species in his collection which is now housed in IRSNB. In conclusion, it is probable that *C. fastidiosus* is the senior name from *C. belus*, but with the doubt over the provenance of the Mniszech specimens and having not located the holotype, this species is placed as *incertae sedis*.



## **Chapter 5: A revision of the Afrotropical taxa of the *C. molossus* species group**

### **Introduction**

The *C. molossus* group comprises 29 African and 7 Asian species and is named after the type species of the genus. The species in this group are all large-bodied and possess ovaline mesa- and metafemurs, a well-defined longitudinal sulcus on the sternum and thick pubescence on the ventrites. Males possess cephalic horns and within the internal sac of the aedeagus, the sclerotised region of the FLP is fused only medially and raspulae are always absent from the sub basal region of the internal sac. With the exception of the horned *C. mirabilis*, all males have an anteriorly carinate pronotal disc.

The species in this group are distributed throughout most of Sub-Saharan Africa (excluding the xeric regions of the Namib and Kalahari deserts and the Nama-Karoo ecoregion) and in Asia from eastern Afghanistan, through most of India and SE Asia as far east as the Philippines and Timor. Within Africa, most of the species in this group are found in open savannas, grasslands and woodlands with the exception of *C. princeps*, *C. gorilloides*, *C. gorilla* and *C. leo*. The Asian members of the genus however are forest-dwelling species with the exception of *C. platypus* which is found in the Thar Desert on the border of Pakistan and India. Many of the species in this group are known to feed exclusively on monogastric herbivore dung and in particular elephant dung (Moretto, 2014), their current distributions being restricted to areas where these animals are found. Aside from digging under elephant dung, these species are only readily collected at light and usually at dusk rather than at dawn (personal observation). Those species that are omnivorous can be regularly trapped using human dung baited pitfall traps and can be very numerous; large numbers of *C. leo* and *C. duciformis* have been collected by the author using this method.

In this chapter, both sexes of each species in the *C. molossus* group is described and re-described in detail, their distribution is outlined, their biology discussed, the associated literature references and information on the type material is provided as well as a key to identification. Furthermore, both sexes of each species are figured in dorsal, lateral and frontal views, together with the male aedeagus. The LC of all species is figured on a single plate to facilitate identification.

### **Materials and methods**

Specimens and taxonomic material

The following abbreviations are used in the text. The name of the curators and collections managers at each of the institutions are, where applicable, provided in parentheses. Specimens from 32 of the 34 institutions and private collections listed below were examined as part of this study:

<b>ANHRT</b>	African Natural History Research Trust collections, Leominster, United Kingdom (R. Smith)
<b>BMNH</b>	The Natural History Museum, London, United Kingdom (M. Barclay)
<b>CMNC</b>	Canadian Museum of Nature, Quebec, Canada (F. Génier)
<b>EMAU</b>	Zoologisches Institut und Museum, Ernst-Moritz-Arndt-Universität, Greifswald, Germany (P. Michalik)
<b>FGIC</b>	François Génier private collection, Gatineau, Canada
<b>HNHM</b>	Natural History Museum, Budapest, Hungary (O. Merkl)
<b>IRSNB</b>	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (A. Drumont)
<b>JFJC</b>	Jean-François Josso private collection, Muzillac, France
<b>JLMC</b>	José Luis Moreno private collection, Barcelona, Spain
<b>LMRZ</b>	Livingstone Museum, Livingstone, Zambia (C. Mateke)
<b>MCG</b>	Museo Civico di Storia Naturale Giacomo Doria, Genoa, Italy (M. Tavano, R. Poggi)
<b>MCST</b>	Museo Civico di Storia Naturale, Trieste, Italy (A. Colla)
<b>MDCL</b>	Michaël Dierkens private collection, Lyon, France
<b>MHNL</b>	Musée de Confluences, Lyon, France (H. Labrique, C. Audibert)
<b>MHPC</b>	Meindert A. Hielkema private collection, Gouda, Netherlands
<b>MNHN</b>	Muséum national d'Histoire Naturelle, Paris, France (O. Montreuil, A. Mantilleri)
<b>MRAC</b>	Musée Royal de l'Afrique Centrale, Brussels, Belgium (S. Hanot, M. De Meyer)
<b>MTD</b>	Museum für Tierkunde, Dresden, Germany (K. Klass, O. Jaeger)
<b>NHRS</b>	Naturhistoriska riksmuseet, Stockholm, Sweden (N. Apelqvist)
<b>NMB</b>	Naturhistorisches Museum, Basel, Switzerland (E. Sprecher, I. Zürcher-Pfander)
<b>NMPC</b>	Národní Museum, Prague, Czech Republic (L. Sekerka, J. Hajek)
<b>NMK</b>	National Museum of Kenya, Nairobi, Kenya (E. Kioko, L. Njoroge)
<b>OUMNH</b>	Oxford University Museum of Natural History, Oxford, United Kingdom (D. Mann)
<b>PMOC</b>	Philippe Moretto private collection, Toulon, France
<b>RMNH</b>	Naturalis Natuurhistorisch Museum, Leiden, Netherlands (H. Huijbregts)
<b>SAMC</b>	South African Museum, Cape Town, South Africa (S. Van Noort, D. Larsen)
<b>SANC</b>	South African National Collection of Insects, Pretoria, South Africa (B. Grobbelaar, R. Staals)
<b>SRPC</b>	Sébastien Rojkoff private collection, Lyon, France
<b>TMSA</b>	Transvaal Museum, Pretoria, South Africa (R. Müller)
<b>UPSA</b>	Scarab Research Group, University of Pretoria, Pretoria, South Africa (C. Deschodt)
<b>USNM</b>	United States National Museum of Natural History, Washington D.C., USA (F. Shockley)
<b>ZMHB</b>	Museum für Naturkunde, Berlin, Germany (J. Frisch, J. Willers, B. Jäger)
<b>ZMUH</b>	Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Hamburg, Germany (K. Schütte)
<b>ZSM</b>	Zoologische Staatssammlung München, München, Germany (M. Balke, D. Balke)

**Terminology:** all name-bearing type label data is transcribed verbatim with “//” denoting a different label and “/” denoting a line break; this is followed by a description of the media for each label in square brackets. If no indication is given, the label is printed on white paper. The length of the specimen is measured from the apex of the pronotum to the apex of the elytra following the midline.

**Plates:** Specimens were photographed using a Canon EOS 5D SR with Macro 100mm or MP-E 65mm lenses. Images were stacked using Helicon Focus 6.0. Genitalia images were photographed through a Leica MS5 stereo microscope. Images were processed and edited using Adobe Photoshop Elements 10. All scale bars on the images unless labelled otherwise, are 5mm.

## 1. *Catharsius platynotus* Felsche, 1907

(Pl. 1: figs. 1-8; Pl. 30: fig. 1)

*Catharsius platynotus* Felsche, 1907: 281; Ferreira, 1960a: 32.

**Type locality:** “Victoria, Kamerun”

**Name-bearing type:** Holotype ♂ (by original monotypy) in MTD:

“// Viktoria / Nyassa [blue card] // platynotus / Felsche / Kamerun [cream paper with green border, handwritten] // Typus. [orange card] // Coll. C. Felsche / Kauf 20, 1918 [blue card] // Senckenberg Natur- / hist. Sammlungen / Dresden, Museum / für Tierkunde (MTD) // HOLOTYPE / CATHARSIUS / platynotus / Felsche / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black; pubescence reddish-brown. **Male** (Pl. 1: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and concave centrally; clypeal margin continuous; clypeal surface rugulate anteriorly, turning more granulose towards the clypeogenal suture. Genal edge rounded and obtusely angled, the lateroposterior edge almost completely arcuate; surface covered evenly with scale-like granules turning more ovaline posteriorly; the genal margin with a distinct emargination at the clypeogenal suture. In dorsal view, the lateral sides of genae parallel-sided. Clypeogenal suture well defined to base of an incomplete clypeal carina. A short, laterally flattened, rectangular, and apically bifidate cephalic horn positioned anteriorly on clypeus; horn gently slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin weakly emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with an angled transverse carina anteriorly; the central portion of disc, as wide as the distance between the eyes, is extended forward, the carina almost straight and interrupted medially; the lateral portions of the carina arcuate from the obtuse angle with the extended central portion and termination point. Surface of pronotal disc covered in circular granules becoming finer posteriorly. Fovea on lateral declivity with a short carina anteriorly running from fovea towards the lateral margin in lateral view. Lateral declivity fully granulose except for a narrow smooth region running from the fovea to the anterior margin. Anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture; elytral striae with evenly-spaced weak punctures. Interstriae with weak fine punctures and alutaceous microsculpture throughout; epipleural carina well-developed, extending less than half of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 1: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 1).

**Female** (Pl. 1: figs. 3, 4, 6): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and emarginate centrally; clypeal margin continuous; clypeal surface with short transverse rugulae,

turning more granulose towards the clypeogenal suture. Genal edge rounded and acutely angled, surface covered with ovaline granules turning finer posteriorly; the genal margin with a weak emargination at the clypeogenal suture. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, all three tubercles positioned along the same transverse plane, the apically rounded central tubercles rising higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin weakly emarginate centrally. Lateroanterior margin rounded and obtusely angled, lateral margin arcuate. Pronotal disc with a short, slightly arcuate transverse carina anteriorly, interrupted medially; carina length shorter than the distance between the eyes; surface of pronotal disc covered in circular granules, tightly packed centrally on each side of the midline, becoming more spaced out towards the posterior margin. Lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture; elytral striae with evenly-spaced weak punctures. Interstriae with weak fine punctures and alutaceous microsculpture throughout; epipleural carina well-developed, extending less than half of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 19-27mm; female 20-25mm.

**Variation:** in smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the pronotal carina is reduced to a short arcuate carina interrupted medially. In smaller females, the tridentate clypeal carina is reduced and the pronotal carina less arcuate and straighter.

#### **Other material examined (149♂♂ 142♀♀):**

**ANGOLA:** **ZAIRE:** San Salvador [=M'banza-Kongo] (6°16'S, 14°14'E) (1♂ MNHN); **CAMEROON:** **LITTORAL:** Edea (3°47'N, 10°08'E) (1♂ ZMHB); Etombo [=Etamba] (5°11'N, 9°59'E), 28.ii.1908 (1♀ ZMHB); **SOUTH:** Akonangi (2°12'N, 11°21'E), iii-iv.1909, G. Tessmann (1♀ ZMHB); **CENTRAL AFRICAN REPUBLIC:** **KEMO:** Fort Sibut (5°44'N, 19°05'E) (2♀♀ MNHN); **SANGHA-MBAÉRÉ:** Bayanga (2°55'N, 16°16'E), iv.1996, P. Moretto (3♂♂ 1♀ MNHL); Parc National Ndoki, Lac 1 (2°29'N, 16°13'E), 28-29.ii.2002, P. Moretto (2♀♀ PMOC); **CONGO:** **NIARI:** Mayoko, 285km NE of Pointe-Noire, 635m (2°24'S, 12°54'E), 21.xi.2013, L. Niemand & C. Ngoulou (1♂ PMOC); **PLATEAUX:** Lefinie Reservation, bungalow near Mpo (2°24'S, 15°30'E), 13.i.1964, S. Endrödy-Younga (2♂♂ NMPC); Lefinie Reservation, Nambouli River (2°30'S, 15°29'E), 7.i.1964, S. Endrödy-Younga (1♂ NMPC); **D.R. CONGO:** Region des Lacs [=between Lake Edward and Lake Kivu], Dr. Sagona (1♂ MRAC); **BAS-UELE:** Bambesa (3°27'N, 25°41'E), 16.iv.1937, J. Vrydagh (1♀ MRAC); Bambesa (3°27'N, 25°41'E), 8.vi.1937, J. Vrydagh (1♂ 2♀♀ MRAC); Bambesa (3°27'N, 25°41'E), 21.vi.1937, J. Vrydagh (2♀♀ MRAC); Bambesa (3°27'N, 25°41'E), x.1937, J. Vrydagh (6♂♂ 3♀♀ IRSNB); Bambesa (3°27'N, 25°41'E), 8.x.1937, J. Vrydagh (3♂♂ 6♀♀ MRAC); Bambesa (3°27'N, 25°41'E), 15-16.x.1937, J. Vrydagh (1♂ NMB); Bambesa (3°27'N, 25°41'E), 11.ix.1937, J. Vrydagh (2♂♂ 3♀♀ MRAC); Bambesa (3°27'N, 25°41'E), iii.1938, J. Vrydagh (5♂♂ 3♀♀ IRSNB); Bambesa (3°27'N, 25°41'E), 15-25.iii.1938, J. Vrydagh (1♀ BMNH); Bambesa (3°27'N, 25°41'E), iv.1938, J. Vrydagh (2♀♀ IRSNB); Bambesa (3°27'N, 25°41'E), v.1938, J. Vrydagh (5♂♂ 2♀♀ IRSNB); Bambesa (3°27'N, 25°41'E), 6-16.v.1938, J. Vrydagh (1♀ NMB); Bambesa (3°27'N, 25°41'E), vi.1938, J. Vrydagh (1♀ MRAC); Bambesa (3°27'N, 25°41'E), vii.1938, J. Vrydagh (2♂♂ IRSNB); Bambesa (3°27'N, 25°41'E), 19-23.vii.1938, J. Vrydagh (1♂ BMNH); Bambesa (3°27'N, 25°41'E), ix.1938, J. Vrydagh (2♂♂ 2♀♀ IRSNB); Bambesa (3°27'N, 25°41'E), x.1938, J. Vrydagh (1♂ 1♀ IRSNB); Bambesa (3°27'N, 25°41'E), xii.1939, J. Vrydagh (2♀♀ IRSNB); Bambesa (3°27'N, 25°41'E), i.1940, J. Vrydagh (1♀ IRSNB); Bambesa (3°27'N, 25°41'E), 6.x.1938, P. Lefèvre (3♀♀ MRAC); Ibembo (2°38'N, 23°37'E), 30.xii.1931, Fr. Hutsebaut (1♀ MRAC); Moto (2°54'N, 29°25'E), 1920, L.

Burgeon (4♂♂ 3♀♀ MRAC; 1♀ BMNH); Moto (2°54'N, 29°25'E), vii.1926, L. Burgeon (1♂ MRAC); Region de Sassa (5°05'N, 25°30'E), 1895-96, Colmant (1♀ MRAC); HAUT-KATANGA: Kasumbalesa (12°14'S, 27°48'E), i.1983, T. Garnier (1♀ PMOC); Kipushya (12°58'S, 29°30'E), i.1948, Mathias (1♀ NMB); HAUT-LOMAMI: Parc National de l'Upemba, Kaswabilenga, 700m (9°09'S, 26°42'E), 8.xii.1948, G.F. de Witte (4♂♂ 3♀♀ MRAC; 1♂ IRSNB); Parc National de l'Upemba, Kaswabilenga, 700m (9°09'S, 26°42'E), 17-24.i.1949, G.F. de Witte (16♂♂ 12♀♀ MRAC; 1♀ ZMHB); Parc National de l'Upemba, Kaswabilenga, 700m (9°09'S, 26°42'E), 31.i.1949, G.F. de Witte (2♂♂ 2♀♀ IRSNB); Parc National de l'Upemba, Kaswabilenga, 700m (9°09'S, 26°42'E), 7-21.ii.1949, G.F. de Witte (8♂♂ 4♀♀ MRAC); Parc National de l'Upemba, Kaswabilenga, 700m (9°09'S, 26°42'E), 30.xii-3.i.1949, G.F. de Witte (1♂ MRAC); Parc National de l'Upemba, piste Kaswabilenga, Mabwe, 585m (8°39'S, 26°31'E), 24.x.1947, G.F. de Witte (1♂ MRAC); Parc National de l'Upemba, Mabwe, 585m (8°39'S, 26°31'E), 12.i.1949, G.F. de Witte (1♂ MRAC); Parc National de l'Upemba, Mukana, 1810m (9°15'S, 27°12'E), 16-24.iii.1949, G.F. de Witte (1♂ 2♀♀ MRAC); HAUT-UELE: Abimva (3°09'N, 29°50'E), 17.viii.1925, L. Burgeon (1♂ MRAC); Dungu (3°36'N, 28°34'E), vi.1922, D.J. Bussey (1♂ BMNH); ITURI: Plaine Semliki (0°54'N, 30°10'E), xi.1931, Mme. L. Lebrun (2♂♂ 2♀♀ MRAC); LUALABA: Kafakumba (9°40'S, 23°46'E), xii.1928, F.G. Overlaet (1♀ MRAC); Kafakumba (9°40'S, 23°46'E), iv.1931, F.G. Overlaet (1♂ 2♀♀ MRAC); Kafakumba (9°40'S, 23°46'E), xii.1931, F.G. Overlaet (2♂♂ 5♀♀ MRAC); Kafakumba (9°40'S, 23°46'E), xii.1932, F.G. Overlaet (3♂♂ MRAC; 1♂ BMNH; 1♂ NMPC); Kafakumba (9°40'S, 23°46'E), xii.1933, F.G. Overlaet (2♀♀ MRAC); Sandoa [=Sanduwa] (9°42'S, 22°53'E), iii.1931, F.G. Overlaet (1♀ MRAC); NORD-KIVU: Beni (0°30'N, 29°27'E), Lt. Borgenhoff (2♂♂ 2♀♀ MRAC; 1♀ IRSNB); Beni (0°30'N, 29°27'E), x-xii.1931, Mme. L. Lebrun (1♂ 1♀ MRAC); Kilo (1°49'N, 30°06'E) (1♂ 1♀ IRSNB); Parc National Albert, Mabenga, Mont Kasale, 1000m (1°01'S, 29°21'E), xi.1934, G.F. de Witte (1♂ MRAC; 1♀ IRSNB); Parc National Albert, Mabenga, Mont Mabenga, 1000m (1°01'S, 29°21'E), vi.1935, G.F. de Witte (1♀ MRAC); Parc National Albert, Kikyo pres Kalonge (0°20'N, 29°48'E), 2180m, 3.ix.1952, P. Vanshuytbroeck & J. Kekenbosch (3♂♂ MRAC); Parc National Albert, Katanda, 950m (0°50'S, 29°22'E), x.1934, G.F. de Witte (1♀ IRSNB); Parc National Albert, Secteur Nord, Riviere Ngokoi, 1160m (0°19'N, 29°45'E), 18.vi.1952, G.F. de Witte (1♂ MRAC); Parc National Albert, NE Rutshuru, region Binza, 1100m (0°52'S, 29°23'E), x.1934, G.F. de Witte (3♀♀ MRAC; 2♂♂ 1♀ IRSNB); Parc National Albert, Plaine Semliki, 900-1000m (0°06'S, 29°34'E), iv-x.1937, Hackars (1♂ 2♀♀ MRAC); EQUATORIAL GUINEA: CENTRO-SUR: Nkolentangan (1°35'N, 10°30'E), xi.1907-v.1908, G. Tessmann (6♂♂ 2♀♀ ZMHB); LITORAL: Uelleburg [=Mbinil] (1°35'N, 9°37'E), vi-viii.1908, G. Tessmann (3♂♂ 2♀♀ ZMHB); GABON: ESTUAIRE: Monts de Cristal, Tchimbele (0°37'N, 10°24'E), ii.2011, G. Faravel (1♂ PMOC); NGOUNIÉ: Sindara (1°02'S, 10°39'E), 11.ix.1985, J.L. Moreno & T. Mestre (1♂ JLMC); Sindara (1°02'S, 10°39'E), 14.xii.1985, J.L. Moreno & T. Mestre (2♀♀ JLMC); Sindara (1°02'S, 10°39'E), 16.xii.1985, J.L. Moreno & T. Mestre (1♀ JLMC); Waka (1°04'S, 11°00'E), 2007 (1♂ 1♀ PMOC); OGOOUÉ-IVINDO: Booué (0°06'S, 11°57'E), vii.1990 (1♀ MDCL); Booué, chantier (0°06'S, 11°57'E), vii.1986, Marinano & Teisier (4♂♂ 2♀♀ PMOC); Ivindo, Station d'Ipassa (0°31'N, 12°48'E), xii.2004, T. Bouyer (1♂ PMOC); Parc National Lopé (0°27'S, 11°38'E), 9-13.xii.2009, G. Lecourt (1♀ PMOC); Makokou (0°34'N, 12°51'E), iv-v.1963, G. Bernardi (1♂ 3♀♀ MNHN); Makokou (0°34'N, 12°51'E), 21.xi.1973, Mission Balachowsky-Menier (1♀ MNHN); OGOOUÉ-MARITIME: Bongo (2°10' S, 10°12'E), iii.1996, Poulard (1♀ MHNL); WOLEU-NTEM: Oyem (1°36'N, 11°34'E), 20.iii.1991, Filippi (1♀ PMOC); UGANDA: [no precise locality] (2♂ MTD); CENTRAL: Entebbe (0°05'N, 32°29'E) (1♀ MTD); Entebbe (0°05'N, 32°29'E), 2.v.1910, C.C. Gowdey (1♂ BMNH); WESTERN: Bundongo Forest (1°46'N, 31°33'E), vii.1952, V.G.L. van Someren (1♀ BMNH); E of Butiaba, 3200ft. (1°48'N, 31°27'E), 9-10.xii.1911, S.A. Neave (1♀ BMNH); Toro, xi.1905, Lady Jackson (32♂♂ 15♀♀ BMNH); ZAMBIA: NORTHERN: Kalundu (10°18'S, 29°23'E), 23.ii.1943, H.J. Brédo (1♀ IRSNB); Mporokoso (9°23'S, 30°08'E), i.1945, H.J. Brédo (2♀♀ IRSNB); Mweru-Wantipa (8°46'S, 29°32'E), i.1945, H.J. Brédo (3♀♀ IRSNB); Tupele [=Lupele], Mweru-Wantipa (9°07'S, 29°37'E), 21.i.1945, H.J. Brédo (1♂ 2♀♀ IRSNB).

**Notes:** the holotype specimen carries labels stating the specimen to have been collected in “Victoria Nyassa”, which likely refers to Victoria Nyanza [=Lake Victoria] rather than the type locality stated in the description of Victoria, Cameroon. It may be possible that Felsche confused the two localities but if the label on the holotype is to be believed, the type locality is not Cameroon but Lake Victoria.

A long series of this species was collected in the Toro region of western Uganda by Lady Aline Louise Jackson and housed in the BMNH. It is important to note that all of these specimens are incorrectly labelled as originating from Toro in Nigeria, the mistake likely arising from an error by museum staff in the early 20<sup>th</sup> century. Lady Jackson was the wife of Sir Frederick John Jackson, Governor of the Uganda Protectorate and an ornithologist, often collecting alongside her husband in the field (Anonymous, 1929).

**Diagnosis:** males of this species are easily identified, possessing a unique pronotal carina which is angled anteriorly with a central flat portion. In no other species does the carina expand forward in this

manner. The female is similar in appearance to the female of *C. adamastor* but the elytral interstriae are covered in weak fine punctures whereas in *C. adamastor*, the interstriae are well punctured.

**Biology:** this species is found in lowland forest and forest-savanna mosaic habitats surrounding the Congo basin. Specimens have been collected in elephant dung and are attracted to light. One specimen in the PMOC was caught in tall Okoume (*Aucoumea klaineana*) lowland forest in Chimpanzee dung. Specimens have been caught throughout the year.

**Distribution** (Pl. 1: fig. 8): Angola, Cameroon, Central African Republic, Equatorial Guinea, Gabon, Congo, D.R. Congo, Uganda, Zambia.

## 2. *Catharsius gibbicollis* Gerstaecker, 1884 **stat. res.**

(Pl. 2: figs. 1-8; Pl. 30: fig. 2)

*Catharsius gibbicollis* Gerstaecker, 1884: 50.

**Type locality:** “Massai”

### **Name-bearing type:**

Type lost. Although *C. gibbicollis* was described in the period when Gerstaecker was based at the University of Greifswald (Peter Michalik, EMAU, pers. comm.), the type was listed as being present in the Hamburg Naturhistorisches Museum according to the type catalogue of Coleoptera published by Gebien in 1907. The Hamburg museum was heavily bombed during the Second World War and the dry collections were almost completely destroyed (Kai Schütte, ZMH, pers. comm. 2016). The type is not listed in the most recent type catalogue by Weidner in 1976. A topotypical specimen in IRSNB which was compared to the type by Gillet, together with notes on the type labels, is here **designated as the neotype** in order to stabilise the taxonomy of this and closely related species.

“// Massai / E. Africa. [handwritten] // gibbicollis ♂ / Gerst. / comp. type Mus / Hambourg – [handwritten] // gibbicollis ♂ / Gerst. / type au Mus du Hambourg / porte 4 etiquettes dont / voici le detail: / voir au verso [handwritten] / [on the reverse of the same label:] Original / 57 } etiquette rouge / magenta / Massailand / G.A. Fischer leg. / Geogr. gesl. ded. 1884 } etiquette blanche / Catharsius / gibbicollis / Gerst. } etiquette bl. / encadrée noir / platycerus Kl. / C. Felsche det. 1901 } 1a ligne à / l’encore rouge [handwritten] // gibbicollis / ♂ Gerst. / comp. type Hamb. / J.J.E. Gillet det. [partially handwritten] // NEOTYPE / CATHARSIVS / gibbicollis / Gerst. / det. H Takano 2017 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black; pubescence yellowish-brown. **Male** (Pl. 2: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and concave centrally; clypeal margin continuous; clypeal surface transversely rugulate anteriorly, turning more granulose towards the

clypeogenal suture. Genal edge rounded and obtusely angled, surface covered evenly with longitudinal granules turning more ovaline posteriorly; the genal margin with a distinct emargination at the clypeogenal suture. In dorsal view, the lateral sides of genae parallel-sided. Clypeogenal suture well defined to base of an incomplete clypeal carina. A laterally flattened, narrow, parallel-sided and apically pointed cephalic horn positioned anteriorly on clypeus; horn slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin interrupted medially, with the interruption as wide as the width of the cephalic horn. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with a transverse carina anteriorly, clearly emarginate medially; on each side of the emargination is a short rounded protuberance from whence the carina angles back to where it terminates; the carina slightly bowed internally before flattening and arcing to its termination; posterior surface of pronotal disc covered in circular granules, becoming more scale-like anteriorly; lateral declivity with fovea and surface completely granulose; anterior declivity perpendicular to the pronotal disc in lateral view; central portion of anterior declivity completely granulose, with a large wide “V” shaped depression medially. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae with weak punctures. Interstriae smooth, with frequent fine punctures and minimal alutaceous microsculpture centrally; epipleural carina well-developed, extending half the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia with three external rounded projections; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 15: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 2).

**Female** (Pl. 2: figs. 3, 4, 6): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and slightly concave centrally; clypeal margin continuous; clypeal surface with short transverse rugulae, turning more granulose towards the clypeogenal suture. Genal edge rounded and obtusely angled, surface covered with longitudinal granules arranged circularly from a point along the lateroposterior edge, turning more ovaline posteriorly; the genal margin with an emargination at the clypeogenal suture. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central tubercle being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin interrupted medially, with the interruption half the width of the clypeal carina. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with wide, transverse undulating carina anteriorly, as wide as the head; the carina bowed on each side of the midline to its terminal point positioned on the same horizontal axis as its midpoint; posterior surface of pronotal disc covered in circular granules, becoming more ovaline and scale-like anteriorly. Lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra

with fine alutaceous microsculpture and slight rugosity; elytral striae with weak punctures. Interstriae smooth, with frequent fine punctures and minimal alutaceous microsculpture centrally; epipleural carina well-developed, extending half the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 21-27mm; female 22-28mm.

**Variation:** in smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the pronotal carina is reduced to a short arcuate carina. In smaller females, the tridentate clypeal carina is reduced.

**Other material examined (56♂♂ 50♀♀):**

**KENYA:** [no precise locality], 13.xi.1911, R.L. Scott (1♀ BMNH); [no precise locality] Lindblom (1♂ NHRS); **KAJIADO:** Ngong (1°21'S, 36°40'E), 1930, G. Babault (1♂ MNHN); Ngong (1°21'S, 36°40'E), v.1940, MacInnes (1♀ NMK); Ngong Forest (1°21'S, 36°40'E), iii.1941, MacInnes (1♂ NMK); **KIAMBURU:** Muguga (1°15'S, 36°39'E), viii.1952, H.J. Brédo (2♂♂ 1♀ IRSNB); Muguga (1°15'S, 36°39'E), vi.1953, H.J. Brédo (1♂ NMPC); Muguga (1°15'S, 36°39'E), 25.iv.1953, B. Verdcourt (1♂ BMNH); Muguga (1°15'S, 36°39'E), vii.1957, B. Verdcourt (1♀ NMK); Muguga (1°15'S, 36°39'E), 30.v.1971, E.S. Brown (1♂ 1♀ BMNH); Muguga (1°15'S, 36°39'E), 5.v.1987, B.L. Parker (1♂ NMK); Muguga (1°15'S, 36°39'E), 25.v.1971, E.S. Brown (1♀ BMNH); Muguga Research Station (1°13'S, 36°39'E), 27.vi.1972, G.F. Bornemissza (1♀ SANC); Muguga Research Station (1°13'S, 36°39'E), 22.vi.1973, A. Macqueen (3♂♂ 4♀♀ SANC); Muguga Research Station, 2090m (1°13'S, 36°39'E), 23.iv.1975, Davis & Dewhurst (1♂ 3♀♀ SANC); **LAIKIPIA:** Naro Moru (0°10'S, 37°01'E), iv.1943, Meneghetti (1♂ 1♀ NMK); Naro Moro [=Naro Moru] (0°10'S, 37°01'E), 8.vii.1991, X. Vazquez (1♂ JLMC); **MURANGA:** Makindi, ca 1500m (0°58'S, 37°06'E), 8.iv.1975, Davis & Dewhurst (2♂♂ SANC); Mont Kinangop, Versant Est, 2200-2400m (0°40'S, 36°49'E), ii.1912, Alluaud & Jeannel (1♀ MNHN); **NAIROBI:** Langata (1°22'S, 36°44'E), xi.1982, M. Ritchie (1♂ NMK); Nairobi (1°19'S, 36°50'E), 8.ii.1909 (1♂ BMNH); Nairobi (1°19'S, 36°50'E), iv.1911, T.J. Anderson (2♂♂ 3♀♀ BMNH); Nairobi (1°19'S, 36°50'E), 1918 (1♀ NMK); Nairobi (1°19'S, 36°50'E), 1919, Dawson (7♂♂ NMK; 1♀ USNM); Nairobi (1°19'S, 36°50'E), 1920, A.F.J. Gedye (1♀ NMK); Nairobi (1°19'S, 36°50'E), 23.xii.1920, A.F.J. Gedye (1♀ NMK); Nairobi (1°19'S, 36°50'E), 24.xii.1920, A.F.J. Gedye (1♀ USNM); Nairobi (1°19'S, 36°50'E), 9.x.1923, J.W. Hunt (1♂ NMK); Nairobi (1°19'S, 36°50'E), 1930, G. Babault (1♀ MNHN); Nairobi (1°19'S, 36°50'E) (1♀ BMNH); **NAKURU:** Naivasha (0°43'S, 36°26'E), xii.1903, C. Alluaud (1♀ MNHN); Nakuru (0°17'S, 36°04'E), Dr. H.A. Bödeker (1♀ BMNH); Nakuru (0°17'S, 36°04'E), v.1950, R. Gray (1♀ NMK); **NAROK:** Keekorok (1°35'S, 35°14'E), i.1986, P. Rahola (1♂ MHNH); Masai Mara (1°28'S, 35°02'E) (1♀ IRSNB); Guaso Nyiro (1°10'S, 35°57'E), ii.1913, G. Babault (1♂ 1♀ MNHN); 26km SW Narok, 1900m (1°15'S, 35°42'E), 26.iv.1975, Davis & Dewhurst (1♂ 1♀ SANC); South Masai Reserve, near Mara River (1°28'S, 35°02'E), 1919, Dr. E.A. Lewis (1♂ 1♀ BMNH); **NYERI:** Nyeri (0°26'S, 36°57'E), i.1948, Miss M. Steele (1♀ NMK); **SAMBURU:** 20km S Maralal, 1825m (0°55'N, 36°42'E), 9.vi.1975, Davis & Dewhurst (2♂♂ 2♀♀ SANC); **TANZANIA:** **ARUSHA:** Arusha (3°23'S, 36°40'E), ii.1905, Oblt. Abel (1♂ ZMHB); Karatu, 1490m (3°20'S, 35°40'E), 30.iv.1975, Davis & Dewhurst (3♂♂ 1♀ SANC); NW Karatu, 1660m (3°20'S, 35°26'E), 12.iii-10.iv.2007, Strole (1♂ PMOC); Lake Ndutu area, Serengeti National Park (2°59'S, 35°01'E), R. Foster (2♂♂ 1♀ OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°01'E), 17.xi.1990, R. Foster (1♀ OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°01'E), 22.xii.1990, R. Foster (1♀ OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°01'E), 30.xii.1990, R. Foster (1♀ OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°01'E), 31.x.1991, R. Foster (1♀ OUMNH); Lake Ndutu area, Serengeti National Park (2°59'S, 35°01'E), 1.iv.1991, R. Foster (1♀ OUMNH); Ngorongoro (3°10'S, 35°34'E), 25.i.1971, G. Fiori (1♂ MCG); Ngorongoro Crater (3°10'S, 35°34'E), iv.1941 (1♀ NMK); Ngorongoro Crater, 2100m (3°10'S, 35°34'E), 9.i.1973, J. Krikken (1♀ RMNH); Ngorongoro-Crater (3°10'S, 35°34'E), xii.2002 (4♂♂ PMOC); Ngorongoro Crater, east rim (3°10'S, 35°41'E), 27.xii.2011, D. Moore (2♂♂ PMOC); Ngorongoro Crater, NW outer slopes, 2010m (3°07'S, 35°30'E), 29.iv.1975, Davis & Dewhurst (2♀♀ SANC); Ngorongoro Crater, NW outer slopes, 2010m (3°07'S, 35°30'E), 30.iv.1975, Davis & Dewhurst (10♂♂ 7♀♀ SANC); Simba Camp, Ngorongoro Crater, 2319m (3°14'S, 35°29'E), 12-14.iv.2012, R. Smith & H. Takano (20♂♂ 13♀♀ BMNH); Serengeti National Park, Lake Ndutu (2°59'S, 35°01'E), 14.v.1985, P.C. Goudswaard (1♂ RMNH); Serengeti National Park, Lake Ndutu (2°59'S, 35°01'E), 15.vi.1986, P.C. Goudswaard (2♀♀ RMNH); Serengeti National Park, Lake Ndutu (2°59'S, 35°01'E), 31.xii.1986, P.C. Goudswaard (2♀♀ RMNH); **KILIMANJARO:** Kibonoto [=Kibongoto] (3°11'S, 37°06'E) (1♂ IRSNB); Madschame [=Machame] (3°12'S, 37°13'E), T. Paesler (1♀ ZMHB); **MARA:** 4km N Serona [=Seroner] (2°25'S,

34°49'E), Serengeti National Park, i-v.1969, H. Hendrichs (1♀ ZSM); SHINYANGA: Serengeti National Park, near Naabi Gate, 1650m (2°50'S, 35°00'E), 28.iv.1975, Davis & Dewhurst (2♂♂ SANC); Serengeti National Park, Seronera/Naabi Gate, 1600m (2°38'S, 34°54'E), 28.iv.1975, Davis & Dewhurst (3♀♀ SANC).

**Diagnosis:** This and the subsequent species have a distinctive pronotal carina which is extended anteriorly further than in any of the other species. *C. gibbicollis* is easily distinguished from *C. chinai* by the depression in the anterior declivity of the pronotum. The females can be separated by the shape of the clypeal carina, with the central tubercle on the clypeal carina elevated much higher in *C. chinai*. These two species are distributed allopatrically, their distribution separated by the Lake Turkana basin of northern Kenya and there is unlikely to be any confusion in specimens with provenance.

**Biology:** This species is associated with the montane forests and the high elevation grasslands of northern Tanzania and southern Kenya. A long series of both sexes was collected by the author at light on the Ngorongoro Crater rim. Some specimens have been caught at dung-baited pitfall traps. Although their specific dung preference is unknown, it is likely that this species feeds primarily on elephant dung. Specimens have been caught between October and August.

**Distribution** (Pl. 2: fig. 8): Kenya, Tanzania.

### 3. *Catharsius chinai* Ferreira, 1960

(Pl. 3: figs. 1-8; Pl. 30: fig. 3)

*Catharsius chinai* Ferreira, 1960a: 14; 1960c: 7.

**Type locality:** "Abissinia"

**Name-bearing type:** Holotype ♂ in BMNH:

"// Holo- / type [white disc with red border] // Raff [handwritten] // Abyssinia / Raffray [cream card with blue horizontal line] // Nevinson Coll. / 1918-14 // HOLOTYPE ♂ / *Catharsius chinai* / n.sp. / M.C.Ferreira det., 1960 [partially handwritten] // NHMUK010367760 [QR code] //"

**Redescription:** Colour: Black; pubescence yellowish-brown. **Male** (Pl. 3: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and concave centrally; clypeal margin continuous; clypeal surface transversely rugulate anteriorly, turning more granulose towards the clypeogenal suture. Genal edge rounded and obtusely angled, surface covered evenly with longitudinal granules turning more ovaline posteriorly; the genal margin with a distinct emargination at the clypeogenal suture. In dorsal view, the lateral sides of genae parallel-sided. Clypeogenal suture well defined to base of an incomplete clypeal carina. A laterally flattened, narrow, parallel-sided and apically pointed cephalic horn positioned anteriorly on clypeus; horn slanted forward in lateral view.

**Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin with a minute interruption medially. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc

with a transverse carina anteriorly, slightly emarginate medially; carina angled back from midline to termination point, almost straight and slightly sinuous; posterior surface of pronotal disc covered in circular granules, becoming more scale-like anteriorly; lateral declivity with fovea and surface completely granulose; anterior declivity slightly sloped but almost perpendicular to the pronotal disc in lateral view; central portion of anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture and slight rugosity; elytral striae with weak punctures. Interstriae with fine punctures and some alutaceous microsculpture centrally; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 3: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 3).

**Female** (Pl. 3: figs. 3, 4, 6): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and concave centrally; clypeal margin continuous; clypeal surface with short transverse rugulae, turning more granulose towards the clypeogenal suture. Genal edge rounded and obtusely angled, surface covered with longitudinal granules arranged circularly from a point along the lateroposterior edge, turning more finer and ovaline posteriorly; the genal margin with an emargination at the clypeogenal suture. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central tubercle being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin emarginate and with minute interruption medially. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with a wide, transverse carina anteriorly, wider than distance between the eyes; the carina bowed very slightly on each side of the midline to its terminal point positioned on the same horizontal axis as its midpoint; a very short carina runs posteriorly along the midline from the carina; posterior surface of pronotal disc covered in circular granules, becoming more ovaline and scale-like anteriorly. Lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae with weak punctures. Interstriae smooth, with frequent fine punctures and minimal alutaceous microsculpture centrally; epipleural carina well-developed, extending half the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 20-27mm; female 20-26mm.

**Variation:** in smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the pronotal carina is reduced to a short arcuate carina. In smaller females, the tridentate clypeal carina is reduced.

**Other material examined** (122♂♂ 104♀♀):

**ERITREA:** [no data] Iwarson (2♂♂ NHRS); [no data] (1♂ IRSNB); **MAEKEL:** Asmara (15°19'N, 38°56'E) (10♂♂ 6♀♀ ZMHB); Asmara (15°19'N, 38°56'E) (3♂♂ MTD); Asmara (15°19'N, 38°56'E) (1♂ IRSNB); Asmara (15°19'N, 38°56'E) (2♂♂ MNHN); **ETHIOPIA:** [no precise locality] 1881, A. Raffray (3♂♂ 1♀ MNHN); [no precise locality] (3♂♂ MNHN); [no precise locality] Laferte (2♂♂ 1♀ MNHN); [no precise locality] 1910, G. Kristensen (3♂♂ 2♀♀ IRSNB); [no precise locality] (2♂♂ IRSNB); [no data] (5♂♂ 3♀♀ MTD); [no data] (1♂ 4♀♀ BMNH); [no data], M.C. Ward (1♂ BMNH); [no data], A. Raffray (1♂ BMNH); [no precise locality] (3♂♂ 3♀♀ ZSM); **ADDIS ABABA:** Addis Ababa (9°00'N, 38°45'E) (1♂ ZMHB); Addis Ababa (9°00'N, 38°45'E), 13.x.1900, Erlanger (1♀ ZMHB); Addis Ababa (9°00'N, 38°45'E), vii.1946, I. Ambjörn (1♂ 2♀♀ NHRS); Addis Ababa (9°00'N, 38°45'E), vii.1987, Rybalov (1♀ OUMNH); **AMHARA:** Abbat (10°38'N, 37°46'E), vi.1902, Degen (1♂ BMNH); 5km E of Bahir Dar (11°36'N, 37°26'E), 19.x.1973, G. de Rougemont (1♂ MRAC); between Djem-Djem and Wouramboulchi, 8000-9000ft. (8°58'N, 39°36'E), 30.ix-1.x.1926, J. Omer Cooper (1♂ BMNH); Mecha (11°30'N, 37°00'E), vii.1902, Degen (1♂ BMNH); **BENISHANGUL-GUMUZ:** 15km NW Hora, 1600m (10°13'N, 34°32'E), vi.1973, G. de Rougemont (1♂ MRAC); **GAMBELLA:** Yambela [=Gambela] (8°15'N, 34°35'E), vii.1987, Rybalov (1♂ 3♀♀ OUMNH); **HARARI:** Harar (9°19'N, 42°07'E) (1♂ NHRS); Harar (9°19'N, 42°07'E) (2♀♀ IRSNB); Harar (9°19'N, 42°07'E) (1♀ MNHN); Harar (9°19'N, 42°07'E), 1911, G. Kristensen (1♂ MNHN); **OROMIA:** Akaki River, 8000ft. (9°03'N, 38°41'E), 22.x.1904, P.C. Zaphiro (3♀♀ BMNH); Assela (7°58'N, 39°08'E), x.1970, S. Persson (3♂♂ 40♀♀ NHRS); Bedele (8°27'N, 36°21'E), xi.1993, R. Lizler (2♀♀ PMOC); Dodola (6°59'N, 39°11'E), 18.xi.1928 (1♂ MCG); Doukham, 6500-7000ft. (8°48'N, 38°54'E), 19.x.1926, Dr. H. Scott (1♂ BMNH); Ejere-dorf (9°55'N, 38°31'E), O. Neumann (1♂ ZMHB); Gimbi, 1880m (9°11'N, 35°50'E), 30.xi.1971, J. Prévost (2♂♂ MNHN); Gimma [=Jimma] (7°40'N, 36°50'E), v.1938, M. Balbis (1♂ MCG); Goba (7°01'N, 38°59'E), R. de Meulenaere (1♀ IRSNB); Hora Salla [=Lake Shala] (7°28'N, 38°31'E) (1♀ MNHN); Jimma, 1800m (7°40'N, 36°50'E), iv-viii, 1971, R.O.S. Clarke (1♂ 1♀ MRAC); Jimma (7°40'N, 36°50'E), vii-viii.1971, G. de Rougemont (1♂ 1♀ MRAC); Kibre Mengist, 1800-2000m (5°53'N, 38°59'E), 17-19.xi.1973, P.C. Rougeot (6♀♀ MNHN); environs Kibre Mengist, 2200m (5°53'N, 38°59'E), 6-7.xi.1976, P.C. Rougeot (1♂ MNHN); near Kibre Mengist (5°53'N, 38°59'E), 16.v.2002, Werner & Sudre (1♂ PMOC); Langano Lake (7°32'N, 38°49'E), v-vi.1971, G. de Rougemont (1♂ MRAC); Managasha [=Menagesha] (9°03'N, 38°34'E), 24.x.1904, P.C. Zaphiro (1♀ BMNH); Mount Antoto [=Entoto] (9°07'N, 38°46'E), 14.x.1904, P.C. Zaphiro (1♀ BMNH); Neghelli [=Negele], 1441m (5°20'N, 39°23'E), Jolivet (2♀♀ NMB); Sodere (8°24'N, 39°23'E), vii.1987, Rybalov (1♂ OUMNH); Yambo [=Ambo] (8°58'N, 37°52'E), iv.1995, Lizler (2♂♂ PMOC; 1♂ MHNL); **SOUTHERN NATONS. NATIONALITIES AND PEOPLES:** Arba Minch (6°02'N, 37°33'E), 1972, H. Rupp (6♂♂ 8♀♀ MRAC); Malghe-Wando farm, Awasa-Meer (7°06'N, 38°30'E), 28.iii-3.iv.1960, Mej. M.J.A. de Koster (1♂ 1♀ RMNH); Bonghe, 9000ft. (6°03'N, 37°20'E), 6.xii.1948, H. Scott (1♀ BMNH); Dilla, 8000ft. (6°25'N, 38°18'E), xii.1941, Meneghetti (3♂♂ 3♀♀ NMK); Dalle [=Yirga Alem] (6°45'N, 38°25'E), 1939, Balbis (1♀ MCG); Dilla (6°25'N, 38°18'E), ix.2000, P. Leonard (1♂ PMOC); near Dorze, 2401m (6°11'N, 37°35'E), 18-31.v.2014, M. Ströhle (3♂♂ 3♀♀ PMOC); Hosaena, 2300m (7°33'N, 37°52'E), 28.v.1974, G. de Rougemont (1♂ MRAC); Maraco [=Marequo] (7°58'N, 38°33'E), 1914 (1♂ IRSNB); between Wubara and Dita, 8500-10000ft. (6°15'N, 37°31'E), 4.xii.1948, H. Scott (1♂ BMNH); **TIGRAY:** Tigre (2♂♂ 1♀ MNHN); Tigre, 1850, Schimper (3♂♂ 1♀ MNHN).

**Diagnosis:** See under *C. gibbicollis*. The lack of a depression on the anterior declivity in the males and the elevated central tubercle of the clypeal carina in the females will distinguish the two species. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** This species is endemic to the montane forests of Ethiopia and Eritrea. There is no information on their behaviour, dung preference or method of capture, but is likely to have similar habits to *C. gibbicollis*. Specimens have been caught between March and December.

**Distributon** (Pl. 3: fig. 8): Ethiopia, Eritrea.

#### 4. *Catharsius gorilloides* Felsche, 1907

(Pl. 4: figs. 1-8; Pl. 30: fig. 4)

*Catharsius gorilloides* Felsche, 1907: 282; Ferreira, 1960a: 24.

**Type locality:** “Stanleypool” [= Pool Malebo (4°17’S, 12°29’E), DRC]

**Name-bearing type:** 3 syntypes (3♂♂) in MTD and 1♂ syntype in NMB. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series is here **designated as the lectotype:**

“// Stanley / Pool [handwritten] // gorilloides / Felsche / W.Africa [cream paper with green border, handwritten] // Typus. [orange card] // Coll. C. Felsche / Kauf 20, 1918 [blue card] // Staatl. Museum für / Tierkunde Dresden // Senckenberg Natur- / hist. Sammlungen / Dresden, Museum / für Tierkunde (MTD) // LECTOTYPE / CATHARSIUS / gorilloides / Felsche / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black; pubescence reddish-brown. **Male** (Pl. 4: figs. 1, 2, 5): **Head:** anterior clypeal edge broadly arcuate with a slight concavity centrally; clypeal margin continuous; clypeal surface with short transverse rugulae turning more granulose towards the clypeogenal suture. Genal edge rounded and obtusely angled, surface covered with ovaline granules anteriorly disappearing completely towards the eyes. Clypeogenal suture well defined to base of an incomplete clypeal carina. A basally rectangular, apically triangular laterally flattened cephalic horn positioned anteriorly of the clypeal carina on clypeus; the triangular portion slightly carinate; horn, erect, gently slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin weakly emarginate centrally. Lateroanterior margin right angled, lateral margin arcuate; Pronotal disc with an angled transverse carina anteriorly; the central portion of carina arcuate and slightly emarginate centrally, before angling back towards the termination point; carina with a gentle concavity half way along between the midpoint and termination point; carina sinuous intermittently; total length of carina wider than the widest point of the pronotum. The lateroposterior edge of pronotal disc at less than 45° to the posterior margin. Anterior two thirds of pronotal disc smooth with fine punctures; the posterior third with fine circular granules and alutaceous microsculpture; lateral declivity granulose with alutaceous microsculpture except in the immediate area around the fovea; the anterior declivity in frontal view with a slight depression under the concavity of the carina on either side of the midline; surface completely granulose, the circular granules turning more transversely ovaline centrally and much finer towards the anterior margin; alutaceous microsculpture throughout. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventriles:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; meso- and metatibia with an undulating apical margin.

Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 4: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 4).

**Female** (Pl. 4: figs. 3, 4, 6): **Head**: anterior clypeal edge evenly arcuate; clypeal margin continuous; clypeal surface with short transverse rugulae turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with ovaline granules disappearing completely towards the eyes. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum**: anterior margin obliquely orientated anteriorly on each side of eyes. Margin weakly emarginate centrally. Lateroanterior margin almost at right-angles, lateral margin arcuate posteriorly; Pronotal disc with a short, straight transverse carina anteriorly, emarginate medially; carina as wide as the distance between the eyes; a very short carina runs posteriorly along the midline from the carina. Surface of pronotal disc completely granulose, larger and more transversely ovaline anteriorly, becoming smaller and circular posteriorly; some alutaceous microsculpture on the disc posteriorly; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulose and with alutaceous microsculpture throughout. **Elytra**: carinate basally; basal portion of elytra with some fine alutaceous microsculpture; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Ventrites**: covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs**: protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence;

**Length**: male 19-26mm; female 23-24mm.

**Variation**: in smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the width of the pronotal carina is reduced to an arcuate carina no wider than the widest point of the pronotum.

#### **Other material examined (66♂♂ 54♀♀):**

**CAMEROON**: [no precise locality], 1898-99, L. Conradt (11♂♂ 12♀♀ MNHN); [no precise locality] (2♂♂ IRSNB); [no precise locality] (1♂ MRAC); [no precise locality] (5♂♂ 4♀♀ MTD); **EAST**: Batouri (4°26'N, 14°22'E), 24.iii.1934, F.G. Merfield (1♂ BMNH); Dja (3°15'N, 13°30'E), 15.v-1.vii.1936, F.G. Merfield (1♂ BMNH); Mimpala (3°25'N, 13°09'E), 24.iii.2012, M-H. Zinque (3♂♂ 3♀♀ IRSNB); **LITTORAL**: Douala (4°02'N, 9°44'E) (5♂♂ 3♀♀ ZMHB); Edea (3°47'N, 10°08'E) (1♂ 2♀♀ ZMHB); Edea (3°47'N, 10°08'E), 1939, P. Lepesme, R. Paulian & A. Villiers (1♂ MNHN); Mont Manengouba, 2000m (5°00'N, 9°51'E), 1939, P. Lepesme, R. Paulian & A. Villiers (1♂ MNHN); **NORTHWEST**: Bali (5°53'N, 10°00'E) (2♂♂ 1♀ ZMHB); Bali (5°53'N, 10°00'E), 5-25.vii.2006, local collector (6♂♂ 4♀♀ PMOC); Baliland [=Bali] (5°53'N, 10°00'E), Museum Lübeck (1♂ ZMHB); Bali-Bamenda (5°56'N, 10°05'E), xi.1965, Straumann (1♂ NMB); Bamenda (5°58'N, 10°09'E) (2♂♂ 2♀♀ ZMHB); Bamenda (5°58'N, 10°09'E), 5.v.1989, D. Bernaud (1♀ MHNH); Nkambe (6°35'N, 10°42'E), vi.2010 (1♂ 1♀ MDCL); Nkambe (6°35'N, 10°42'E), 5-7.vi.2010, J.L. Voma (1♂ 1♀ PMOC); **SOUTH**: Akonangi (2°12'N, 11°21'E), iii-iv.1909, Tessmann (1♀ ZMHB); Lolodorf (3°14'N, 10°44'E) (2♂♂ 3♀♀ NMB); **SOUTHWEST**: Bakassi (4°37'N, 8°36'E) (1♂ 2♀♀ ZMHB; 2♂♂ NMB); Barombi (4°39'N, 9°25'E) (1♂ MTD); Barombi (4°39'N, 9°25'E), Preuss (1♀ ZMHB); Barombi (4°39'N, 9°25'E), Zeuner (6♂♂ 2♀♀ ZMHB); Buea (4°09'N, 9°14'E) (1♀ MTD); Esosung (4°52'N, 9°44'E) (1♀ NMB); Mamfe (5°45'N, 9°19'E), Dr. Guillemain (1♀ ZMHB); **WEST**: Dschang

(5°27'N, 10°03'E), iv.1970 (1♂ NMPC); **CONGO: NIARI:** Tsingidi (2°24'S, 12°58'E), xi.2013, J. Niemand (14♂♂ 10♀♀ TMSA); Vouka (2°35'S, 12°45'E), 15.i.1975, C. Thibaud (1♂ PMOC); **EQUATORIAL GUINEA:** Bioko (1♂ 1♀ MNHN); Fernando Po, xi.1986, J.M. Bousquet (1♂ 2♀♀ MHNL); **CENTRO-SUR:** Nkolentangan (1°35'N, 10°30'E), xi.1907-v.1908, G. Tessmann (2♀♀ ZMHB); **BIOKO-NORTE:** Casa Banana, 800-100m (3°40'N, 8°52'E), xi.1987, J.M. Bousquet (1♂ 1♀ MHNL); **BIOKO-SUR:** Bahia de San Carlos [=Luba], 0-400m (3°27'N, 8°33'E), xii.1901, L. Fea (1♀ MCG); Bioko, Lake Loreto, 900m (3°24'N, 8°40'E), 1.xi.1953, K. Bystrom (1♀ NHRS); Musola, 500-800m (3°26'N, 8°38'E), i-iii.1902, L. Fea (1♂ TMSA; 2♀♀ MCG); **GABON:** Ogowé (1♀ ZMHB); **OGOOUÉ-IVINDO:** Ivindo National Park, Ipassa Research Station, 510m (0°31'N, 12°48'E), i.2006, Forti (1♂ 2♀♀ PMOC); Mpassa [=Ipassa] (0°31'N, 12°48'E), 12-13.xii.1983, P. Walter (1♂ 1♀ JLMC).

**Diagnosis:** This species and the two subsequent species are all very similar in appearance, but there are a number of characters to distinguish among the species. The males of *C. gorilloides* can easily be separated from *C. gorilla* and *C. leo* by the convex anterior portion of the lateral margin of the pronotum and anteriorly smooth pronotal disc. In well-developed males, the cephalic horn is subconical in *C. gorilloides* whilst it is triangular or arcuate in *C. gorilla* and *C. leo*. The females are very similar in appearance but the punctuation of the first abdominal sternite is much finer in *C. gorilloides*.

**Biology:** this species is found in lowland forest habitats in Central Africa. It is sympatric with *C. gorilla* throughout much of its range and both species are often caught in the same pitfall traps. It appears *C. gorilloides* is not found west of the Cross River or east of the Congo River and is also one of the few species to be recorded from Bioko Island. It has been found in elephant dung and collected in human and gorilla dung baited pitfall traps, as well as being attracted to light. Specimens have been caught between November and July.

**Distribution** (Pl. 4: fig. 8): Cameroon, Equatorial Guinea, Gabon, Congo, D.R. Congo (?).

## 5. *Catharsius gorilla* (Thomson, 1858)

(Pl. 5: figs 1-8; Pl. 30: fig. 5)

*Copris gorillus* Thomson, 1858: 51.

*Catharsius gorilla* (Thomson, 1858): Gemminger & Harold, 1869: 1012; Kolbe, 1893: 138; Ferreira, 1960a: 23.

**Type locality:** “Gabon”

**Name-bearing type:** 17 syntypes (10♂♂ 7♀♀) in IRSNB. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the male specimen closest in appearance to that figured by Thomson in his original description is here **designated as the lectotype**: “// Type [grey card with black border; red print] // 1443 // Coll. J. Thomson // *Catharsius* / *gorillus* Thoms. / det. J. Gillet 1913 // LECTOTYPE / COPRIS / *gorillus* / Thomson / det. H Takano 2017 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black; pubescence reddish-brown. **Male** (Pl. 5: figs. 1, 2, 5): **Head:** anterior clypeal edge broadly arcuate with a slight concavity centrally; clypeal margin continuous; clypeal

surface with short transverse rugulae turning more granulose towards the clypeogenal suture. Genal edge rounded and obtusely angled, surface covered with ovaline granules disappearing completely towards the eyes. Clypeogenal suture well defined to base of an incomplete clypeal carina. A triangular laterally flattened cephalic horn positioned anteriorly of the clypeal carina on clypeus; horn, erect, gently slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin emarginate centrally. Lateroanterior margin acutely angled, lateral margin concave anteriorly and arcuate posteriorly; Pronotal disc with an angled transverse carina anteriorly; the central portion of disc, slightly wider than the distance between the eyes, is extended forward, the carina arcuate laterally and gently emarginate centrally; lateral portions of the carina arcuate from the obtuse angle with the extended central portion and termination point. Carina with weak serrations along the lateral portions; total length of carina no wider than the widest point of the pronotum. The lateroposterior edge of pronotal disc at 45° to the posterior margin; Surface of pronotal disc completely granulose, larger and more diamond-shaped anteriorly, becoming more circular posteriorly; lateral declivity with fovea, the surface totally granulose with alutaceous microsculpture in between; the anterior declivity in frontal view with a distinct depression under the obtuse angle of the carina on either side of the midline; surface completely granulose, the circular granules turning more transversely ovaline centrally and with alutaceous microsculpture throughout. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 5: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 5).

**Female** (Pl. 5: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate; clypeal margin continuous; clypeal surface transversely rugulate turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with ovaline granules disappearing completely towards the eyes. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin emarginate centrally. Lateroanterior margin almost at right-angles, lateral margin gently concave anteriorly and arcuate posteriorly; Pronotal disc with a short, straight transverse carina anteriorly, emarginate medially; carina as wide as the distance between the eyes; a very short carina runs posteriorly along the midline from the carina. Surface of pronotal disc completely granulose, larger and more transversely ovaline anteriorly, becoming smaller and circular posteriorly; some alutaceous

microsculpture on the disc posteriorly; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulose and with alutaceous microsculpture throughout. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 20-28mm; female 21-26mm.

**Variation:** the shape of the male cephalic horn is variable, some individuals having an isosceles-shaped triangular horn with concave sides, others having an apically arcuate and parallel-sided horn. In smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the pronotal carina is reduced to a gently arcuate carina. In smaller females, the height of the clypeal carina is reduced and the pronotal carina becomes more arcuate in shape.

**Other material examined (206♂♂ 167♀♀):**

**ANGOLA: CABINDA:** Chiloango, M. Tschuffen (1♂ 1♀ IRSNB); Landana (5°14'S, 12°09'E), L. Petit (1♂ 4♀♀ IRSNB; 1♀ RMNH); Landana (5°14'S, 12°09'E), 1883, L. Petit (2♀♀ MNHN); **CAMEROON:** [no precise locality] 1898-99, L. Conradt (4♂♂ 1♀ MNHN); [no precise locality] (1♂ 3♀♀ MNHN); [no precise locality] (3♂♂ 1♀ BMNH); [no precise locality] (7♂♂ 2♀♀ MTD); [no precise locality] Sjøstedt (24♂♂ 11♀♀ NHRS; 1♂ 1♀ IRSNB); [no precise locality] P. Elsen (1♂ IRSNB); [no precise locality], 1887, Rutherford (2♂♂ NMPC); **CENTRE:** Jaunde-station [=Yaounde] (3°51'N, 11°31'E), Zenker (1♂ 2♀♀ ZMHB); Mont Kala (3°58'N, 11°24'E), 22.viii.1988, D. Bernaud (1♂ MHNL); Region de Samba (3°22'N, 11°01'E), Carret (1♂ MNHN); **EAST:** Akonangi (2°12'N, 11°21'E), iii-iv.1909, Tessmann (1♂ 1♀ ZMHB); 12km Mimpala (3°25'N, 13°09'E), 24.iii.2012, M-H. Zinque (8♂♂ 8♀♀ IRSNB); **LITTORAL:** Dibongo (3°42'N, 10°01'E) (1♂ 1♀ MTD); Dibongo (3°42'N, 10°01'E) (1♂ ZMHB); Douala (4°02'N, 9°44'E) (1♂ 1♀ MNHN); Edea (3°47'N, 10°08'E) (34♂♂ 30♀♀ IRSNB); Edea (3°47'N, 10°08'E), J-J. van Mol (1♀ MRAC); Japoma (4°02'N, 9°49'E), Dr. Schafer (1♂ ZMHB); Nkongsamba (4°58'N, 6°56'E), M. Delpont (1♂ MHNL); **SOUTHWEST:** Barombi-station (4°39'N, 9°25'E), Zeuner (8♂♂ 1♀ ZMHB); Johann Albrechtshöhe (4°39'N, 9°25'E), L. Conradt (2♂♂ 4♀♀ ZMHB); Kumba (4°38'N, 9°27'E), 20.xi.1955, Bechyne (2♂♂ 2♀♀ NMB); Malende (4°20'N, 9°26'E), xii.1957, W. Hartwig (1♂ 1♀ NMB); Rio del Rey (4°34'N, 8°44'E), H.H. Johnston (1♂ BMNH); Victoria (4°00'N, 9°13'E) (1♀ MTD; 1♀ NMB); **SOUTH:** Akoafim (2°19'N, 12°45'E), Tessmann (1♀ ZMHB); Batanga (2°51'N, 9°53'E) (1♂ ZMHB); Bipindi (3°05'N, 10°25'E), G. Zenker (1♂ ZMHB); Region de Kribi (2°57'N, 9°55'E), Carret (1♀ MNHN); Kribi (2°57'N, 9°55'E), 1890, Morgen (1♂ 2♀♀ ZMHB); Kribi (2°57'N, 9°55'E), 20.ii.1906, G. Tessmann (1♂ ZMHB); Lolodorf (3°14'N, 10°44'E), L. Conradt (2♀♀ ZMHB); Lolodorf (3°14'N, 10°44'E), 8.ii-27.iii.1895, L. Conradt (1♂ NMPC); Londji (1♂ ZMHB); Obem (2°42'N, 11°31'E), 15.ii.1989, D. Bernaud (2♀♀ MNHL); **CENTRAL AFRICAN REPUBLIC: OMBELLA-M'POKO:** Bangui (4°23'N, 18°33'E), M. André (1♂ MHNL); **SANGHA-MBAËRÉ:** Parc National Ndoki, Camp I (2°29'N, 16°13'E), 13.ii-6.iii.2002, P. Moretto & A. Monziagou (7♂♂ 9♀♀ BMNH); Bayanga (2°55'N, 16°16'E), 16.iii-6.iv.1996, P. Moretto (4♂♂ 2♀♀ PMOC); **CONGO: CUVETTE:** Diele (1°41'S, 14°45'E), 1886, de Brazza (1♀ MNHN); **KOUILOU:** Zambi [=Nzambi] (3°58'S, 11°17'E), C. Haas (1♂ IRSNB); Zambi [=Nzambi] (3°58'S, 11°17'E), M. Tschuffen (1♂ IRSNB); Thoumby [=Toumby] (4°36'S, 11°55'E), 1883, L. Petit (3♀♀ MNHN); **NIARI:** Tsingidi (2°24'S, 12°58'E), xi.2013, J. Niemand (10♂♂ 13♀♀ TMSA); **D.R. CONGO:** [no precise locality] A. Curror (1♂ 1♀ BMNH); **BANDUNDU:** Beni Bendi (4°17'N, 20°22'E) (1♂ 1♀ IRSNB); **KASAI:** Dekese (3°29'S, 21°23'E), i.1960, F. Francois (1♂ MRAC); Dekese (3°29'S, 21°23'E), xii.1959 (3♂♂ 1♀ RMNH); **KONGO CENTRAL:** Banana (5°59'S, 12°23'E) (1♂ RMNH); Banana (5°59'S, 5°23'E), F. Busschodts (4♂♂ 2♀♀ IRSNB; 1♂ MNHN); Congo da Lemba (5°42'S, 13°40'E) (2♂♂ 1♀ IRSNB); Camp de Lukula (5°24'S, 12°57'E), 1911, Dr. Daniel (1♀ MRAC); Lukula (5°24'S, 12°57'E), iv.1930 (1♂ MRAC); Lukula (5°24'S, 12°57'E), vii.1946, Dr. Darteville (1♂ 1♀ MRAC); Kisantu (5°08'S, 15°05'E), Goosens (1♂ MRAC); Mayumbe (5°27'S, 12°52'E), Deleval (1♀ MRAC); Mayumbe (5°27'S, 12°52'E), Lemire (1♀ IRSNB); Mayumbe (5°27'S, 12°52'E), 19.xi.1912, R. Verschuere (1♂ 1♀ MRAC); Mvuangu (5°32'S, 12°43'E), 21.i.1972, Rambouts (1♀ MHNL); Mvuangu (5°32'S, 12°43'E), 15.xii.1973, Rambouts (1♀ MHNL); Mvuangu (5°32'S, 12°43'E), 6.i.1974, Rambouts (1♀ MHNL); **TSHOPO:** Opala (0°31'S, 24°14'E), xi.1952, Meewis (2♀♀ MRAC); Barumbu (1°15'N, 23°29'E) (3♂♂ MTD); **TSHUAPA:** Etata (0°14'S, 20°42'E), xi-xii.1971, J. Hauwaerts (1♂ MRAC); Etata (0°14'S, 20°42'E), vii-viii.1969, J. Hauwaerts (1♂ MRAC); Ikela (1°03'N, 23°22'E), 1955, Rev. Lootens (1♂ 1♀ NMPC); Ikela (1°03'N, 23°22'E), ix.1956,

Rev. Lootens (1♂ 2♀♀ MRAC); Ikela (1°03'N, 23°22'E), 1956, R. Deguide (2♀♀ MRAC); **EQUATORIAL GUINEA:** [no specific data] L. Petit (1♂ IRSNB); [no specific locality] A. Aniamova (1♀ NHRS); [no precise locality] Tessmann (2♂♂ 1♀ ZMHB); **CENTRO-SUR:** Nkolentangan (1°35'N, 10°30'E), xi.1907-v.1908, G. Tessmann (4♀♀ ZMHB); **LITORAL:** Benito [=Mbini] (1°35'S, 9°37'E) (2♂♂ 3♀♀ ZMHB); Makomo campogebiet (1°44'N, 9°46'E), 1-15.iv.1906, G. Tessmann (2♂♂ ZMHB); Mongo (1°52'N, 10°10'E), 13.vi.1947, J. Palau (2♂♂ 3♀♀ MRAC); San-Benito [=Mbini] (1°35'S, 9°37'E), 1885, Guiral (1♂ 6♀♀ MNHN); Uelleburg [=Mbini] (1°35'S, 9°37'E), vi-viii.1908, G. Tessmann (3♀♀ ZMHB); **GABON:** [no precise locality] (2♂♂ 1♀ MNHN); [no precise locality] (2♂♂ 2♀♀ IRSNB); [no precise locality] (1♂ MTD); [no precise locality] (1♂ BMNH); **ESTUAIRE:** Libreville environs (0°20'N, 9°29'E), vi.1914, G. Babault (11♂♂ MNHN); **HAUT-OGOOUÉ:** Haut-Ogooue (1♂ IRSNB); **NGOUNIÉ:** Mouila (1°52'S, 11°03'E), G. Le Testu (1♂ MNHN); **NYANGA:** Tschibanga (2°55'S, 11°00'E), G. Le Testu (1♂ MNHN); **OGOOUÉ-IVINDO:** region du Haut-Ivindo, 1906, Dr. J. Gravot (1♂ MNHN); Talagouga pres N'jole [=Ndjole] (0°11'S, 10°46'E), E. Ellenberger (1♂ MNHN); Ivindo, Station d'Ipasa (0°31'N, 12°48'E), 15-17.xi.2009, G. Lecourt (1♂ PMOC); Belinga (1°08'N, 13°07'E), 9.ii.1963, H. Coiffai (1♂ MNHN); Ivindo National Park, Ipasa Research Station, 450m (0°31'N, 12°48'E), 14-26.vi.2006, E. Ruzzier & T. Tassane (2♂♂ 12♀♀ BMNH); **OGOOUÉ-LOLO:** Dilo, 600m (0°01'S, 13°02'E), iv.1992, Pageix (1♂ PMOC); Lastoursville (0°49'S, 12°44'E), G. Le Testu (2♂♂ MNHN); **OGOOUÉ-MARITIME:** Bas-Ogoue (4♂♂ 3♀♀ IRSNB); Bas-Ogoue, Favarel (1♀ NMB); Kivoro (2°17'S, 10°09'E), vii.1965 (1♀ MHNL); entre Lambarene et la Mer (0°53'S, 9°34'E), 1901, E. Haug (1♂ 1♀ MNHN); Milango (0°24'S, 9°38'E), vii.1965 (1♀ MHNL); Wonga-Wongué (0°29'S, 9°18'E), 15.iii.1972, J. Wyon (3♂♂ 3♀♀ MHNL); **NIGERIA:** [no precise locality] F. Winn Sampson (1♀ BMNH); [no precise locality] J.D. Kennedy (1♀ BMNH); [no specific data] (1♂ MTD); **ANAMBRA:** Onitsha (6°08'N, 6°47'E), 1903 (1♂ BMNH); **CROSS RIVER:** Calabar (4°57'N, 8°20'E), 1916, J.G. Sol (1♀ MNHN); Calabar (4°57'N, 8°20'E), Dr. J. Currie (2♀♀ BMNH); Old Calabar (4°57'N, 8°20'E) (2♂♂ IRSNB); Old Calabar (4°57'N, 8°20'E) (5♂♂ 1♀ MNHN); Old Calabar (4°57'N, 8°20'E) (2♂ BMNH); Old Calabar (4°57'N, 8°20'E) (1♀ NHRS); Old Calabar (4°57'N, 8°20'E) (2♂♂ NMPC); Old Calabar (4°57'N, 8°20'E), J.W. Cockburn (1♂ 1♀ BMNH); Old Calabar (4°57'N, 8°20'E), Miss M. Kingsley (2♂♂ 1♀ BMNH); Oban district (5°13'N, 8°33'E), P.A. Talbot (1♂ 1♀ BMNH); **LAGOS:** Lagos (6°27'N, 3°24'E) (1♂ MNHN); Lagos district (6°27'N, 3°24'E), viii.1949, W.E.S. Merrett (1♂ 1♀ BMNH); Oni (6°32'N, 4°14'E), 1.vi.1912, W.A. Lamborn (1♀ OUMNH).

**Notes:** the type specimens were collected by Henri Deyrolle in “Gabon” under the auspices of Count Georges de Mniszech and James Thomson. Gabon in this historical context refers to the region in the Bight of Biafra to the south of the southern border of Cameroon. At the time of this expedition, French occupation had continued to expand northwards along the coastline from Libreville into modern day Equatorial Guinea, despite the Spanish sovereignty in this region (Deschamps, 1963). Deyrolle stepped foot onto mainland Africa on 6<sup>th</sup> September 1856 at Benito, situated “25 leagues” or 100km from Presqu’ile Louis Philippe [=Cap Santa Clara] (Thomson, 1859). The type locality is therefore likely to be in Equatorial Guinea in the vicinity of Benito [=Mbini] at the mouth of the Benito River, rather than in Gabon.

**Diagnosis:** see under *C. gorilloides*. Very similar in appearance to *C. leo* but the lateroposterior edge of the pronotal disc is angled further forward at 45° to the posterior margin in *C. gorilla*. As these two species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** this species is found in lowland forest habitats east of the Dahomey Gap. It has been found in elephant dung and collected in human and gorilla dung baited pitfall traps, as well as regularly being attracted to light. Specimens have been caught throughout the year.

**Distribution** (Pl. 5: fig. 8): Angola, Gabon, Equatorial Guinea, Congo, D.R. Congo, Central African Republic, Cameroon, Nigeria.

## 6. *Catharsius leo* sp. nov.

(Pl. 6: figs. 1-8; Pl. 30: fig. 6)

**HOLOTYPE** ♂ (BMNH):

“// SIERRA LEONE 420m / Loma Mountains / farmland/forest mosaic / N09°07'47”; W11°05'24” / 11-15.vi.16 Dung Pitfall / leg. Takano, Miles & Goff //”

**Description:** Holotype ♂ (Pl. 6: figs. 1, 2, 5): Body: Colour: Black, pubescence reddish-brown. Length: 27mm.

**Head:** anterior clypeal edge broadly arcuate with a slight concavity centrally; clypeal margin continuous; clypeal surface with short transverse rugulae turning more granulose towards the clypeogenal suture. Genal edge rounded and obtusely angled, surface covered with ovaline granules anteriorly disappearing completely towards the eyes. Clypeogenal suture well defined to base of an incomplete clypeal carina. A triangular, basally parallel-sided, laterally flattened cephalic horn positioned anteriorly of the clypeal carina on clypeus; horn, erect, gently slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin emarginate centrally. Lateroanterior margin acutely angled, lateral margin concave anteriorly and arcuate posteriorly; Pronotal disc with an angled transverse carina anteriorly; the central portion of carina arcuate and slightly emarginate centrally, before angling back towards the termination point; carina with a slight concavity half way along between the midpoint and termination point; carina sinuous intermittently; total length of carina wider than the widest point of the pronotum. The lateroposterior edge of pronotal disc at less than 45° to the posterior margin; Surface of pronotal disc with evenly-spaced circular granules, turning more diamond shaped and tighter-packed in the very anterior regions near the carina; alutaceous microsculpture throughout the central and posterior regions of the disc; lateral declivity with fovea, the surface totally granulose with alutaceous microsculpture in between; the anterior declivity in frontal view with a distinct depression under the concavity of the carina on either side of the midline; surface completely granulose, the circular granules turning more transversely ovaline centrally and with alutaceous microsculpture throughout; a very short and narrow region along the midline near the anterior margin of the pronotum smooth, without granules or any microsculpture. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 6: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 6).

**FEMALE PARATYPE** (Pl. 6: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate; clypeal margin continuous; clypeal surface transversely rugulate turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with ovaline granules disappearing completely towards the eyes. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin emarginate centrally. Lateroanterior margin almost at right-angles, lateral margin gently concave anteriorly and arcuate posteriorly; Pronotal disc with a short, slightly arcuate transverse carina anteriorly, emarginate medially; carina as wide as the distance between the eyes; a very short carina runs posteriorly along the midline from the carina. Surface of pronotal disc completely granulose, larger and more transversely ovaline anteriorly, becoming smaller and circular posteriorly; some alutaceous microsculpture on the disc posteriorly; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulose and with alutaceous microsculpture throughout. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 25-28mm; female 23-26mm.

**Variation:** the shape of the male cephalic horn is variable, some individuals having an isosceles-shaped triangular horn with concave sides, others having an equilateral shaped horn with arcuate sides. In smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the width of the pronotal carina is reduced to no wider than the widest point of the pronotum.

**PARATYPES** (44♂♂ 51♀♀):

**GUINEA:** SEREDOU: Foret de Ziama (8°11'N, 9°16'W), 28.x.2013, J. Pennancier (1♂ 2♀♀ PMOC); Seredou (8°22'N, 9°17'W) (1♂ ZMHB); **IVORY COAST:** ABIDJAN: Abidjan (5°19'N, 4°02'W), iv.1997, P. Moretto (2♂♂ 1♀ MHNH); Banco (5°23'N, 4°03'W), A. Ture (4♂♂ 1♀ PMOC); Parc National du Banco, Banco Forest, 39-48m (5°23'N, 4°03'W), 23-30.iv.2017, A. Aristophanous, M. Aristophanous, M. Geiser & P. Moretto (3♂♂ 3♀♀ BMNH); COMOE: Assinie (5°09'N, 3°19'W), 1885, Treich (1♂ 1♀ IRSNB; 1♀ MNHN); Assinie (5°09'N, 3°19'W), 1886, C. Alluaud (2♂♂ 2♀♀ IRSNB); LAGUNES: Adiopodoumé (5°20'N, 4°08'W), 16.vii.1966, D. Thys & W. Verheyen (1♀ MRAC); Adiopodoumé (5°20'N, 4°08'W), 1967, P.J. Hummelen (1♀ RMNH); Akoupé (5°29'N, 4°09'W), vi.1962, J. Decelle (1♂ 1♀ MRAC; 1♂ NMPC); IRHO [=l'Institut de Recherches pour les Huiles et Oleagineux], Route d'Alepe, A. Ture (1♂ PMOC); MONTAGNES: ca 3km W Tai Research Station (SRET), 205m (5°51'N, 7°21'W), 8-14.iv.2017, Aristophanous, A., Aristophanous, M., Geiser, M. & Moretto, P. (1♀ BMNH); Yéalé village, Mt Nimba, track before reserve border, 376m (7°32'N, 8°25'W), 18-29.iv.2016, M. Aristophanous, M. Geiser & P. Moretto (12♂♂ 2♀♀ BMNH); **LIBERIA:** LOFA: Foya Proposed Protected Area, 530m (7°57'N, 10°17'W), 10-19.xi.2017, M. Aristophanous, S. Safian, G. Simonics & L. Smith (16♂♂ 27♀♀ BMNH); Mount Wologizi base camp, 611m (8°07'N, 9°58'W), 20.xi-1.xii.2017, M. Aristophanous, S. Safian, G. Simonics & L. Smith (6♂♂ 4♀♀ BMNH); Mount Wologizi ridge camp, 865m (8°07'N, 9°57'W), 24-29.xi.2017, M. Aristophanous, S. Safian, G. Simonics & L. Smith (2♀♀ BMNH); **SIERRA LEONE:** NORTHERN: Loma Mountains, 420m (9°08'N, 11°05'W), 11-15.vi.2016, Takano, Miles & Goff (8♂♂ 5♀♀ BMNH).

**Diagnosis:** see under *C. gorilloides* and *C. gorilla*. Very similar in appearance to *C. gorilla* with which it has been confused in the past but can be separated by the lateroposterior edge of the pronotal disc which is angled at less than 45° to the posterior margin in *C. leo*. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** this species is found in lowland forests to the west of the Dahomey Gap. The author has caught this species in disturbed forests at the foothills of the Loma Mountains in Sierra Leone, to human dung baited pitfall traps, rotting snake and at light. Specimens have been caught between April and December.

**Derivatio nominis:** this species is named after the lion; in reference to the similar *C. gorilla* and *C. rhinoceros* being named after iconic African animals, as well as the country of the type locality, Sierra Leone.

**Distribution** (Pl. 6: fig. 8): Sierra Leone, Guinea, Liberia, Ivory Coast.

## 7. *Catharsius rhinoceros* (Klug, 1855)

(Pl. 7: figs. 1-8; Pl. 30: fig. 7)

*Copris rhinoceros* Klug, 1855: 655; Peters, 1862: 239.

*Catharsius rhinoceros* (Klug, 1855): Gemminger & Harold, 1869: 1013; Péringuey, 1901: 328; Ferreira, 1960a: 37; 1967: 247.

**Type locality:** “Tette” [= Tete (16°10’S, 33°36’E), Mozambique]

**Name bearing type:** 5 syntypes (3♂♂ 2♀♀) in ZMHB. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series is here **designated as the lectotype**:

“// Type [orange card] // 9345 // rhinoceros / Kl. / Tette Peters. [turquoise card with black border; handwritten] // LECTOTYPE / COPRIS / rhinoceros / Klug / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription: Male** (Pl. 7: fig. 1, 2, 5): Colour: Slaty-black; pubescence dark brown. **Head:** anterior clypeal edge broadly arcuate with a slight concavity centrally; clypeal margin continuous; clypeal surface granulate, becoming finer and more spaced out towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with diamond-shaped granules becoming finer and disappearing completely towards the eyes. Clypeogenal suture well defined to base of an incomplete clypeal carina. A basally rectangular, apically triangular laterally flattened cephalic horn positioned anteriorly of the clypeal carina on clypeus; the triangular portion slightly carinate, the rectangular portion slightly truncate; horn, erect, gently slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin acutely angled,

lateral margin deeply concave anteriorly turning arcuate posteriorly. Pronotal disc with an arcuate transverse carina anteriorly; slightly emarginate centrally and arcing back almost to the posterior margin of the disc; the lateral portions follow the outline of the posterior margin the lateral-most point projecting beyond the widest point on the pronotum; carina with intermittent serrations, more frequently centrally and laterally; The lateroposterior edge of pronotal disc at less than 45° to the posterior margin; Surface of pronotal disc completely granulose, larger and more ovaline anteriorly, becoming more spaced out and circular posteriorly; fine alutaceous microsculpture throughout disc; lateral declivity with fovea; surface of lateral and anterior declivity granulose with alutaceous microsculpture in between; a narrow ovaline region of the anterior declivity following the midline near the anterior margin lacks granules. **Elytra**: carinate basally; elytral striae shallow with very indistinct punctures. Interstriae with irregularly-shaped vesicular granules and alutaceous microsculpture throughout; epipleural carina well-developed, extending three quarters of the length of the elytra. **Pygidium**: transverse, fully margined, rugose with deep punctures and alutaceous microsculpture. **Ventrites**: covered in dark brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with some short pubescence. **Legs**: protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence; **Aedeagus** (Pl. 7: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 7).

**Female** (Pl. 7: figs. 3, 4, 6): **Head**: anterior clypeal edge evenly arcuate; clypeal margin continuous; clypeal surface with short transverse rugulae turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with elongate granules disappearing completely towards the eyes. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum**: anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin almost at right-angles, lateral margin gently concave anteriorly and arcuate posteriorly; Pronotal disc with a short, gently arcuate transverse carina anteriorly, emarginate medially; carina as wide as the distance between the eyes; a very short carina runs posteriorly along the midline from the carina. Surface of pronotal disc completely granulose, larger and more transversely ovaline anteriorly, becoming smaller and circular posteriorly; alutaceous microsculpture throughout the disc; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulose and with alutaceous microsculpture throughout. **Elytra**: carinate basally; elytral striae shallow with very indistinct punctures. Interstriae with irregularly-shaped vesicular granules and alutaceous microsculpture throughout; epipleural carina well-developed, extending three quarters of the length of the elytra. **Pygidium**: transverse, fully margined, rugose with deep punctures and alutaceous microsculpture. **Ventrites**: covered in dark brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with some short pubescence. **Legs**: protibia

quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 20-30mm; female 19-30mm.

**Variation:** in smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the pronotal carina is reduced to a gently arcuate carina.

### Other material examined (101♂♂ 91♀♀):

**KENYA:** **KILIFI:** Arabuko Forest (3°15'S, 39°58'E), 16.viii.2000, M. Mungai, C. Lange & D. Karanja (1♀ NMK); Dida (3°26'S, 39°48'E), vii.1941, H.F. Stoneham (2♂♂ 1♀ NMK); Kilifi (3°30'S, 39°55'E), 1944, V.G.L. van Someren (2♂♂ BMNH); Malindi (3°13'S, 40°07'E), 19.v.1941, G.W. Jeffery (1♂ 1♀ BMNH); Sokoke (3°32'S, 39°49'E), A. Turner (4♂♂ NMK); Sokoke Forest, SW of Kararacha (3°25'S, 39°53'E), 5.x.1979, C. Smeenk (2♀♀ RMNH); **KITUI:** Ikutha (2°04'S, 38°11'E), F. Schneider (1♂ IRSNB); **KWALE:** Kwale (4°10'S, 39°27'E), iv.1987, G. Lecourt (8♂♂ 5♀♀ MHNL; 3♂♂ 1♀ PMOC; 2♂♂ JLMC); Shimba Hills, 1000ft. (4°15'S, 39°23'E), vii.1939 (2♀♀ NMK); Shimba Hills (4°15'S, 39°23'E), iii.1941, V.G.L. van Someren (1♂ 2♀♀ BMNH); Shimba Hills, Makadara Forest (4°14'S, 39°23'E), 17.x.1979, C. Smeenk (2♂♂ 4♀♀ RMNH); Shimba Hills, Makadara Forest (4°14'S, 39°23'E), 26.x.1979, C. Smeenk (4♂♂ 1♀ RMNH); Shimba Hills National Park (4°15'S, 39°23'E), 14.xii.1989, Moreno & Mestre (9♀♀ JLMC); **MOZAMBIQUE:** **CABO DELGADO:** Kionga [=Quionga] (10°36'S, 40°30'E) (1♂ MTD); Namaluco (site 1), Parque Nacional das Quirimbas, 130m (12°19'S, 40°17'E), 29.xii.2012, F. & S. Génier (4♀♀ FGIC); Namaluco (site 2), Parque Nacional das Quirimbas, 160m (12°19'S, 40°17'E), 29.xii.2012, F. & S. Génier (3♂♂ 6♀♀ FGIC); Namaluco (site 4), Parque Nacional das Quirimbas, 180m (12°19'S, 40°15'E), 29.xii.2012, F. & S. Génier (8♂♂ 8♀♀ FGIC); Namaluco (site 5), Parque Nacional das Quirimbas, 190m (12°18'S, 40°15'E), 29.xii.2012, F. & S. Génier (11♂♂ 15♀♀ FGIC); Porto Amelia [=Pemba] (12°58'S, 40°29'E), v.1959, F. Gomes (1♂ TMSA); Ravia (site 1), Parque Nacional das Quirimbas, 380m (12°40'S, 39°25'E), 3.i.2013, F. & S. Génier (1♀ FGIC); Ravia (site 2), Parque Nacional das Quirimbas, 340m (12°40'S, 39°26'E), 3.i.2013, F. & S. Génier (1♀ FGIC); Ravia (site 3), Parque Nacional das Quirimbas, 380m (12°40'S, 39°26'E), 3.i.2013, F. & S. Génier (1♂ 3♀♀ FGIC); Ravia (site 4), Parque Nacional das Quirimbas, 380m (12°40'S, 39°27'E), 3.i.2013, F. & S. Génier (11♂♂ 10♀♀ FGIC); Ravia (site 5), Parque Nacional das Quirimbas, 390m (12°41'S, 39°27'E), 3.i.2013, F. & S. Génier (5♂♂ 4♀♀ FGIC); Taratibu (site 2), Parque Nacional das Quirimbas, 350m (12°49'S, 39°42'E), 8.i.2013, F. & S. Génier (2♀♀ FGIC); Taratibu (site 2), Parque Nacional das Quirimbas, 350m (12°49'S, 39°42'E), 9.i.2013, F. & S. Génier (2♂♂ 2♀♀ FGIC); Taratibu (site 2), Parque Nacional das Quirimbas, 350m (12°49'S, 39°42'E), 10.i.2013, F. & S. Génier (1♂ 1♀ FGIC); Taratibu (site 3), Parque Nacional das Quirimbas, 340m (12°48'S, 39°42'E), 8.i.2013, F. & S. Génier (15♂♂ 9♀♀ FGIC); Taratibu (site 3), Parque Nacional das Quirimbas, 340m (12°48'S, 39°42'E), 9.i.2013, F. & S. Génier (7♂♂ 5♀♀ FGIC); Taratibu (site 3), Parque Nacional das Quirimbas, 340m (12°48'S, 39°42'E), 10.i.2013, F. & S. Génier (1♂ FGIC); Taratibu (site 6), Parque Nacional das Quirimbas, 300m (12°50'S, 39°42'E), 10.i.2013, F. & S. Génier (2♂♂ 1♀ FGIC); **MANICA:** Amatongas (19°15'S, 33°50'E) (1♀ TMSA); Amatonga Forest (19°15'S, 33°50'E), ii.1950 (1♂ TMSA); Espungabera (20°27'S, 32°47'E), 22.x.1954, M.C. & G.V. Ferreira (1♂ TMSA); 10mi E Gondola (19°05'S, 33°49'E), 9.i.1972, Bornemissza & Kirk (9♂♂ 4♀♀ SANC; 1♀ BMNH); **SOFALA:** 15mi N Beira (19°37'S, 34°51'E), 19.i.1972, Bornemissza & Kirk (1♂ SANC); Chinizua (18°57'S, 35°08'E), v.1957, G. de Sousa (1♂ TMSA); 5mi NW Dondo (19°34'S, 34°41'E), 19.i.1972, Bornemissza & Kirk (6♂♂ 23♀♀ SANC; 1♂ BMNH; 1♂ MNHN); Marromeu (18°18'S, 35°56'E), van Eldik (2♀♀ RMNH); **TANZANIA:** [no precise locality] (2♂♂ 1♀ NMPC); [no precise locality] H.J. Schreiber (1♂ MTD); [no precise locality] (2♂♂ NHRS); **DAR ES SALAAM:** Dar es Salaam (6°49'S, 39°17'E) (1♂ 2♀♀ IRSNB); Dar es Salaam (6°49'S, 39°17'E), V.M. Duchon (3♂♂ 2♀♀ IRSNB); Dar es Salaam (6°49'S, 39°17'E) (3♂♂ MNHN); Dar es Salaam (6°49'S, 39°17'E), R. von Bennigsen (1♂ MTD); Dar es Salaam (6°49'S, 39°17'E) (7♂♂ 2♀♀ ZMHB); Dar es Salaam (6°49'S, 39°17'E) (6♂♂ 2♀♀ MTD); **LINDI:** Lindi (10°00'S, 39°42'E) (1♂ MTD); Rondo Plateau, 769m (10°07'S, 39°14'E), 20.vii.2011, P. Darge (5♂♂ 24♀♀ MHNL); **MOROGORO:** Morogoro (6°50'S, 37°40'E) (1♂ MTD; 2♀♀ NMB); Udzungwa Mountains (7°40'S, 36°59'E), vi.2000 (1♂ BMNH); Uluguru Mountains (7°01'S, 37°44'E), iii.1995, R. Minetti (1♂ PMOC); Uhehe (1♂ 1♀ ZSM); **PWANI:** 15km W Kibiti (7°43'S, 39°04'E), 15-17.i.2007, A. Kudurna Jr. (1♂ PMOC); Madinula [=Madimola] (6°43'S, 38°44'E), S.P. Illaire (1♀ ZMHB); Matumbi Highlands, R. Mwengei ponds, 1050ft. (8°21'S, 38°58'E), 30.xi.1989, W.R.B. Hynd (1♀ BMNH); Pugu (6°52'S, 39°10'E), xii.1913 (1♀ ZMHB); Rufiji, 150m (7°47'S, 38°15'E), ii.2015, local collector (3♂♂ 3♀♀ BMNH); Zaraninge Forest, Sadaani National Park, 200m (6°09'S, 38°36'E), x-xi.1994 (4♀♀ BMNH); **RUVUMA:** Kigonsera (10°48'S, 35°04'E) (1♂ 1♀ NHRS); **MTWARA:** Mikindani (10°17'S, 40°07'E) (4♂♂ 2♀♀ ZMHB); **TANGA:** Usambara (5°07'S, 38°32'E) (5♂♂ 6♀♀ ZMHB; 1♂ NMB); Usambara Mountains (5°07'S, 38°32'E), A.J. Bois (1♂ 1♀ RMNH); **ZIMBABWE:** [no precise locality] T. Bent (1♂ BMNH); **MANICALAND:** Christmas Pass (18°57'S, 32°38'E), 1892, F.C. Selous (1♂ SANC; 1♀ SAMC); Chirinda, 3800ft. (20°25'S, 32°42'E), iv.1908 (1♂ 1♀ BMNH); Mount Chirinda (20°25'S, 32°42'E), xii.1901, G.A.K. Marshall (1♂ BMNH); Mount Chirinda (20°25'S, 32°42'E), 1906, Swynnerton (3♂♂ 2♀♀ BMNH; 1♂ IRSNB); Mount Chirinda (20°25'S, 32°42'E), xi-xii.1906, D. Odendaal (1♂ 1♀ BMNH); Mount Chirinda (20°25'S, 32°42'E), xi.1907, D. Odendaal (2♂♂ 1♀ BMNH).

**Notes:** Specimens collected by Walter von Saint Paul-Illaire labelled as “Madinula” in the ZMHB refer undoubtedly to Madimola (6°43’S, 38°44’E), the station founded by him in the Ruvu River valley (Anonymous, 1887). The incorrectly transcribed “Madinula” labels were printed and seem to be attached to a small collection of beetles referred to by Kolbe (1897).

**Diagnosis:** an unmistakable species. The males possess a uniquely shaped serrated pronotal carina, whilst the distinctive sculpture of the elytra make both sexes easy to identify.

**Biology:** this species is found in coastal regions from south-eastern Kenya as far south as the Save River in Mozambique. This species is regularly attracted to light. In Kenya, one specimen from Arabuko Forest was found in elephant dung and a number of individuals were caught in mist nets set up in the Shimba Hills. Specimens have been caught between October and August.

**Distribution** (Pl. 7: fig. 8): Mozambique, Zimbabwe, Tanzania, Kenya.

## 8. *Catharsius dominus* sp. nov.

(Pl. 8: figs. 1-8; Pl. 30: fig. 8)

**HOLOTYPE** ♂ (BMNH):

“// Uganda Prot. / Mbale-Kumi Rd. / 3,700ft. S. of / L. Salisbury. Aug. 15-17, 1911. / S.A. Neave. // 1912-193. //”

**Description:** Holotype ♂ (Pl. 8: figs. 1, 2, 5): Body: Colour: Black, pubescence reddish-brown. Length: 34mm.

**Head:** anterior clypeal edge unevenly arcuate, rounded laterally and almost straight centrally; clypeal margin continuous; clypeal surface granulose except for some transverse rugulae centrally between the cephalic horn and the anterior margin; Genal edge rounded and obtusely angled, surface covered with circular granules becoming finer towards the eyes; Clypeogenal suture well defined to base of indistinct clypeal carina; carina with a single short tubercle medially positioned anteriorly to the start point of the carina; A laterally flattened, narrow, parallel-sided and apically pointed cephalic horn positioned anteriorly, very near the anterior margin; horn slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin right angled, lateral margin arcuate with a small fold raised apically, half way along the length of the margin; Pronotal disc with a triangular carina anteriorly; central portion arcuate and weakly emarginate centrally; carina serrated centrally, less so laterally; the total length slightly wider than the widest point of the pronotum; Surface of pronotal disc evenly covered with circular granules; some alutaceous microsculpture centrally and posteriorly; lateral declivity with fovea, the surface granulose with alutaceous microsculpture in between; anterior declivity completely granulose, the circular granules turning more transversely ovaline basally and only in the very central portion; alutaceous

microsculpture throughout. **Elytra**: carinate basally; elytral striae shallow with very weak punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs**: protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with an undulating apical margin; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 8: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 8).

**FEMALE PARATYPE** (Pl. 8: fig. 3, 4, 6): **Head**: anterior clypeal edge evenly arcuate; clypeal margin continuous; clypeal surface with transversely rugulate turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with diamond-shaped granules becoming finer towards the eyes. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum**: anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin obtusely angled, lateral margin arcuate; Pronotal disc with transverse arcuate carina anteriorly, with the width greater than the distance between the eyes; the carina almost straight centrally, bowed gently laterally to its terminal point positioned along the same lateral plane as the midpoint; a very short carina runs posteriorly along the midline from the carina. Surface of pronotal disc completely granulose, larger and more transversely ovaline anteriorly, becoming smaller and circular posteriorly; some alutaceous microsculpture posteriorly; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulose with some alutaceous microsculpture towards the anterior margin. **Elytra**: carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs**: protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with an undulating apical margin; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence;

**Length**: male 26-34mm; female 26-32mm.

**Variation**: in smaller males, the cephalic horn is reduced to a short point to the anterior of the clypeal carina and the pronotal carina is reduced to a gently arcuate carina.

**PARATYPES** (219♂♂ 145♀♀):

**CAMEROON:** ADAMAWA: Babua [=Baboua] (6°59'N, 14°15'E), 4.v.1914 (2♀ BMNH); Galim, 1200m (7°06'N, 12°28'E), viii.1979, P.M. Elsen (1♂ MRAC); Goungel (7°16'N, 11°51'E), iv.1985 (1♂ 1♀ MHNH); environs de Ngaoundere (7°19'N, 13°35'E), vi.1991, Dr. Laurent (2♂ MHNH); Ngaoundere, Bini Dang (7°25'N, 13°32'E), iii-v.2003, M. Dongmo (1♂ 1♀ MDCL); CENTRE: Eseka (3°38'N, 10°47'E) (1♂ MNHN); Jaunde-station [=Yaounde] (3°51'N, 11°31'E), Zenker (1♀ ZMHB); Joko [=Yoko] (5°32'N, 12°19'E), A. Heyne (2♂ 1♀ RMNH); 1♂ 1♀ MTD; 1♂ IRSNB; 3♀ NMB); Joko [=Yoko] (5°32'N, 12°19'E) (1♂ 1♀ IRSNB; 2♂ 2♀ MRAC); Joko [=Yoko] (5°32'N, 12°19'E) (6♂ 1♀ ZMHB; 6♂ 9♀ MTD; 20♂ 18♀ ZSM; 1♂ 2♀ NMB); Joko [=Yoko] (5°32'N, 12°19'E) (1♂ NMPC); Joko [=Yoko] (5°32'N, 12°19'E), Colin (2♀ MTD; 1♂ NMB); Joko [=Yoko] (5°32'N, 12°19'E), v.1910 (2♂ ZSM); Joko [=Yoko] (5°32'N, 12°19'E), vii.1910 (1♀ ZSM); Joko [=Yoko] (5°32'N, 12°19'E), ix.1910 (1♂ ZSM); Joko [=Yoko] (5°32'N, 12°19'E), ix.1912 (1♀ ZSM); Nkolbisson, 600m (3°52'N, 11°27'E), ii.1964, W.J.J.O. de Wilde (1♀ RMNH); Tina (5°29'N, 12°23'E), L. Colin (1♂ ZMHB); Yaounde (3°51'N, 11°31'E), 26.xii.1968, J. Wyon (1♂ MHNH); Yaounde (3°51'N, 11°31'E), xi.1969, J. Wyon (1♂ MHNH); EAST: Batouri (4°26'N, 14°22'E) (13♂ MNHN); LITTORAL: Bare (5°01'N, 9°58'E) (1♂ 1♀ MTD); NORTHWEST: Bafut (6°05'N, 10°07'E), 1-2.vi.2010, local collector (1♂ 1♀ PMOC); Bafut (6°05'N, 10°07'E), vi.2010, J.L. Voma (6♂ 2♀ PMOC); Bali (5°53'N, 10°00'E), vii.2006, J.L. Voma (6♂ PMOC); region de Bali (5°53'N, 10°00'E), 5-25.vii.2006, local collector (1♂ 1♀ PMOC); Baliland [=Bali] (5°53'N, 10°00'E), Museum Lübeck (1♀ ZMHB); Bamenda (5°58'N, 10°09'E) (6♂ 1♀ ZMHB); region de Bamenda (5°58'N, 10°09'E), 10-11.ix.2008, local collector (1♂ PMOC); WEST: Banjun [=Bandjoun] (5°22'N, 10°25'E), 5.vii.1905 (2♂ 4♀ ZMHB); Bamum [=Foumban] (5°44'N, 10°54'E) (1♂ ZMHB; 1♀ TMSA); Dschang (5°27'N, 10°03'E), iv.1910 (1♀ MTD); Ndzi'è [=Ndzihi], plantation de Djuttisa (5°35'N, 10°07'E), 7.viii.2002, B. Dongmo (2♂ MDCL); **CENTRAL AFRICAN REPUBLIC:** BAMINGUI-BANGORAN: Sangba (7°34'N, 20°25'E), 1977, Heck (8♂ 7♀ MRAC); HAUT-KOTTO: Yalinga (6°31'N, 23°15'E), G. Le Testu (4♂ MNHN); KEMO: Fort Sibut (5°44'N, 19°05'E), G. Favarel (3♂ 3♀ MHNH); Fort Sibut (5°44'N, 19°05'E), 1909, G. Favarel (3♂ MNHN); Fort Sibut (5°44'N, 19°05'E), 1904, Dr. J. Decorse (1♂ MNHN); Fort Sibut (5°44'N, 19°05'E), 1912, G. Favarel (1♂ 1♀ MNHN); Fort Sibut (5°44'N, 19°05'E), J.J. van Mol (1♂ MRAC); Fort Sibut (5°44'N, 19°05'E) (1♂ 1♀ BNMH; 2♂ ZMHB; 1♂ NMB); Fort Sibut (5°44'N, 19°05'E) (23♂ 16♀ IRSNB); MBOMOU: Rafai (4°58'N, 23°56'E) (1♂ PMOC); NANA-MAMBÉRÉ: Bouar (5°57'N, 15°36'E), viii-ix.1970, S. Bahuchet (1♂ 1♀ MNHN); OUHAM: Bouca (6°30'N, 18°17'E), 1909, Lefevre (4♂ 1♀ MNHN); OUHAM-PENDÉ: Bossum [=Bozoum] (6°19'N, 16°22'E), v.1913, Houy (1♂ ZMHB); CHAD: LOGONE OREINTAL: Bebedija (8°40'N, 16°34'E), 29.ii.1964, L. Brader (1♂ 1♀ RMNH); **D.R. CONGO:** BAS-UELE: Bambesa (3°27'N, 25°41'E), v.1933, H.J. Brédo (2♂ 1♀ MRAC); Bambesa (3°27'N, 25°41'E), xi.1934, J.V. Leroy (2♂ MRAC); Bambesa (3°27'N, 25°41'E), iii.1937, J. Vrydagh (1♂ 2♀ MRAC); Bambesa (3°27'N, 25°41'E), 8.x.1937, J. Vrydagh (2♀ MRAC); Bambesa (3°27'N, 25°41'E), xi.1937, J. Vrydagh (1♂ 1♀ MRAC); Bambesa (3°27'N, 25°41'E), 5-10.iii.1938, J. Vrydagh (9♂ 5♀ IRSNB); Bambesa (3°27'N, 25°41'E), v.1938, J. Vrydagh (2♂ IRSNB); Bambesa (3°27'N, 25°41'E), v.1938, P. Henrard (1♀ MRAC); Bambesa (3°27'N, 25°41'E), 6.x.1938, P. Lefevre (1♂ 1♀ MRAC); Bambesa (3°27'N, 25°41'E), i.1940, J. Vrydagh (1♀ MRAC); Bambesa (3°27'N, 25°41'E), 2.ii.1940, J. Vrydagh (1♂ IRSNB); Buta (2°48'N, 24°45'E), 1932, Fr. Hutsebaut (1♂ MRAC); Region de Sassa (5°05'N, 25°30'E), 1895-96, Colmant (10♂ 3♀ MRAC); HAUT-UELE: Doruma (4°43'N, 27°41'E), 1934, De Graer (1♀ MRAC); Kapili (3°42'N, 27°53'E), v.1927, F.S. Patrizi (8♂ 4♀ MCG); Moto (2°54'N, 29°25'E) (1♂ MRAC); Moto (2°54'N, 29°25'E), 1920, L. Burgeon (1♂ 3♀ MRAC); Moto (2°54'N, 29°25'E), 1923, L. Burgeon (4♂ 6♀ MRAC); Moto (2°54'N, 29°25'E), 29.viii.1926, L. Burgeon (1♂ 1♀ MRAC); Moto (2°54'N, 29°25'E), 1926, L. Burgeon (2♀ MRAC); Faradje (3°44'N, 29°43'E), vi.1915, Blommaert (1♀ MRAC); Watsa (3°02'N, 29°32'E), 1922, L. Burgeon (2♀ MRAC); ITURI: Aru (2°52'N, 30°50'E), 6.vii.1931, H.J. Brédo (1♂ MRAC); Aru (2°52'N, 30°50'E), 1938, Bastiaens (2♀ MRAC); Aru (2°52'N, 30°50'E), vi.1952, M. Winand (1♂ 1♀ MRAC); Aru (2°52'N, 30°50'E), 1953, M. Winand (3♀ MRAC); Luma (2°35'N, 30°35'E), 1939, Gerard (2♀ MRAC); Mahagi à Niarembe (2°16'N, 31°04'E), 1935, C. Scops (1♂ MRAC); Nioka (2°06'N, 30°37'E), x.1952, J. Hecq (1♀ MRAC); Nioka (2°06'N, 30°37'E), x.1953, J. Hecq (2♀ MRAC); NORD-KIVU: Beni (0°30'N, 29°27'E), Lt. Borgenhoff (1♂ MRAC); Beni (0°30'N, 29°27'E), i.1895, L. Cloetens (3♂ IRSNB); NORD-UBANGI: Banzville [=Mobayi-Mbongo] (4°18'N, 21°11'E), 24-29.i.1932, H.J. Brédo (1♀ MRAC); SUD-UBANGI: Libenge (3°39'N, 18°38'E), viii.1937, Leontovitch (1♀ MRAC); Libenge (3°39'N, 18°38'E), 15.i.1947, R. Cremer & M. Neuman (4♂ 1♀ IRSNB); **KENYA:** BUNGOMA: Mount Elgon (1°08'N, 34°42'E), iv.1954, T.H.E. Jackson (1♂ 1♀ NMK); E Mount Elgon (1°08'N, 34°46'E), vii.1949, V.G.L. van Someren (1♂ BMNH); KAKAMEGA: 31km NW Eldoret, 2220m (0°42'N, 35°05'E), 16.iv.1975, Davis & Dewhurst (1♂ SANC); Kakamega (0°17'N, 34°45'E), vi.1921 (1♂ NMK); Kakamega (0°17'N, 34°45'E), x.1937, Jackson (1♂ NMK); Kakamega (0°17'N, 34°45'E), 15.ix.1949, R.A. Maas Geesteranus (1♀ RMNH); Kakamega (0°17'N, 34°45'E), vi.1950, Mrs. Adamson (2♂ NMK); Kakamega (0°17'N, 34°45'E), iii.1957, Mrs. Board (1♂ NMK); Kakamega (0°17'N, 34°45'E), v.1967, R.H. Carcasson (1♀ NMK); 13-15km N Kakamega, 1550m (0°23'N, 34°40'E), 17.iv.1975, Davis & Dewhurst (5♂ 3♀ SANC); Kakamega Forest (0°16'N, 34°52'E), vii.1976, J. Miskell (1♀ NMK); Kakamega Forest Station (0°16'N, 34°52'E), iv.1981, J. Krikken (1♂ RMNH); Kisumu to Mumias Road (0°07'N, 34°35'E), viii.1912, Dr. A.D. Milne (1♂ BMNH); Kwisero [=Khwisero] (0°10'N, 34°36'E), 2.xii.1965, W. Geirmaert (1♂ RMNH); Mumias to Kisumu Road, 3800-4800ft. (0°07'N, 34°35'E), 25-26.vi.1911, S.A. Neave (1♀ BMNH); 14km E of Mumias, 4500ft. (0°20'N, 34°37'E), 18-21.vi.1911, S.A. Neave (1♂ BMNH); KERICHO: Kapsoit (0°19'N, 35°13'E), 23.iii.1982, A. Bjornstad (1♀ NMK); NANDI: Baraton Animal Husbandry Research Station (0°15'N, 35°05'E), 10.ix.1976, H. Straat (1♂ RMNH); Baraton, University College of East Africa (0°15'N, 35°05'E), 6.viii.1982, G. Girsha (1♂ NMK); North Nandi Forest, near Chemiesia [=Chomisia] (0°15'N, 35°01'E), xii.1979, North Nandi Expedition (2♀ NMK); TRANS-NZOIA: East Surrey Estates (1°09'N, 35°02'E), 18.vi.1932, H.F. Stoneham (1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 10.x.1932, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 23.iii.1936, H.F. Stoneham (1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 29.v.1936, H.F. Stoneham (1♂ 1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 19.vii.1936, H.F. Stoneham (1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 4.x.1936, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 2.iv.1937, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 5.viii.1937, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N,

35°02'E), 5.xi.1937, H.F. Stoneham (1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 27.iv.1938, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 26.v.1938, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 24.vi.1938, H.F. Stoneham (1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 3.vi.1944, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 28.iv.1948, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 30.iv.1961, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 18.v.1961, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 21.v.1961, H.F. Stoneham (1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 20.viii.1961, H.F. Stoneham (1♂ NMK); East Surrey Estates (1°09'N, 35°02'E), 29.ix.1961, H.F. Stoneham (1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 12.x.1961, H.F. Stoneham (1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 20.xi.1961, H.F. Stoneham (1♀ NMK); East Surrey Estates (1°09'N, 35°02'E), 8.ix.1962, H.F. Stoneham (1♂ 1♀ NMK); Kitale (1°01'N, 35°00'E), v-vi.1932, V.G.L. van Someren (1♂ 1♀ NMK); Kitale (1°01'N, 35°00'E), ii.1934, T.H.E. Jackson (1♂ NMK); Kitale (1°01'N, 35°00'E), vi.1952, C. Howard (1♂ NMK); SIAYA: Ndori (0°01'S, 34°26'E), 10.v.1966, W. Geinaert (1♂ RMNH); VHIGA: Kaimosi (0°07'N, 34°51'E), iii-iv.1932, A. Turner (6♂♂ 7♀♀ NMK); Kaimosi (0°07'N, 34°51'E), v.1952, E. Pinhey (1♀ NMK); environs de Kaimosi (0°07'N, 34°51'E), Forêt de Kakamegoes [=Kakamega], 2000m, 1913, G. Babault (2♂♂ MNHN); Maragoli district (0°05'N, 34°43'E), xi.1937, S. Blom Bjerne (2♀♀ NMK); **NIGERIA**: TARABA: Gembu General Hospital (6°43'N, 11°15'E), 3.viii-7.x.1977, E.P. Meijer (1♂ RMNH); **UGANDA**: [no precise locality], 1906-7, A.F.R. Wollaston (1♂ BMNH); CENTRAL: Entebbe (0°05'N, 32°29'E), 6.vii.1911, C.C. Gowdey (1♀ BMNH); Entebbe (0°05'N, 32°29'E), xii.1912, C.C. Gowdey (1♂ BMNH); EASTERN: Bussu (0°34'N, 33°27'E), 1909, Dre. E. Bayon (3♂♂ 4♀♀ MCG; 1♂ IRSNB); Bussu (0°34'N, 33°27'E), v.1909, Dre. E. Bayon (1♀ MCG); Bussu (0°34'N, 33°27'E), 24.vi.1910, Dre. E. Bayon (2♀♀ MCG); Buvuma Island (0°14'N, 33°17'E), 1908, Dre. E. Bayon (1♂ MCG); Buvuma Island, Magyo (0°11'N, 33°17'E), iii.1968, E. Vertriest (1♀ MRAC); Iganga Forest (0°36'N, 33°28'E), 8.viii.1931, H.F. Stoneham (1♂ NMK); Jinja (0°26'N, 33°12'E), x.1930, V.G.L. van Someren (1♀ NMK); Jinja (0°26'N, 33°12'E), iii-iv.1932, V.G.L. van Someren (1♀ BMNH); Kigulu (0°37'N, 32°50'E), x.1968, J.J. Rwabuneza (3♂♂ 1♀ ANHRT); Northern shore of Lake Salisbury (1°41'N, 33°57'E), 13.viii.1913, C.A. Wiggins (1♀ OUMNH); Magunga (0°31'N, 33°27'E), 26-27.ii.1913, C.C. Gowdey (1♂ BMNH); Mbale, 3800ft. (1°05'N, 34°10'E), 6.viii.1911, S.A. Neave (1♂ BMNH); Mount Elgon (1°07'N, 34°19'E), Sir H.H. Johnston (1♂ BMNH); Mount Elgon (1°07'N, 34°19'E), xii.1978, B. Watulege (1♂ NMK); Nakajo [=Nakagyo] (0°39'N, 33°15'E), i.1969, J.J. Rwabuneza (1♀ ANHRT); Serere (1°30'N, 33°34'E), Ford (1♀ BMNH); Tororo (0°41'N, 34°11'E), v.1951, V.G.L. van Someren (1♂ BMNH); NORTHERN: Gulu (2°46'N, 32°18'E) (1♂ 1♀ ZSM); WESTERN: Toro, i-ii.1902, F.J. Jackson (1♂ BMNH); Toro, 1909, C. Alluaud (1♀ MNHN); Budongo Forest, 3400ft. (1°48'N, 31°34'E), 11-15.xii.1911, S.A. Neave (1♂ BMNH); N of Fort Portal, 4700ft. (0°45'N, 30°16'E), 24.xi.1911, S.A. Neave (1♂ BMNH); Hoima (1°26'N, 31°21'E), Dr. Ansoorge (1♂ MTD).

**Diagnosis:** similar in appearance to *C. dux* and *C. duciformis* but males can easily be separated by the shape of the clypeal horn, which is wider and flatter in *C. dux* whilst reduced to a miniscule tubercle in *C. duciformis*. The females of these three species are also very similar but *C. dominus* sp. nov. has a distinctly wider pronotal carina than *C. dux*, whilst *C. duciformis* has a slightly more angled carina. As the three species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** this species is found in the forest-savanna mosaics north of the Congo basin. It has been caught in human dung-baited pitfall traps as well as at light. Specimens have been caught throughout the year.

**Derivation nominis:** this species is named *dominus* (translated as *Lord*), in reference to the similar *C. dux* (translated as *Duke*).

**Distribution** (Pl. 8: fig. 8): Nigeria, Cameroon, Chad, Central African Republic, D.R. Congo, Uganda, Kenya.

## 9. *Catharsius dux* Harold, 1878

(Pl. 9: figs. 1-8; Pl. 30: fig. 9)

*Catharsius dux* Harold, 1878: 101; Harold, 1879: 38; Quedenfeldt, 1884: 271; Kolbe, 1893: 138; Ferreira, 1959: 22; 1960a: 18; 1967: 231; Genier & Josso, 2016: 338.

**Type locality:** “im inneren Guinea”

**Name-bearing type:** Lectotype ♀ in ZMHB:

“// Pogge! [green card; handwritten] // 60062 // Type [orange card] // dux / Harold\* / Regn. Lunda [green card with black border; handwritten] // 1285 [light green paper] // SYNTYPUS / Catharsius / dux Harold, 1878 / labelled by MNHUB 2014 [red card] // LECTOTYPE ♀ / *Catharsius* / dux / Harold, 1878 / dés.: F. Génier, 2014 [red card with black border; partially handwritten] //”

**Redescription:** Colour: Black; pubescence reddish-brown. **Male** (Pl. 9: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and almost straight centrally; clypeal margin continuous; clypeal surface granulose except for some transverse rugulae centrally between the cephalic horn and the anterior margin; Genal edge rounded and obtusely angled, surface covered with circular granules becoming finer towards the eyes; Clypeogenal suture well defined to base of indistinct clypeal carina; carina with a single short tubercle medially positioned anteriorly to the start point of the carina; A basally broad, triangular, laterally flattened cephalic horn positioned anteriorly, very near the anterior margin; horn slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin right angled, lateral margin arcuate with a small fold raised apically, half way along the length of the margin; Pronotal disc with a triangular carina anteriorly; central portion arcuate and weakly emarginate centrally; the carina with a slight concavity one third of the way along from the midline; carina weakly serrated, the total length no wider than the widest point of the pronotum; Surface of pronotal disc completely granulose, larger and more diamond-shaped anteriorly, becoming more circular posteriorly; some alutaceous microsculpture centrally and posteriorly; lateral declivity with fovea, the surface granulose with alutaceous microsculpture in between; anterior declivity completely granulose, the circular granules turning more transversely ovaline centrally and with alutaceous microsculpture throughout. **Elytra:** carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout; **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with an undulating apical margin; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 9: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 9).

**Female** (Pl. 9: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate; clypeal margin continuous; clypeal surface with transversely rugulate turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with diamond-shaped granules becoming

finer towards the eyes. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin obtusely angled, lateral margin arcuate; Pronotal disc with transverse arcuate carina anteriorly, with the width greater than the distance between the eyes and slightly emarginate medially; the carina bowed from the midline to its terminal point positioned along the same lateral plane; a very short carina runs posteriorly along the midline from the carina. Surface of pronotal disc completely granulate, larger and more transversely ovaline anteriorly, becoming smaller and circular posteriorly; some alutaceous microsculpture posteriorly; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulate with some alutaceous microsculpture towards the anterior margin. **Elytra:** carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with an undulating apical margin; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 25-34mm; female 23-33mm.

**Variation:** in smaller males, the cephalic horn is reduced to a short point to the anterior of the clypeal carina and the pronotal carina is reduced to a gently arcuate carina.

#### **Other material examined (353♂♂ 302♀♀):**

**ANGOLA:** [no precise locality] 1000-2000ft., Dr. Welwitsch (2♂♂ 1♀ BMNH); [no precise locality] (1♂ 2♀♀ BMNH); **BENGUELA:** Cubal (13°02'S, 14°15'E), E. Robins (1♀ BMNH); Benguela (12°35'S, 13°24'E), ix.1991, L. Hilburger (1♂ 1♀ NMPC; 1♀ BMNH); Benguela (12°35'S, 13°24'E), x.1980 (1♂ OUMNH); Benguela (12°35'S, 13°24'E), iv.1991, I. Arburger (1♂ OUMNH); Ebanga (12°44'S, 14°44'E), xi.1932, Mission Scientifique Suisse (2♂♂ NMB); **BIÉ:** Bihe, Master L. Sanders (1♂ 1♀ BMNH); Catabola (12°09'S, 17°17'E), 15-25.xi.2012, T. Lackner (3♂♂ 3♀♀ BMNH); S of Quarenta, 1693m (10°38'S, 16°05'E), 17.xi.2013, P. Schüle (1♀ PMOC); **CUANZA NORTE:** Salazar, Instituto de Investigação Agronomica (9°18'S, 14°55'E), 9-15.iii.1972, Southern African Expedition (1♂ BMNH); **CUANZA SUL:** Quirimbo (10°38'S, 14°20'E), v.1934, K. Jordan (1♀ BMNH); Calulo (10°00'S, 14°54'E), 9.xi.1966, E. Junger (3♂♂ NMB; 1♂ PMOC); [no precise locality] iii-iv.1999, T. Bouyer & M. Hasson (1♂ PMOC); **HUAMBO:** Bimbi (11°49'S, 15°50'E), x.1932, Mission Scientifique Suisse (3♂♂ 3♀♀ NMB); **HUILA:** Huila (1♂ 1♀ MNHN); Caconda (13°44'S, 15°04'E) (1♂ ZSM); 3.5km SW Negola (14°09'S, 14°28'E), 8.xii.2012, P. Schüle (1♂ 1♀ PMOC); 3.5km SW of Negola (14°09'S, 14°28'E), 11-12.xi.2013, P. Schüle (2♂♂ PMOC); 3km N of Nova Moncao (13°26'S, 15°20'E), 12-14.xi.2013, T. Lackner (1♀ BMNH); **LUNDA NORTE:** Dundo (7°23'S, 20°50'E), xi.1948 (1♂ 1♀ NHRS); **MALANJE:** Quango strom [=Kwango stream], Major. W. Mechow (1♂ 1♀ MNHN); Malange [=Malanje] (9°33'S, 16°21'E), Mechow (1♂ 1♀ ZMHB); Malange [=Malanje] (9°33'S, 16°21'E), Pogge (1♀ ZMHB); Malange [=Malanje] (9°33'S, 16°21'E), 1879, von Mechow (1♂ 1♀ MNHN); **CONGO:** [no precise locality] Dannfelt (4♂♂ NHRS); [no precise locality] Sjöholm (1♂ 2♀♀ NHRS); [no precise locality] (2♂♂ 1♀ NHRS); [no precise locality] (1♂ IRSNB); [no precise locality] (1♂ MNHN); [no precise locality] 1886, Thollon (5♂♂ 3♀♀ MNHN); [no precise locality] 1883, Guiral (2♂♂ 1♀ MNHN); **POOL:** Musana [=Mousana] (4°33'S, 14°41'E), M. Lundgren (1♂ 1♀ NHRS); Voka (4°40'S, 14°40'E), iii.1893 (2♀♀ ZMHB); Voka (4°40'S, 14°40'E), 4.i.1975 (6♂♂ 4♀♀ MHNL); Voka (4°40'S, 14°40'E), 2.ii.1975 (7♂♂ 7♀♀ MHNL); Voka (4°40'S, 14°40'E), 23.iv.1973 (1♀ MHNL); Voka (4°40'S, 14°40'E), i.1980, G. Onore (1♂ PMOC); Voka (4°40'S, 14°40'E), xii.1977 (2♂♂ 1♀ RMNH); Voka [=Vouka] par Boko (4°43'S, 14°39'E), 30.v.1974, G. Onore (4♂♂ 4♀♀ OUMNH); **BRAZZAVILLE:** Brazzaville (4°16'S, 15°15'E), Unsgaard (1♂ 1♀ NHRS; 1♂ 1♀ IRSNB); Brazzaville (4°16'S, 15°15'E)

(1♂ 1♀ BMNH); Brazzaville (4°16'S, 15°15'E), xii.1958 (2♂♂ 4♀♀ NMB); Brazzaville (4°16'S, 15°15'E), viii-xii.1909, H. Eltringham (1♂ OUMNH); environs de Brazzaville (4°16'S, 15°15'E), 1907, E. Roubaud & A. Weiss (1♂ MNHN); Brazzaville (4°16'S, 15°15'E), 1904, Dr. J. Decorse (3♀♀ MNHN); Brazzaville (4°16'S, 15°15'E), iii-v.1965, L. Detaille (1♂ MRAC; 1♂ NMB); Brazzaville (4°16'S, 15°15'E), xi.1965, R. Paulian (1♂ MNHN); Brazzaville, ORSTOM Park [=Office de la Recherche Scientifique et Technique Outre-Mer] (4°11'S, 15°10'E), 2.i.1964, S. Endrödy-Younga (4♂♂ 1♀ NMPC; 1♂ TMSA); **CUVETTE**: Diele (1°41'S, 14°45'E), 1886, de Brazza (2♂♂ MNHN); **D.R. CONGO: HAUT-LOMAMI**: Kabongo (7°21'S, 25°35'E), 1952, M. Dierckx (28♂♂ 18♀♀ MRAC; 5♂♂ 2♀♀ NMPC); Kamina (8°44'S, 25°00'E), 1930, R. Massart (2♂♂ 3♀♀ MRAC); Kamina (8°44'S, 25°00'E), 8.ii.1955, M. Ledieu (1♂ MRAC); Kamina (8°44'S, 25°00'E), ii-iii.1960, A. Froidebise (2♂♂ MRAC); Kinda (9°18'S, 25°03'E) (11♂♂ 16♀♀ MTD); Kinda (9°18'S, 25°03'E) (9♂♂ 4♀♀ IRSNB); Kinda (9°18'S, 25°03'E), 1930 (1♂ 1♀ IRSNB); Kinda (9°18'S, 25°03'E), 1934, Mme. Warroux (1♀ MRAC); Kinda (9°18'S, 25°03'E), 1951, M. Dierckx (2♂♂ 4♀♀ MTD); Kisamba (7°21'S, 24°02'E), i.1931, P. Quarre (1♂ MRAC); Tshibamba (8°12'S, 24°21'E), iii.1933, F.G. Overlaet (4♂♂ MRAC); **KASAI**: Dekese (3°29'S, 21°23'E), x.1959 (1♂ RMNH); Dekese (3°29'S, 21°23'E), xii.1959 (4♂♂ 2♀♀ RMNH); Dekese (3°29'S, 21°23'E), viii.1959, F. Francois (1♀ MRAC); Dekese (3°29'S, 21°23'E), i.1960, F. Francois (1♂ 1♀ MRAC); Kabwe (4°33'S, 21°09'E), 1937, Soeur Louise du Carmel (2♀♀ MRAC); Luebo (5°21'S, 21°25'E), G. Babault (2♂♂ MRAC); Luebo (5°21'S, 21°25'E), x.1930, J.P. Colin (1♂ MRAC); Luebo (5°21'S, 21°25'E), 1943-44, Dr. Hautmann (1♂ 1♀ MRAC); Muteba (6°11'S, 21°34'E), iii.1932, F.G. Overlaet (1♂ 1♀ MRAC); Port-Francqui [=Ilebo] (4°20'S, 20°35'E), x.1937, Mme. Gillardin (1♂ MRAC); Tshikapa (6°26'S, 20°47'E), i.1932, van Risseghem (1♂ MRAC); **KINSHASA**: Bombo-Lumene (4°25'S, 16°00'E), ii-iii.1996, P. Oremans (3♂♂ 3♀♀ PMOC); Guma (4°07'S, 15°40'E), 11.ii.1968, P.M. Elsen (1♂ MRAC); Kinshasa (4°21'S, 15°18'E), 13.i.1970, P.M. Elsen (1♀ MRAC); Kinshasa (4°21'S, 15°18'E), 15.x.1899, Waelbroeck (1♀ IRSNB); Kinshasa (4°21'S, 15°18'E), xii.1975, L. Segers (34♂♂ 46♀♀ ZSM); Leopoldville [=Kinshasa] (4°21'S, 15°18'E) (1♀ BMNH); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), Dr. Houssiaux (2♂♂ MRAC); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), Sohal (2♀♀ MRAC); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), v-vi.1899, E. Clavareau (2♂♂ 2♀♀ IRSNB); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), 22.vi.1911, Dr. A. Dubois (1♀ MRAC); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), 13.x.1911, Dr. A. Dubois (1♂ 1♀ MRAC); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), v.1912, Dr. Christy (2♀♀ MRAC); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), 1933, Dr. C. Henard (1♂ MRAC); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), 1942, R. Fiasse (1♀ MRAC); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), 1948, Dr. E. Darteville (1♀ MRAC); Leopoldville [=Kinshasa] (4°21'S, 15°18'E), 3.vi.1903, Wilmin (1♂ IRSNB); Menkao, Plateau Bateke (4°12'S, 15°42'E), 1.iv.1974, P. Walter (3♂♂ 3♀♀ MRAC); Menkao, Plateau Bateke (4°12'S, 15°42'E), 11.v.1974, P. Walter (1♀ MRAC); **KONGO CENTRAL**: Banana (5°59'S, 12°23'E), 1948, Dr. E. Darteville (1♀ MRAC); Cattier (5°26'S, 14°45'E), 1946, Delafaille (2♂♂ MRAC); Congo da Lemba (5°42'S, 13°40'E), 4.v.1911, R. Mayne (4♂♂ 5♀♀ MRAC); Congo da Lemba (5°42'S, 13°40'E), 21.xi.1911 (1♂ MRAC); Congo da Lemba (5°42'S, 13°40'E), x-xii.1911, R. Mayne (1♂ MRAC); Congo da Lemba (5°42'S, 13°40'E), v.1913, R. Mayne (2♂♂ 1♀ MRAC); Inkisi (5°08'S, 15°03'E), iv-viii.1948, van der Broeck (1♂ MRAC); Kiniati (5°20'S, 12°56'E), xi-xii.1970, Lesire (3♂♂ MHNH); Kiniati (5°20'S, 12°56'E), iv.1971, Lesire (1♀ MHNH); Kisantu (5°08'S, 15°05'E) (1♂ ZMHB); Kisantu (5°08'S, 15°05'E), 1909 (2♂♂ IRSNB); Kisantu (5°08'S, 15°05'E), P. Gillet (1♂ MRAC); Kisantu (5°08'S, 15°05'E), Goosens (4♂♂ 2♀♀ MRAC); Kisantu (5°08'S, 15°05'E), Van Wing (1♀ MRAC); Kisantu (5°08'S, 15°05'E), 1930-31, Englebert (1♂ MRAC); Kisantu (5°08'S, 15°05'E), 15.xii.1920, Dr. H. Schouteden (1♂ MRAC); Kisantu (5°08'S, 15°05'E), v.1945, Rev. F. Anastase (1♂ 1♀ MRAC); Lemfu (5°18'S, 15°13'E), 1931, Van Eyen (1♂ 1♀ MRAC); Lemfu (5°18'S, 15°13'E), vi.1945, Rev. L. de Beir (2♀♀ MRAC); Lukula (5°24'S, 12°57'E), 1911, Dr. Daniel (1♀ MRAC); Matadi (5°50'S, 13°27'E) (1♂ NHRS); Matadi (5°50'S, 13°27'E), 24.v.1888, J. Duviervier (1♂ IRSNB); Matadi (5°50'S, 13°27'E) 1948, Dr. Bervoets (2♀♀ MRAC); Mayidi (5°11'S, 15°09'E), 1942, van Eyen (4♂♂ 5♀♀ MRAC); Mpese (5°14'S, 15°33'E), xi.1935, Coosemans (1♂ MRAC); Thysville [=Mbanza-Ngungu] (5°15'S, 14°51'E), xii.1939, Mevr. Bequaert (1♀ MRAC); **KWANGO**: Panzi (7°12'S, 17°57'E), 17.ii.1939, Mevr. Bequaert (2♂♂ MRAC); **KWILU**: Ipamu (4°10'S, 19°38'E), 1922, P. Vanderijst (1♂ 1♀ MRAC); Kikwit (5°02'S, 18°48'E), xi.1920, P. Vanderijst (2♀♀ MRAC); Kikwit (5°02'S, 18°48'E), 29.xii.1952, J. Ruelle (1♂ 1♀ MRAC); Kikwit (5°02'S, 18°48'E), 28.ii.1985, P. Walter (1♂ JLMC); Kimbau [=Kimbao] (5°08'S, 17°37'E), 1931, van der Velgen (1♀ MRAC); Kingungi (5°25'S, 17°56'E), xii.1937, Rev. M. Reguier (1♂ MRAC); Kingungi (5°25'S, 17°56'E), viii.1939, Renier (1♂ MRAC); Leveville [=Lusanga] (4°50'S, 18°43'E), de Walsche (1♀ PMOC); Leveville [=Lusanga] (4°50'S, 18°43'E), 1923, Mme. J. Tinant (2♂♂ 3♀♀ MRAC); Madibi (4°18'S, 18°25'E), vi-vii.1913, R. Verschueren (1♂ MRAC); Mukila (5°01'S, 16°59'E), x.1952, M. Bequaert (1♂ 2♀♀ MRAC); Zaba (4°20'S, 18°15'E), 1941, Mlle. B. D'Oliveira (1♂ MRAC); **LOMAMI**: Kabinda (6°08'S, 24°29'E), Dr. Schwetz (1♂ 1♀ MRAC); Kabinda (6°08'S, 24°29'E), i.1926, C. Seydel (1♂ MRAC); Kabinda (6°08'S, 24°29'E), xii.1934, Mme. Gillardin (3♂♂ 1♀ MRAC); Kabinda (6°08'S, 24°29'E), 1945-46, Dr. Hautmann (7♂♂ 9♀♀ MRAC); Kambaye (6°53'S, 23°44'E), x.1930, P. Quarre (1♀ MRAC); Katoto (6°44'S, 23°50'E), 1952, R. Roiseux (1♀ MRAC); Mwene-Ditu (7°01'S, 23°27'E), Doutreleport (34♂♂ 28♀♀ MRAC); **LUALABA**: Kafakumba (9°40'S, 23°46'E), xii.1932, F.G. Overlaet (1♀ MRAC); Kapanga (8°21'S, 22°39'E), xii.1931, F.G. Overlaet (2♂♂ 2♀♀ MRAC); Kapanga (8°21'S, 22°39'E), x.1932, F.G. Overlaet (8♂♂ 8♀♀ MRAC; 2♂♂ 1♀ NMPC); Kapanga (8°21'S, 22°39'E), 30.xi.1932, F.G. Overlaet (2♂♂ 1♀ MRAC); Kapanga (8°21'S, 22°39'E), xii.1932, F.G. Overlaet (1♂ MRAC); Kapanga (8°21'S, 22°39'E), i.1933, F.G. Overlaet (10♂♂ 5♀♀ MRAC); Kapanga (8°21'S, 22°39'E), ii.1933, F.G. Overlaet (9♂♂ 10♀♀ MRAC); Kapanga (8°21'S, 22°39'E), iii.1933, F.G. Overlaet (3♂♂ 3♀♀ MRAC); Kapanga (8°21'S, 22°39'E), iv.1933, F.G. Overlaet (1♂ 1♀ MRAC); Kapanga (8°21'S, 22°39'E), v.1933, F.G. Overlaet (3♂♂ 1♀ MRAC); Kapanga (8°21'S, 22°39'E), ix.1933, F.G. Overlaet (10♂♂ 7♀♀ MRAC); Kapanga (8°21'S, 22°39'E), x.1933, F.G. Overlaet (13♂♂ 12♀♀ MRAC; 1♂ NMB); Kapanga (8°21'S, 22°39'E), xi.1933, F.G. Overlaet (1♂ MRAC); Kapanga (8°21'S, 22°39'E), iv.1934, F.G. Overlaet (1♂ MRAC); Kapanga (8°21'S, 22°39'E), 1935, Dr. Richard (2♀♀ MRAC); Kolwezi (10°43'S, 25°30'E), viii.1951, Dr. V. Allard (1♂ MRAC); Kolwezi (10°43'S, 25°30'E), 10.xi.1991, T. Bouyer (1♂ 1♀ PMOC); Koni (10°46'S, 25°41'E), xii.1988-ii.1989, A. Chaminade (1♂ PMOC); Luashi (10°56'S, 23°37'E), xii.1933, Freyne (1♂ 1♀ MRAC); Sandoa [=Sanduwa] (9°42'S, 22°53'E), iii.1931, F.G. Overlaet (1♂ MRAC); Tshibalaka (8°36'S, 23°03'E), xii.1933, F.G. Overlaet (1♀ MRAC); Zilo (10°31'S, 25°28'E),

iii.1980, J. Remy (1♂ 1♀ PMOC); LULUA: Kananga (5°54'S, 22°25'E), 1937, Schouteden (1♂ 1♀ MRAC); Kele (6°55'S, 23°11'E), i.1953, R. Roiseux (2♂♂ MRAC); de Luebo à Luluabourg [=Kananga] (5°35'S, 21°55'E), 1921, Lt. J. Ghesquiere (1♂ MRAC); Luluabourg [=Kananga] (5°54'S, 22°25'E), P. Callewaert (6♂♂ 8♀♀ MRAC); Luluabourg [=Kananga] (5°54'S, 22°25'E), K. Vaillmans (1♀ MRAC); Luluabourg [=Kananga] (5°54'S, 22°25'E), 1926 (1♂ NMB); Luluabourg [=Kananga] (5°54'S, 22°25'E), 1938, Van Kerckhoven (1♂ MRAC); Luluabourg [=Kananga] (5°54'S, 22°25'E), 1939, Van Kerckhoven (1♀ MRAC); Luluabourg [=Kananga] (5°54'S, 22°25'E), 15.iv.1939, J.J. Deheyn (2♀♀ MRAC); Mukenge (6°01'S, 22°19'E) (2♂♂ MTD); Mukenge (6°01'S, 22°19'E), Pogge (1♂ ZMHB); Hemptinne St-Benoit (6°18'S, 22°31'E), 1912, P. Callewaert (12♂♂ 15♀♀ MRAC; 1♀ IRSNB); Tshibala (6°22'S, 21°52'E), 1949, Zusters van Heule (2♂♂ MRAC); MAI-NDOMBE: Bolobo (2°09'S, 16°14'E), Dr. H. Schouteden (1♂ MRAC); Bokoro (2°48'S, 18°14'E), 1952, Jans (1♂ MRAC); Kwamouth (3°11'S, 16°12'E) (1♀ MRAC); Kwamouth (3°11'S, 16°12'E), vi.1921, Lebrun (1♂ 3♀♀ MRAC); MANIEMA: Kasongo (4°26'S, 26°40'E), Lt. van Deft (1♀ MRAC); Kasongo (4°26'S, 26°40'E), viii-ix.1959, P.L.G. Benoit (6♂♂ 3♀♀ MRAC); entre Kindu et le Lomami (3°06'S, 25°28'E) (1♀ MRAC); Nyangwe (4°17'S, 26°15'E), 1894 (1♂ MRAC); SANKURU: Djeka (3°17'S, 23°59'E), i.1954, R. Roiseux (2♂♂ 2♀♀ MRAC); Komi (3°31'S, 23°23'E), v.1930, J. Ghesquiere (1♂ MRAC); Kondue (4°58'S, 23°19'E), Leonard (2♂♂ 4♀♀ MRAC); Kondue (4°58'S, 23°19'E), E. Lujja (3♂♂ 1♀ MRAC); entre Lodja et Kole (3°29'S, 22°59'E), Mme. Lebrun (2♂♂ 1♀ MRAC); Lodja (3°31'S, 23°36'E), 1909, Demptinne (1♂ 1♀ IRSNB); Lusambo (4°58'S, 23°26'E), 1921, Lt. Ghesquiere (1♀ MRAC); Lusambo (4°58'S, 23°26'E), i.1926, C. Seydel (1♀ MRAC); Lusambo (4°58'S, 23°26'E), vii-viii.1949, Dr. M. Fontaine (1♂ 2♀♀ MRAC); Lusambo (4°58'S, 23°26'E), 1950, P. Hostie (2♀♀ MRAC); ZAMBIA: [no precise locality] Lindblom (3♂♂ 1♀ NHRS); NORTHWESTERN: Nchila Wildlife Reserve (11°16'S, 24°19'E), 13-16.xi.2003, K. Werner & P. Smrž (2♂♂ PMOC); Hillwood, Ikelenge, 1400m (11°16'S, 24°19'E), 21-28.x.2013, R. Smith, H. Takano, L. Chmurova & L. Smith (2♂♂ 1♀ BMNH); Lukwakwa, West Lunga National Park, 1147m (12°40'S, 24°26'E), 4-8.xi.2013, R. Smith, H. Takano & D. Oram (2♀♀ BMNH); Lukwakwa, West Lunga National Park, 1147m (12°40'S, 24°26'E), 28-29.iv.2014, R. Smith, H. Takano, L. Chmurova & L. Smith (1♀ BMNH).

**Notes:** the type specimen was collected by Paul Pogge on his expedition with Alexander von Homeyer through Angola and D.R. Congo in the early 1870's. Ferreira (1960) refers to the type locality as Guinea which is likely a misinterpretation of Harold's type locality of "im inneren Guinea" as discussed by Genier & Josso (2016).

**Diagnosis:** see under *C. dominus* sp. nov.. Very similar in appearance to *C. dominus* but can be distinguished by the wider and flatter clypeal horn in the male and the narrower pronotal carina in the female. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** this species is widely distributed throughout the forest-savanna mosaics south of the Congo basin. It appears *C. dux* is found to the west of the Lualaba-Kabompo river system and is replaced by *C. duciformis* to the east. There are no records of both species being caught at the same site. The author has caught this species in Zambia on forest edges in human dung baited pitfall traps. Specimens have been caught between October and June.

**Distribution** (Pl. 9: fig. 8): Angola, Gabon (?), Congo, D.R. Congo, Zambia.

## 10. *Catharsius duciformis* Ferreira, 1959

(Pl. 10: figs. 1-8; Pl. 30: fig. 10)

*Catharsius duciformis* Ferreira, 1959: 18; 1960a: 17.

**Type locality:** "Kaziba" [Kaziba Gorge, Upemba National Park, DRC]

**Name-bearing type:** Holotype ♂ in MRAC:

“// HOLOTYPUS [orange card with black border] // Congo belge: P.N.U. / Kaziba (1,140m.) / 19-27-II-1948 / Mis. G.F. de Witte. 1314a // HOLOTYPUS ♂ / *Catharsius duci-* / *formis* n.sp. / 1958 Maria C. Ferreira [partially handwritten] //”

**Redescription:** Colour: Black; pubescence reddish-brown. **Male** (Pl. 10: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and almost straight centrally; clypeal margin continuous; clypeal surface granulose except for some transverse rugulae centrally between the cephalic horn and the anterior margin; Genal edge rounded and obtusely angled, surface covered with circular granules with a smooth narrow region posteriorly along the clypeogenal suture; suture well defined to base of clypeal carina; carina strongly raised centrally and tridentate, the central tubercle being positioned anteriorly and slightly higher than the tubercles on either side; A miniscule, tubercular cephalic horn positioned anteriorly, very near the anterior margin; horn slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin right angled, lateral margin arcuate with a small fold raised apically, half way along the length of the margin; Pronotal disc with a triangular carina anteriorly; central portion arcuate and weakly emarginate centrally; the carina with a slight concavity one third of the way along from the midline; carina weakly serrated, the total length no wider than the widest point of the pronotum; Surface of pronotal disc completely granulose, with some larger and more diamond-shaped granules anteriorly, becoming more circular posteriorly; some alutaceous microsculpture centrally and posteriorly; lateral declivity with fovea, the surface granulose with alutaceous microsculpture in between; anterior declivity completely granulose, the circular granules turning more transversely ovaline centrally and with weak alutaceous microsculpture. **Elytra:** carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventriles:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with an undulating apical margin; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 10: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 10).

**Female** (Pl. 10: fig. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate; clypeal margin continuous; clypeal surface with transversely rugulate turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with diamond-shaped granules becoming finer towards the eyes. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes.

Lateroanterior margin obtusely angled, lateral margin arcuate; Pronotal disc with transverse arcuate carina anteriorly, as wide as the distance between the eyes and slightly emarginate medially; the carina bowed from the midline to its terminal point positioned posteriorly; a very short carina runs posteriorly along the midline from the carina. Surface of pronotal disc completely granulose, larger more transversely ovaline granules closely arranged anteriorly, becoming smaller, circular and spaced out posteriorly; some alutaceous microsculpture in the extreme posterior and central portion of disc; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulose with some alutaceous microsculpture towards the anterior margin. **Elytra**: carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs**: protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence.

**Length**: male 25-34mm; female 22-33mm.

**Variation**: in smaller males, the cephalic horn disappears completely; the pronotal carina is reduced to a gently arcuate carina. In smaller females the pronotal carina is reduced to a short arcuate carina.

**Other material examined (42♂♂ 49♀♀):**

**D.R. CONGO**: **TANGANYIKA**: Baudouinville [=Kirungu] (7°05'S, 29°44'E), 1937, Debbaudt (1♀ MRAC); **HAUT-KATANGA**: Kipopo (11°39'S, 27°27'E), 31.x.1961, R. Maréchal (1♂ NMB); Pweto-Kilwa (8°49'S, 28°35'E), iv-vi.1923, A. Pilette (2♂♂ 2♀♀ MRAC); **HAUT-LOMAMI**: Parc National de l'Upemba, Kimilombo (8°55'S, 27°11'E), 25.x-5.xi.2002, Mission Hasson & Bouyer (1♂ PMOC); Parc National de l'Upemba, Kaziba, 1140m (9°10'S, 26°50'E), 7-12.ii.1948, G.F. de Witte (1♂ TMSA); Parc National de l'Upemba, Kaziba, 1140m (9°10'S, 26°50'E), 19-27.ii.1948, G.F. de Witte (*allotype*♀, 2♂♂ 1♀ *paratypes* MRAC; 2♀♀ *paratypes* IRSNB); Parc National de l'Upemba, riviere Ntumbwa (8°56'S, 27°03'E), 1-14.iv.2001, Mission Hasson & Bouyer (2♂♂ 2♀♀ PMOC); **MALAWI**: **CENTRAL**: Dzalanyama Forest Reserve (14°20'S, 33°31'E), i.1991, C. Dudley (1♂ 1♀ PMOC); **NORTHERN**: Chisasira (11°54'S, 34°04'E), 3.i.1978, R. Jocqué (1♂ MRAC); Vwaza Game Reserve, Kazuni Camp (11°08'S, 33°39'E), i.1993, C. Dudley (1♂ MHNH); **TANZANIA**: **RUKWA**: Bismarckburg [= Kasanga] (8°28'S, 31°08'E), von Reinzenstein (1♂ ZSM); Kalambo Forest Reserve, 1587m (8°22'S, 31°15'E), 22.xi.2009, P. Darge (2♂♂ 1♀ MHNH); **ZAMBIA**: [no precise locality], 31.i.1910, Duchessa E. d'Aosta (1♂ MCG); **CENTRAL**: Chisanga (13°50'S, 27°50'E), 10.v.1915, H.C. Dollman (1♂ 6♀♀ BMNH); Kacheleko, Kafue National Park, 1260m (15°00'S, 26°26'E), 21-26.xi.2013, R. Smith, H. Takano & D. Oram (1♂ BMNH); Mfwanta (13°07'S, 30°20'E), 17.i.2009, R. Minetti (1♂ PMOC); Kafue National Park, Mayukuyuku, 1080m (14°55'S, 26°04'E), 21-26.xi.2013, R. Smith, H. Takano & D. Oram (7♂♂ 7♀♀ BMNH); Mkushi environs (13°37'S, 29°23'E), 15-18.xii.2004, Snížek & Tichy (1♀ NMPC); **COPPERBELT**: Kashitu (13°44'S, 28°39'E) xii.1914, H.C. Dollman (1♀ BMNH); Kashitu (13°44'S, 28°39'E), 26.iii.1915, H.C. Dollman (1♀ BMNH); **LUAPULA**: W of Medona [=Madona] (11°08'S, 28°33'E), D. MacDonald (1♂ BMNH); Ntumbachushi Falls, 1166m (9°51'S, 28°57'E), 12-13.v.2013, R. Smith, H. Takano & D. Oram (2♂♂ 1♀ BMNH); **MUCHINGA**: Chinsali, 4000ft. (10°33'S, 32°04'E), 22.iv.1908, S.A. Neave (1♀ OUMNH); Kalungu, 1280m (9°41'S, 32°43'E), 22-24.xi.2016, R. Smith, H. Takano & D. Oram (2♂♂ 1♀ BMNH); Kapishya Hot Springs, Shiwa N'gandu Estate, 1437m (11°10'S, 31°36'E), 24-27.iv.2013, R. Smith, H. Takano & D. Oram (1♀ BMNH); Kapishya Hot Springs, Shiwa N'gandu Estate, 1437m (11°10'S, 31°36'E), i.2015, M.T. Harvey (1♂ BMNH); Lavushi Manda Hills, Lavushi Manda National Park, 1441m (12°23'S, 30°52'E), 27-29.xi.2012, R. Smith & H. Takano (1♀ BMNH); Mpika (11°50'S, 31°27'E), ii.1905, F.H. Wellard (1♂ BMNH); Mutinondo Wilderness Area, 1460m (12°27'S, 31°17'E), 26-29.xi.2016, R. Smith, H. Takano & D. Oram (2♂♂ 2♀♀ BMNH); **NORTH-WESTERN**: Congo-Zambezi watershed, 1928, Dr. H.S. Evans (1♀ BMNH); Jiwundu Swamp, 1340m (11°52'S, 25°33'E), 21-24.xi.2014, R. Smith & H. Takano (3♂♂ 2♀♀ BMNH); **NORTHERN**: Abercorn [=Mbala] (8°51'S, 31°22'E), xii.1942, H.J. Brédo (2♂♂ 2♀♀ IRSNB); Abercorn [=Mbala] (8°51'S, 31°22'E), 12.v.1943, H.J. Brédo (1♂ IRSNB); Abercorn [=Mbala] (8°51'S, 31°22'E), vii.1944, H.J. Brédo (1♀ IRSNB); Abercorn [=Mbala] (8°51'S, 31°22'E), 1.ii.1951, H.J. Brédo (1♂ IRSNB); Abercorn [=Mbala] (8°51'S, 31°22'E), ii.1945, H.J. Brédo (1♀ IRSNB); Abercorn [=Mbala] (8°51'S, 31°22'E), 1949, H.J. Brédo (1♀

MRAC); Lumangwe Falls, 1187m (9°33'S, 29°23'E), 20-22.xi.2012, R. Smith & H. Takano (7♂♂ 8♀♀ BMNH); N'koli [=Nkole] (10°35'S, 31°11'E), 16.i.1938, H.J. Brédo (1♀ MRAC); Ubemba, 1900, Guilleme (1♂ 1♀ MNHN).

**Diagnosis:** see under *C. dominus* sp. nov.. The male is superficially similar to *C. dux* and *C. dominus* sp nov. but can easily be distinguished by the cephalic horn which is reduced to a miniscule tubercle and the clypeal carina which is strongly raised centrally. The female is very similar to *C. dux* but the pronotal carina is slightly more angled in *C. duciformis*. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** this species is widely distributed in the Central Zambezian Miombo woodland habitat to the east of the Lualaba and Kabompo Rivers and as far north as the Albertine Rift just to the north of the Tanzania-Zambia border. It is attracted to light and despite being uncommon in collections, the author has collected long series in human dung baited pitfall traps throughout north-eastern Zambia. Specimens have been caught between October and May.

**Distribution** (Pl. 10: fig. 8): Zambia, D.R. Congo, Malawi, Tanzania.

## 11. *Catharsius spectabilis* Gillet, 1918

(Pl. 11: figs. 1-8; Pl. 30: fig. 11)

*Catharsius spectabilis* Gillet, 1918: 146; Ferreira, 1960a: 44.

**Type locality:** “Usagara” [Usagara Mountains, Tanzania]

### **Name-bearing type:**

The type of *C. spectabilis* could not be located in Gillet’s collection (IRSNB). The only specimen of this species in his collection and the whole of the IRSNB collections is a female from “Umbulu”. Ferreira apparently studied the type (1960a) but is now presumed lost. In order to stabilise the taxonomy of this and closely related species by fixing the published name to a single specimen, a topotypical male specimen with a determination label of Gillet in the BMNH is here **designated as the neotype**:

“// Afr. Or. / Usagara [handwritten] // 71274 [pink paper; handwritten] // Fry Coll. / 1905-100. // Catharsius / spectabilis, m. / Gillet det. [handwritten] // NEOTYPE / CATHARSIUS / spectabilis / Gillet / det. H Takano 2017 [white card with red border; partially handwritten] //”

**Redescription:** Black; pubescence reddish-brown. **Male** (Pl. 11: figs. 1, 2, 5): Colour: **Head:** anterior clypeal edge almost straight with an emargination centrally, rounded laterally and obtusely angled; clypeal margin continuous; clypeal surface granulose except for some transverse rugulae centrally between the cephalic horn and the anterior margin; Genal edge rounded and obtusely angled, surface covered with ovaline granules; suture well defined to base of incomplete carina; a short conical cephalic horn positioned to anteriorly of clypeus; horn gently slanted forward in lateral view.

**Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate; Pronotal disc with a triangular carina anteriorly; the carina with a raised angular projection one third of the way along the midline on each side; carina intermittently sinuous, the total length no wider than the widest point of the pronotum; Surface of pronotal disc covered with circular granules and alutaceous microsculpture, except for the extreme anterior portions where the granules are larger and more diamond-shaped; lateral declivity with fovea, the surface granulose with alutaceous microsculpture in between; anterior declivity completely granulose, the circular granules turning more transversely ovaline centrally and with alutaceous microsculpture. **Elytra:** carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with an undulating apical margin; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 11: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 11).

**Female** (Pl. 11: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate; clypeal margin continuous; clypeal surface with transversely rugulate turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with diamond-shaped granules becoming finer towards the eyes. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin obtusely angled, lateral margin arcuate; Pronotal disc with transverse arcuate carina anteriorly, with the width greater than the distance between the eyes; the carina almost straight centrally, gently bowed laterally to its terminal point positioned along the same lateral plane as the midpoint; Surface of pronotal disc completely granulose, larger more transversely ovaline granules closely arranged anteriorly, becoming smaller, circular and spaced out posteriorly; some alutaceous microsculpture in the extreme posterior and central portion of disc; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulose with some alutaceous microsculpture towards the anterior margin. **Elytra:** carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia

quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 23-33mm; female 23-30mm.

**Variation:** in smaller males, the cephalic horn is reduced to a short point to the anterior of the clypeal carina and the pronotal carina is reduced to a gently arcuate carina.

**Other material examined (34♂♂ 22♀♀):**

**BURUNDI:** [no precise locality], von Langenn-Steinkeller (1♂ ZMHB); **BUJUMBURA MAIRIE:** environ de Bujumbura (3°23'S, 29°22'E), iv.1990, H. Bomans (1♂ MHNL); **BURURI:** Bururi (3°57'S, 29°37'E), xi.1937, A. Lestrade (1♂ MRAC; 1♂ TMSA); Bururi (3°57'S, 29°37'E), xii.1959 (1♂ 2♀♀ NMB; 2♀♀ MRAC); **GITEGA:** Kitega [=Gitega] (3°45'S, 30°10'E), v.1969, Père Giraudin (1♂ 1♀ PMOC); Kitega [=Gitega] (3°45'S, 30°10'E), vi.1972, Père Giraudin (1♂ PMOC); **NGOZI:** Ngozi (2°54'S, 29°49'E) (2♂♂ ZSM); Ngozi (2°54'S, 29°49'E), v.1970 (1♂ MCG); Ngozi (2°54'S, 29°49'E), 25.xi.1970, M. Galant (1♀ MHNL); Ngozi (2°54'S, 29°49'E), 28.xi.1970, M. Galant (1♂ 1♀ MHNL); Ngozi (2°54'S, 29°49'E), 3.xii.1970 (1♂ PMOC; 1♀ MHNL); Ngozi (2°54'S, 29°49'E), 3.xii.1970, M. Galant (2♂♂ MHNL); Ngozi (2°54'S, 29°49'E), v.1971 (1♂ PMOC); **RWANDA:** **KIGALI CITY:** Kigali (1°58'S, 30°06'E), iii.1973, V. Allard (3♂♂ 1♀ PMOC); **SOUTHERN:** Nyanza (2°21'S, 29°45'E), 13.xii.1932, L. Burgeon (1♀ MRAC); **TANZANIA:** **KAGERA:** Bukoba (1°20'S, 31°49'E), i.1913 (3♂♂ ZMHB; 1♂ 1♀ MTD); Bukoba (1°20'S, 31°49'E), 15.i.1922, N.C.E. Miller (1♂ BMNH); Bukoba (1°20'S, 31°49'E), Gudowius (1♂ ZMHB); Kiyamyulwa, 1157m (2°09'S, 31°37'E), 26.iii.2010, P. Darge (1♂ MHNL); **KIGOMA:** Mkuyu (5°30'S, 29°51'E), ii.1966, Japanes Primate Research Expedition (1♀ NMK); Uha [=Kibondo] (3°31'S, 30°43'E), x.1912 (1♂ ZMHB); **MANYARA:** Mbulu (3°51'S, 35°33'E) (1♀ IRSNB); Giting, Mount Hanang, 1964m (4°24'S, 35°25'E), 21-24.v.2012, R. Smith & H. Takano (1♂ 1♀ BMNH); Mount Hanang, versant sud, 2300-2400m (4°28'S, 35°24'E), 29-30.v.1957 (1♂ MRAC); Ufiome (4°14'S, 35°48'E), 6.xii.1911, E. Obst (1♂ 1♀ MTD; 1♂ MNHN); **MOROGORO:** Nguru Mountains (6°06'S, 37°30'E) Holtz (1♀ ZMHB); Njia Panda, Udzungwa Mountains National Park, 970m (7°47'S, 36°50'E), 12-14.iv.2011, R. Smith & H. Takano (1♀ BMNH); Njia Panda, Udzungwa Mountains National Park, 970m (7°47'S, 36°50'E), 27-30.xi.2010, R. Smith & H. Takano (1♀ BMNH; 1♀ NMPC); Nongwe, Ukaguru Mountains, 1500m (6°28'S, 36°54'E), xi.2013, local collector (1♀ BMNH); **MWANZA:** Geita Forest, 1230m (2°55'S, 32°06'E), 24.x.2011, P. Darge (3♂♂ 1♀ MHNL); Ukerewe Island (2°06'S, 33°05'E), Father Conrads (1♀ NMK); **SINGIDA:** Saranda (5°43'S, 34°59'E), 4.ii.1918, G.D.H. Carpenter (1♂ OUMNH).

**Diagnosis:** this species is superficially similar in appearance to *C. satyrus* but can easily be distinguished by the shape of the anterior clypeal edge which is arcuate in *C. satyrus*, but clearly angled in *C. spectabilis*. The cephalic horn of *C. satyrus* is laterally flattened and bifid whilst in *C. spectabilis*, the horn is short and pointed. The females of these two species are very similar but the central tubercle on the clypeal carina is elevated much higher in *C. satyrus*. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** this species is uncommon in collections and is found in open woodland and grassland habitats. The author dug up a male and a female from underneath cattle dung at the foothills of Mount Hanang in Tanzania, in an open area of grassland and farmland. Aside from this, no other information is available on their natural history. Specimens have been caught between October and June.

**Distribution** (Pl. 11: fig. 8): Tanzania, Burundi, Rwanda.

## 12. *Catharsius satyrus* Kolbe, 1893

(Pl. 15: figs. 1-8; Pl. 30: fig. 12)

*Catharsius satyrus* Kolbe, 1893: 137; Ferreira, 1960a: 39; Ferreira, 1967: 249.

**Type locality:** “Conde-Gebiet” [=Konde Region, Tanzania]

**Name bearing type:** 4 syntypes (2♂♂ 2♀♀) in ZMHB. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series is here **designated as the lectotype:**

“// Type [orange card] // N. Nyassa / Conde-G / Linnaea V. [blue card; handwritten] // 64852 // LECTOTYPE / CATHARSIUS / satyrus / Kolbe / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black; pubescence reddish-brown. **Male** (Pl. 15: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and slightly emarginate centrally; clypeal margin continuous; clypeal surface granulose except for some transverse rugulae centrally between the cephalic horn and the anterior margin; Genal edge rounded and obtusely angled, surface covered with ovaline granules; suture well defined to base of incomplete carina; A laterally flattened, basally truncate and apically bifidate cephalic horn positioned anteriorly, very near the anterior margin; horn slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate; Pronotal disc with a triangular carina anteriorly; the carina with a raised angular projection one third of the way along the midline on each side; carina intermittently sinuous, the total length no wider than the widest point of the pronotum; Surface of pronotal disc covered with circular granules and alutaceous microsculpture, except for the extreme anterior portions where the granules are larger and more diamond-shaped; lateral declivity with fovea, the surface granulose with alutaceous microsculpture in between; anterior declivity completely granulose, the circular granules turning more transversely ovaline centrally and with alutaceous microsculpture. **Elytra:** carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventriles:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with an undulating apical margin; Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 15: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 12).

**Female** (Pl. 15: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate; clypeal margin continuous; clypeal surface with transversely rugulate turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with diamond-shaped granules becoming finer towards the eyes. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and higher than the tubercles

on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin obtusely angled, lateral margin arcuate; Pronotal disc with transverse arcuate carina anteriorly, with the width greater than the distance between the eyes; the carina almost straight centrally, gently bowed laterally to its terminal point positioned along the same lateral plane as the midpoint; Surface of pronotal disc completely granulose, larger more transversely ovaline granules closely arranged anteriorly, becoming smaller, circular and spaced out posteriorly; some alutaceous microsculpture in the extreme posterior and central portion of disc; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulose with some alutaceous microsculpture towards the anterior margin. **Elytra:** carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia quadridentate, the fourth and most posterior tooth weakly developed; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 23-34mm; female 25-33mm.

**Variation:** in smaller males, the cephalic horn is reduced to a short point to the anterior of the clypeal carina and the pronotal carina is reduced to a gently arcuate carina. The shape of the cephalic horn varies in males although it is always bifidate; some individuals have horns with very arcuate sides where the apex of the horn is much wider than the base whilst others have horns with arcuate sides but the apex is as wide as the base. Specimens from southern Malawi tend to belong to the latter where even the biggest males have quite parallel-sided horns but as they have identical internal sac sclerites as the typical form, this is considered as intraspecific variation.

**Other material examined** (142♂♂ 82♀♀):

**D.R. CONGO:** [no precise locality] (1♀ IRSNB); **HAUT-KATANGA:** Kapiri (9°42'S, 27°13'E), ix.1912, Mission Agricole (1♂ 1♀ MRAC); Lubumbashi (11°40'S, 27°29'E), 20.xi-13.xii.2002, T. Bouyer (1♂ PMOC); **HAUT-LOMAMI:** Kaluli-Nord [=Kalule-Nord] (9°47'S, 26°00'E), i.1934, C. Seydel (1♀ MRAC); Mukishi (8°30'S, 24°43'E), A. Buquet (2♂♂ MRAC); Parc National de l'Upemba, 1320m (8°50'S, 26°50'E), 26.iv-5.v.1948, G.F. de Witte (1♂ MRAC); Parc National de l'Upemba, Kabwe sur Muye, 1320m (8°50'S, 26°50'E), 26.iv-5.v.1948, G.F. de Witte (1♂ TMSA); Parc National de l'Upemba, Kaziba, 1140m (9°10'S, 26°50'E), 19-27.ii.1948, G.F. de Witte (1♀ as *paratype* of *Catharsius duciformis* Ferreira: MRAC); Parc National de l'Upemba, Mubale, 1480m (8°45'S, 26°54'E), 1-5.v.1947, G.F. de Witte (2♂♂ 1♀ IRSNB); Parc National de l'Upemba, Munoi, 890m (9°16'S, 26°46'E), 31.v-2.vi.1948, G.F. de Witte (1♀ as *paratype* of *Catharsius duciformis* Ferreira: MRAC); **LUALABA:** Kapanga (8°21'S, 22°39'E), x.1932, F.G. Overlaet (1♂ NMPC); Kapanga (8°21'S, 22°39'E), ix.1933, F.G. Overlaet (3♂♂ 1♀ MRAC); Kapanga (8°21'S, 22°39'E), ii.1934, F.G. Overlaet (2♂♂ MRAC); Kapanga (8°21'S, 22°39'E), 1935, Dr. Richard (1♂ MRAC); **TANGANYIKA:** Baudouinville [=Kirungu] (7°05'S, 29°44'E), 23.i.1933, Debbaudt (1♀ MRAC); **MALAWI:** [no precise locality] (2♂♂ 1♀ ZMHB); [no precise locality] (4♂♂ NHRS); **CENTRAL:** Misuku Hills (9°40'S, 33°33'E), iv.1993, C. Dudley (1♂ 1♀ MHNL); Ntchisi (13°22'S, 33°55'E), 20-30.i.1998, Mracek (1♂ PMOC); Ntchisi (13°22'S, 33°55'E), 26.i.1998, Bacovsky (1♂ PMOC); Ntchisi Forest Reserve (13°22'S, 34°01'E), 25.xii.1974, H.R. Frijen (1♂ RMNH); **NORTHERN:** Jembya Forest Reserve (10°08'S, 33°27'E), xi.1989, C. Dudley (1♀ PMOC); Misuku Hills (9°40'S, 33°33'E), iv.1993, M. Chirwa (1♀ JLMC); Mzuzu (11°27'S, 34°01'E), 3.ii.1978, R. Jocqué (1♀ MRAC); Nkhata Bay (11°37'S, 34°18'E), 1.xii.1994, M. Chirwa (1♂ JLMC); Viphya Forest Reserve (12°07'S, 33°43'E), xii.1981, C. Dudley (1♂ PMOC); **SOUTHERN:** Bvumbwe (15°56'S, 35°05'E), 21.iii.1971, Gowing-Scopes (2♂♂ BMNH); Bvumbwe (15°56'S, 35°05'E), xi.1972, Gowing-Scopes (2♀♀)

BMNH); Bvumbwe Research Station (15°56'S, 35°05'E), 20.xi.1972, G.F. Bornemissza (1♂ 1♀ SANC); Lujeri (16°02'S, 35°40'E), 14.xi.1972, G.F. Bornemissza (3♂♂ 1♀ SANC); Mlanje [=Mulanje] (16°01'S, 35°31'E), 27.xii.1912, S.A. Neave (1♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 21.i.1913, S.A. Neave (1♂ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 6.ii.1913, S.A. Neave (1♂ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 17.ii.1913, S.A. Neave (1♂ 1♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 18.ii.1913, S.A. Neave (1♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 6.v.1913, S.A. Neave (1♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 1.xii.1913, S.A. Neave (1♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 21.xii.1913, S.A. Neave (1♂ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 20.i.1914, S.A. Neave (2♀♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 4.ii.1914, S.A. Neave (2♂♂ 1♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 5.ii.1914, S.A. Neave (2♀♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 16.ii.1914, S.A. Neave (1♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 24.ii.1914, S.A. Neave (1♀ BMNH); Mlanje [=Mulanje] (16°01'S, 35°31'E), 27.ii.1914, S.A. Neave (1♀ BMNH); Mulanje (16°01'S, 35°31'E) (1♀ BMNH); Mulanje (16°01'S, 35°31'E), S.A. Neave (2♀♀ BMNH); Zomba (15°23'S, 35°19'E), A. Whyte (1♂ 1♀ BMNH); Zomba, 2000-3000ft. (15°23'S, 35°19'E), ix.1893, A. Whyte (1♀ BMNH); **MOZAMBIQUE**: Nyassa, F.A.A. Simons (1♂ 1♀ BMNH); **ZAMBEZIA**: E of Mount Chipirone, Valley of Kola River, 1500-2000ft. (16°29'S, 35°46'E), 7.iv.1913, S.A. Neave (1♀ BMNH); **TANZANIA**: **IRINGA**: Kidugala (9°08'S, 34°32'E) (2♀♀ ZMHB); Idetero, 1793m (8°32'S, 35°01'E), 7.ii.2013, P. Darge (14♂♂ 7♀♀ MHNL); **MBEYA**: Konde-Unyika, i.1900, Fülleborne (2♂♂ 1♀ ZMHB; 1♂ BMNH); Conde [=Konde] (9°29'S, 33°53'E) (1♂ MTD); Langenburg [=Lumbira] (9°35'S, 34°09'E) (1♂ ZMHB); Manow (9°16'S, 33°47'E) (1♂ RMNH); Manow (9°16'S, 33°47'E) (5♂♂ ZMHB); Manow (9°16'S, 33°47'E) (1♂ NMPC); Manow (9°16'S, 33°47'E) (3♂♂ 2♀♀ MTD); Manow (9°16'S, 33°47'E) (2♂♂ 1♀ ZSM; 3♂♂ NMB); Masewe-Kivira Fluss (9°25'S, 33°37'E), 25.xi.1899, Götze (5♂♂ 1♀ ZMHB; 3♂♂ ZSM; 1♂ IRSNB); Rutenganio (9°21'S, 33°37'E) (1♂ ZMHB); **RUKWA**: Msamwia [=Msambia] (8°24'S, 31°52'E), Fromm (2♂♂ ZMHB); Mbizi Forest, Sumbawanga, 1236m (7°54'S, 31°41'E), x.2013, local collector (1♂ BMNH); **RUVUMA**: Kigonsera (10°48'S, 35°04'E) (1♂ ZMHB); Kigonsera (10°48'S, 35°04'E) (4♀♀ NHRS); Kigonsera (10°48'S, 35°04'E) (2♂♂ 1♀ IRSNB); Kigonsera (10°48'S, 35°04'E) (1♂ RMNH); Kigonsera (10°48'S, 35°04'E), P.C. Hartl (13♂♂ 6♀♀ ZSM); Kigonsera, 1949, Hartl (14♂♂ 11♀♀ NMB); Kigonsera, 1950, Hartl (1♂ NMB); Kigonsera, i.1950, Hartl (2♂♂ 1♀♀ NMB); Kigonsera, 1952, Hartl (5♂♂ 6♀♀ NMB); Kigonsera, 1959, Hartl (1♂ NMB); Kigonsera, 1960, Hartl (1♂ NMB); Lac Rukwa (8°20'S, 32°15'E), i.1945, H.J. Brédo (1♂ IRSNB); Peramiho (10°38'S, 35°28'E), 1905 (4♂♂ 1♀ ZSM); Songea, 3800ft. (10°40'S, 35°39'E), 2.xi.1933, R.F. Johnstone (1♂ BMNH); near Songea (10°40'S, 35°39'E), 9-13.xii.1997, K. Werner & R. Lizler (3♂♂ 1♀ PMOC); **ZAMBIA**: **CENTRAL**: Mayukuyuku, Kafue National Park, 1080m (14°55'S, 26°04'E), 21-26.xi.2013, R. Smith, H. Takano & D. Oram (1♂ BMNH); Mfwanta (13°07'S, 30°20'E), 17.i.2009, R. Minetti (1♂ PMOC).

**Diagnosis:** see under *C. spectabilis*. These two species can easily be separated by the shape of the anterior clypeal edge which is arcuate in *C. satyrus*. The females are similar in appearance but the central tubercle on the clypeal carina is elevated much higher in *C. satyrus*. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** the distribution of this species is centred around the Central Zambesian Miombo woodland habitat and although the dung preference is unknown, the author collected one individual in a human dung-baited pitfall trap in Kafue National Park, Zambia. Other specimens with collecting data show that this species is attracted to light. Specimens have been caught between September and June.

**Distribution** (Pl. 15: fig. 8): Zambia, D.R. Congo, Tanzania, Malawi, Mozambique.

### 13. *Catharsius hertli* Ferreira, 1964

(Pl. 13: figs. 1-8; Pl. 30: fig. 13)

*Catharsius hertli* Ferreira, 1964: 3.

**Type locality:** “Deutsch Ost Afrika”

**Name-bearing type:** Holotype ♂ in MTD:

“// Deutsch Ost / Afrika [blue card] // D.O.Africa [cream paper with green border, handwritten] // Coll. C. Felsche / Kauf 20, 1918 [blue card] // Staatl. Museum für / Tierkunde Dresden // Senckenberg

Natur- / hist. Sammlungen / Dresden, Museum / für Tierkunde (MTD) // HOLOTIPO, ♂ / Catharsius hertli / n.sp. / M.C.FERREIRA, 1964 [pink paper; handwritten] //”

**Redescription:** Colour: Black; pubescence reddish-brown. **Male** (Pl. 13: figs. 1, 2, 5): **Head:** anterior clypeal arcuate, clypeal margin continuous; clypeal surface granulose except for some transverse rugulae centrally between the cephalic horn and the anterior margin; Genal edge rounded and obtusely angled, surface covered with ovaline granules disappearing towards the eyes; suture well defined to base of incomplete carina; A short, laterally flattened, rectangular cephalic horn positioned anteriorly, very near the anterior margin; horn arcuate in dorsal view and slanted forward in lateral view. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin right angled, lateral margin arcuate; Pronotal disc with a triangular carina anteriorly; carina weakly sinuous the total length no wider than the widest point of the pronotum; Surface of pronotal disc completely granulose, with some larger and more diamond-shaped granules anteriorly, becoming more circular posteriorly; some alutaceous microsculpture centrally and posteriorly; lateral declivity with fovea, the surface of lateral and anterior declivities completely granulose with some alutaceous microsculpture. **Elytra:** carinate basally; elytral striae shallow with very indistinct punctures. Interstriae rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate, mesa- and metatibia with an undulating apical margin; tarsomeres with reddish-brown pubescence; **Aedeagus** (Pl. 13: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 13).

**Female** (Pl. 13: 3, 4, 6): **Head:** anterior clypeal edge arcuate with slight emargination centrally; clypeal margin continuous; clypeal surface with transversely rugulate turning more granulose towards the clypeogenal suture; Genal edge rounded and obtusely angled, surface covered with ovaline granules disappearing towards the eyes; Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central point being positioned slightly to the posterior of and much higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Lateroanterior margin right angled, lateral margin arcuate; Pronotal disc with transverse carina anteriorly, with the width as wide as the head; the carina almost straight centrally and slightly emarginate, gently bowed laterally to its terminal point positioned along the same lateral plane as the midpoint; Surface of pronotal disc completely granulose, larger more transversely ovaline granules closely arranged anteriorly, becoming smaller, circular and spaced out posteriorly; some alutaceous microsculpture in the extreme posterior and central portion of disc; Lateral declivity with fovea; surface of lateral and anterior declivity completely granulose with alutaceous microsculpture throughout. **Elytra:** carinate basally; elytral striae shallow with very indistinct punctures. Interstriae

rugose with alutaceous microsculpture throughout; epipleural carina well-developed, extending two-thirds the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout; **Ventrites:** covered in reddish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate, mesa- and metatibia with a smooth apical margin; tarsomeres with reddish-brown pubescence.

**Length:** male 24-29mm; female 22-28mm.

**Variation:** in smaller males, the clypeal margin is emarginate centrally and the cephalic horn is reduced to a short point just to the anterior of the clypeal carina.

**Other material examined** (23♂♂ 25♀♀):

**TANZANIA:** [no precise locality] (1♂ *paratype*, MTD); **MOROGORO:** Itumba (6°20'S, 37°00'E) (1♀ BMNH); Itumba (6°20'S, 37°00'E), Rev. A.N. Wood (2♂♂ 1♀ BMNH); Mahenge Mountains (8°41'S, 36°43'E) (1♂ ZMHB); Mahenge Mountains (8°41'S, 36°43'E), v.1995, R. Minetti (2♂♂ PMOC); Maskati, Nguru Mountains, 1759m (6°03'S, 37°29'E), iv-v.2011, R. Smith & H. Takano (3♀♀ BMNH); Mizimu, Udzungwa Mountains National Park, 850m (7°48'S, 36°51'E), 9-11.iv.2011, R. Smith & H. Takano (1♂ 2♀♀ BMNH; 1♂ 1♀ NMPC); Mwanhiana, Udzungwa Mountains National Park, 1350m (7°49'S, 36°50'E), 15.iv.2011, R. Smith & H. Takano (1♂ 5♀♀ BMNH); Nguru-Mpwapwa, Rohrbeck (2♂♂ 2♀♀ ZMHB); Njia Panda, Udzungwa Mountains National Park, 970m (7°47'S, 36°50'E), 12-14.iv.2011, R. Smith & H. Takano (6♂♂ 5♀♀ BMNH); Sali Forest, Mahenge Mountains, 1137m (8°56'S, 36°40'E), 25-27.iv.2011, R. Smith & H. Takano (1♀ BMNH); Udzungwa Gebirge, 1450m (7°40'S, 36°59'E), Missionar Neuberger (2♂♂ 1♀ ZMHB); Udzungwa Mountains National Park (7°40'S, 36°59'E), 10.xii.2009, J.L. Moreno (1♂ 1♀ JLMC); Usagara (1♂ MTD); Usegua (2♀♀ MTD); **TANGA:** Usambara (5°07'S, 38°32'E) (1♂ IRSNB); Usambara (5°07'S, 38°32'E) Mountains (1♂ ZMHB).

**Notes:** the holotype specimen is a minor male with poorly developed cephalic armature. This may have led to confusions between this species and *C. satyrus*.

**Diagnosis:** this species is similar in appearance to the larger *C. satyrus*, but the right-angled lateroanterior pronotal margin and the tridentate protibia of *C. hertli* will distinguish both the males and females of the two species. The two species are distributed allopatrically and are unlikely to be found together despite their distributional ranges being very close.

**Biology:** this species is rare in collections and appears to be restricted to the forests of the Eastern Arc Mountains in Tanzania. The author has collected this species in cattle dung baited pitfall traps and under elephant dung in riverine forest at the foothills of the Udzungwa Mountains in Tanzania, as well as at light. Specimens have been caught between December and May.

**Distribution** (Pl. 13: fig. 8): Tanzania.

#### 14. *Catharsius adamastor* Gillet, 1932

(Pl. 14: figs. 1-8; Pl. 30: fig. 14)

*Catharsius adamastor* Gillet, 1932: 323; Ferreira, 1960a: 10.

**Type locality:** "Mont Kénia"

**Name-bearing type:** 2 syntypes (1♂ 1♀) in IRSNB. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the male specimen is here **designated as the lectotype:**

“// TYPE [pink card with black border] // Kenia – Afr. / Orient. Angl. / (Alluaud) [handwritten] // Catharsius / adamastor / Gillet / J.J.E. Gillet det. [partially handwritten] // J.J.E. Gillet det., vend.: / Catharsius / adamastor Gillet / R.M.H.N. Belg. 10.640 [partially handwritten] // LECTOTYPE / CATHARSIUS / adamastor / Gillet / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black; pubescence reddish-brown. **Male** (Pl. 14: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and concave centrally; clypeal margin continuous; clypeal surface rugulate anteriorly, turning more granulose towards the clypeogenal suture. Genal edge rounded and obtusely angled, surface covered evenly with scale-like granules turning more ovaline posteriorly; the genal margin with a distinct emargination at the clypeogenal suture. In dorsal view, the lateral sides of genae parallel-sided. Clypeogenal suture well defined to base of an incomplete clypeal carina. A laterally flattened, narrow, parallel-sided and apically pointed cephalic horn positioned anteriorly on clypeus; horn slanted forward in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin weakly emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with an angular transverse carina anteriorly, slightly emarginate medially; carina very slightly arcuate centrally with an obtuse angle between the midline and termination point. Surface of pronotal disc covered in circular granules, with alutaceous microsculpture in between the granules on the posterior portion; lateral declivity with fovea; lateral portion of anterior declivity with a narrow smooth region extending from just under the carina to the lateroanterior margin; anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture and slight rugosity; elytral striae with evenly spaced punctures encroaching on intervals; Interstriae with some alutaceous microsculpture and deep punctures throughout; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventriles:** covered in thick yellowish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 14: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 14).

**Female** (Pl. 14: figs. 3, 4, 6): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and concave centrally; clypeal margin continuous; clypeal surface with short transverse rugulae, turning more granulose towards the clypeogenal suture. Genal edge rounded and acutely angled, surface covered with ovaline granules arranged circularly from a point along the lateroposterior edge, turning

finer posteriorly; the genal margin with an emargination at the clypeogenal suture. Clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central tubercle being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin weakly emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with a short, slightly arcuate transverse carina anteriorly, interrupted medially; carina length shorter than the distance between the eyes; surface of pronotal disc covered in circular granules, becoming more spaced out towards the posterior margin; some alutaceous microsculpture throughout the disc. Lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture and slight rugosity; elytral striae with evenly spaced punctures encroaching on intervals; Interstriae with some alutaceous microsculpture and deep punctures throughout; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick yellowish brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 21-25mm; female 20-25mm.

**Variation:** in smaller males, the cephalic horn is reduced to a and the pronotal carina is reduced to an arcuate carina without any distinct angles. In smaller females, the tridentate clypeal carina is reduced.

#### **Other material examined (52♂♂ 44♀♀):**

**ETHIOPIA:** [no precise locality], 1910, G. Kristensen (1♀ IRSNB); [no precise locality], 1914, Schabelitz (1♂ NMB); **OROMIA:** Awash National Park, vii-viii.1971, G. de Rougemont (1♀ NMB); Awash National Park, 1000m, 14-15.viii.1971, R.O.S. Clarke (1♂ 1♀ MRAC); 39km SEE Goro (6°55'N, 40°51'E), 2-3.v.2013, I. Martinů (1♀ OUMNH); 76km S Hagera Mariam (4°59'N, 38°12'E), 8.v.2013, I. Martinů (1♂ OUMNH); Irgalem [=Yirga Alem] - Kibre Mengist (6°19'N, 38°40'E), iv.1993, K. Werner (1♂ PMOC); Yavello [=Yabelo] (4°54'N, 38°06'E), iv.1994, K. Werner (1♀ MHNL); 35km SW Yabelo (4°49'N, 38°21'E), 9-10.v.2013, I. Martinů (1♂ 1♀ OUMNH); 5km W Yabelo, 1750m (4°50'N, 38°03'E), 6.v.2008, S. Naumann & H. Schnitzler (1♂ Hielkma Collection); **SOUTHERN NATONS, NATIONALITIES AND PEOPLES:** Arba Minch (6°02'N, 37°33'E), ix.1971, G. de Rougemont (1♀ MRAC); Arba Minch (8°58'N, 40°07'E), 1972, H. Rupp (1♂ MRAC); Arba Minch (6°02'N, 37°33'E), iv.1994, Werner (1♀ PMOC); 5km S of Arba Minch (5°59'N, 37°33'E), iv.1993, K. Werner (1♂ PMOC); Maraquo [=Marequo] (7°58'N, 38°33'E) (1♂ MNHN); **TIGRAY:** Tigray, 1850, Schimper (1♂ 1♀ MNHN); **SOMALI:** Aware (8°15'N, 44°09'E), 10.v.1955, E.J. van Ingen (1♀ BMNH); **KENYA:** **ISIOLO:** Meru National Park, Leopard Rock Swamp/Bisanandi Plains, ca 600-700m (0°14'N, 38°13'E), 14-15.xi.1975, C.F. Dewhurst (1♂ SANC); **KITUI:** Ikutha (2°04'S, 38°11'E) (5♂♂ 1♀ ZMHB); Ikutha (2°04'S, 38°11'E), i.1991, Werner (1♀ NMPC); **LAMU:** Lamu (2°16'S, 40°54'E) (1♂ NMB); **MAKUENI:** Chyulu Hills (2°35'S, 37°50'E), 2.vi.1974 (1♀ SANC); Emali Range, Sultan Hamud (2°01'S, 37°22'E), 4900-5900ft., iii.1940 (2♀♀ NMK); 7km SE Sultan Hamud, Nzai Farm, ca 1300m (2°03'S, 37°25'E), 30.v.1975, Davis & Dewhurst (1♀ SANC); Kibwezi (2°25'S, 37°58'E) (1♂ ZMHB); Kibwezi (2°25'S, 37°58'E), R.A. Dummer (1♂ MNHN); Mito Andei (2°41'S, 38°10'E), vii.1991, K. Werner (1♂ 1♀ PMOC); **MERU:** Meru National Park, Bisanandi Plains, 700m (0°15'N, 38°10'E), 13.xi.1975, C.F. Dewhurst (1♂ SANC); Meru National Park, Leopard Rock Swamp, ca 610m (0°12'N, 38°12'E), 2.xii.1975, C.F. Dewhurst (1♀ SANC); Meru National Park, Tana River post 96, ca 275m (0°04'S, 38°23'E), 13.xi.1975, C.F. Dewhurst (1♀ SANC); **MURANGA:** 6km NE Fort Hall [=Muranga], ca 1200m (0°41'S, 37°12'E), 10.v.1975, Davis & Dewhurst (2♂♂ SANC); Makuyu (0°54'S, 37°11'E), x-xi.1989, F. Ferrero (2♂♂ 1♀ PMOC); Makuyu (0°54'S, 37°11'E), xi.1989, R. Minetti (1♂ MHNL); **SANKURU:** 20km S Maralal, 1825m (0°55'N, 36°42'E), 9.vi.1975, Davis & Dewhurst (4♂♂ SANC); **TAITA-TAVETA:** Mbuyuni (3°24'S, 37°53'E), 1100m, iii.1912, Alluaud & Jeannel (3♂♂ 6♀♀ MNHN); Sagala Hills (3°28'S, 38°35'E), xii.1993, Werner (1♂ PMOC); Lake Jipe (3°36'S, 37°47'E), vi.1913, Dr. Bayer (1♀ MRAC); Tsavo (3°00'S, 38°28'E), 1982 (1♀ OUMNH); **MERU:** Meru National Park (0°13'N, 38°10'E), 9.iv.1981, J. Krikken (1♀ RMNH); Meru National Park, 650m (0°13'N, 38°10'E), 13.iv.1981, J. Krikken (1♂ RMNH); **SOMALIA:** [no precise locality], Greenfield (1♂ BMNH);

**HIRSHABELLE:** Giohar [=Jowhaar] (2°47'N, 45°30'E), 18-28.iv.1968, L. Simonetta (1♂ NMB); Giohar [=Jowhaar] (2°47'N, 45°30'E), 21.iv.1968, L. Simonetta (1♂ NMB); **TANZANIA:** **ARUSHA:** 19km W Arusha, 1325m (3°22'S, 36°31'E), 2.v.1975, Davis & Dewhurst (3♂♂ 1♀ SANC); Karatu, 1490m (3°20'S, 35°40'E), 30.iv.1975, Davis & Dewhurst (4♂♂ 4♀♀ SANC); Karatu, 1540m (3°20'S, 35°40'E), 20.xi.2011, R. Smith & H. Takano (1♂ 1♀ BMNH); Lake Ndotu (2°59'S, 35°01'E), i.1994 (1♂ 1♀ MHNH); Lake Ndotu area, Serengeti National Park (2°59'S, 35°01'E), R. Foster (1♂ OUMNH); Lake Ndotu area, Serengeti National Park (2°59'S, 35°01'E), 17.xii.1990, R. Foster (1♂ OUMNH); Lake Ndotu area, Serengeti National Park (2°59'S, 35°01'E), 20.i.1991, R. Foster (1♀ OUMNH); Lake Ndotu area, Serengeti National Park (2°59'S, 35°01'E), 5.ii.1991, R. Foster (1♂ OUMNH); Lake Ndotu area, Serengeti National Park (2°59'S, 35°01'E), 29.iii.1991, R. Foster (1♀ OUMNH); Lake Ndotu area, Serengeti National Park (2°59'S, 35°01'E), 14.v.1991, R. Foster (1♂ 1♀ OUMNH); Lake Ndotu area, Serengeti National Park (2°59'S, 35°01'E), 31.x.1991, R. Foster (2♂♂ OUMNH); Mto wa Mbu, 963m (3°23'S, 35°53'E), 21.x.2011, R. Smith & H. Takano (4♂♂ 2♀♀ BMNH); Ndotu Camp (2°59'S, 34°58'E), 18.xi-4.xii.1994, M. Homolac (2♂♂ 2♀♀ NMPC); Ngorongoro Crater (3°10'S, 35°34'E), 20.iv.1987, P.C. Goudswaard (1♀ RMNH); Serengeti National Park, Lake Ndotu (2°59'S, 35°01'E), 15.v.1985, P.C. Goudswaard (1♂ RMNH); Serengeti National Park, Lake Ndotu (2°59'S, 35°01'E), 15.v.1985, P.C. Goudswaard (3♂♂ 3♀♀ RMNH); Serengeti National Park, Lake Ndotu (2°59'S, 35°01'E), 15.vi.1986, P.C. Goudswaard (4♂♂ 10♀♀ RMNH); Serengeti National Park, Ndotu Safari Lodge (3°01'S, 35°00'E), 11.i.1974, H. Hazewinkel (2♂♂ RMNH); Usa River near Arusha (3°22'S, 36°51'E), iv.1982, G. Leach (1♀ ZSM); **DODOMA:** Dodoma (6°10'S, 35°45'E), i.1963, E. Haaf (1♂ NHB); **KILIMANJARO:** Kisangiro (3°38'S, 37°33'E), 23.x.2004, R. Minetti (1♂ PMOC); Madschame [=Machame] (3°38'S, 37°33'E) (2♂♂ 1♀ NMB); Moshi (3°21'S, 37°20'E), 24.iv.1963, B. Salwegter (3♂♂ 1♀ NMK); Moshi (3°21'S, 37°20'E), 2.v.1963, B. Salwegter (1♂ NMK); Ndarakwai, 1310m (3°01'S, 36°59'E), 5-7.iv.2012, R. Smith & H. Takano (1♂ BMNH); **MANYARA:** Tarangire National Park camp (3°46'S, 36°01'E), i.1987, Burmeister (1♀ ZSM); Tarangire National Park lodge (3°46'S, 36°01'E), ii.1979, E.J. Fittkan (1♀ ZSM); **SHINYANGA:** Shinyanga (3°40'S, 33°26'E), 19-31.xii.1955, Dr. E. Burt (1♀ BMNH).

**Diagnosis:** the male may be confused with *C. gibbicollis* and *C. chinai* and the female with *C. platynotus* but both sexes can easily be distinguished by the well punctured elytra interstriae. This species is often found together with *C. gibbicollis* and *C. chinai* within their respective ranges.

**Biology:** this species is found in the East African montane forests and high elevation grasslands of Kenya, Tanzania and Ethiopia. They are regularly attracted to light and have also been caught in unspecified dung baited pitfall traps. Their dung preference is unknown. Specimens have been caught between March and December.

**Distribution** (Pl. 14: fig. 8): Eritrea (?), Ethiopia, Somalia, Kenya Tanzania.

## 15. *Catharsius ulysses* Boheman, 1857

(Pl. 15: figs. 1-8; Pl. 30: fig. 15)

*Catharsius ulysses* Boheman, 1857: 219; Péringuey, 1901: 331; Ferreira, 1960a: 46.

**Type locality:** “Caffraria tota”

**Name bearing type:** 9 syntypes (5♂♂ 4♀♀) in NHRS. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series is here **designated as the lectotype:**

“// Caffra / ria. // J. Wahlb. // Type. // Ulysses Bhm [handwritten] // Typus [red card with black border] // 25 / 54 [pink paper; partially handwritten] // 5231 / E92 + [light blue paper] // NHRS-JONI / 000000255 // LECTOTYPE / CATHARSIUS / ulysses / Boheman / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black, pubescence reddish-brown. **Male** (Pl. 15: figs: 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and very slightly concave centrally; clypeal margin continuous; clypeal surface with transverse rugulae centrally turning more granulose towards the edges; Genal edge rounded and obtusely angled, the posterior lateral margin almost parallel-sided, the surface covered evenly with ovaline granules becoming more indistinct towards the eyes; clypeogenal suture well defined to base of cephalic horn; cephalic horn stout and straight, wide on basal third with edges converging evenly; horn gently slanting forward in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin almost at right angles, lateral margin arcuate. Pronotal disc with an interrupted transverse carina anteriorly with four short projections along the same plane; the two central projections placed either side of the midline with an angular concavity in between. Either side of the central projections are two lateral projections, one on each side, linked to the central projections by a deeper rounded concavity. The lateral portion of the carina arcuate, terminating well before the lateral margin of the pronotum; carina forms just above the fovea in lateral view; anterior surface of pronotal disc with a posteriorly semi-circular smooth region on each side of the midline, extending laterally as far as the lateral projection and two thirds the distance from the carina to the posterior pronotal margin. The posterior and lateral surface covered evenly in circular granules, the granules becoming larger towards the edge; lateral declivity with fovea, the surface granulose with the exception of a small area surrounding the fovea; anterior declivity completely granulose except for the extreme anterior basal region which is smooth; **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae deep with inconsistent punctures indenting into the interstriae. Interstriae with irregular fine punctures and very minimal alutaceous microsculpture; epipleural carina well-developed, extending half of the length of the elytra; **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout; **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence; **Aedeagus** (Pl. 15: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 15).

**Female** (Pl. 15: figs: 3, 4, 6):: **Head:** anterior clypeal edge broadly arcuate with continuous clypeal margin; clypeal surface transversely rugulate posterior portion behind clypeal carina granulose; genal edge rounded and acutely angled, surface covered with ovaline granules becoming finer towards the eyes; clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central tubercle being positioned slightly to the posterior of and higher than the tubercles on either side; **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with short transverse carina anteriorly; carina arcuate and slightly flattening towards the edge, shorter than the distance between the eyes; a short carina runs posteriorly along the midline from the carina. Posterior surface

of pronotal disc with well-defined circular granules, with a circular area on each side of the midline where the granules are poorly-defined; the distinct boundary between these two areas forming a concave arc on each side of the midline, starting near the carina and terminating on the posterior margin. The rest of the pronotal disc is covered in granules arranged circularly towards the lateral and anterior edges from the region of poorly-defined granules. Lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra**: carinate basally; only the extreme basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae deep with weak punctures. Interstriae smooth with well-spaced fine punctures; epipleural carina well-developed, extending two-thirds of the length of the elytra; **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout; **Ventrites**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence; **Legs**: protibia tridentate; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length**: male 18-27mm; female 18-25mm.

**Variation**: in smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the pronotal carina is reduced to a smooth arcuate carina without projections. In smaller females, the tridentate clypeal carina is reduced.

#### **Other material examined** (117♂♂ 115♀♀):

**BOTSWANA**: **CENTRAL**: Mahalapye (23°06'S, 26°50'E), 21.iii.1979, A.M. Camerith (1♂ TMSA); between Francistown and Makadikadi Lake (20°54'S, 26°41'E) (1♂ TMSA); **NAMIBIA**: Herero, Lübbert (1♀ ZMHB); **ERONGO**: 33mi. ENE Omaruru (21°15'S, 16°27'E), 10-13.ii.1972, Southern African Expedition (1♂ BMNH); Ondongantje, 12mi. SE Omaruru (21°32'S, 16°04'E), ii.1958 (1♀ TMSA); **KHOMAS**: Hoffnung, 1850m (22°32'S, 17°12'E), 5.i.1934, K. Jordan (2♂♂ BMNH); Khomashochland, Farm Hochenheim (23°20'S, 16°20'E), 10.iii.1975, Endrödy-Younga (1♂ 1♀ TMSA); Khomashochland, Farm Hochenheim (23°20'S, 16°20'E), 19.i.1975, Endrödy-Younga (1♀ TMSA); Khomashochland, Farm Wissenfels (23°20'S, 16°25'E), 8.iii.1975, Endrödy-Younga (1♂ TMSA); Lichtenstein-Süd (22°46'S, 16°59'E), 10.ii.1959, Niethammer (2♂♂ 1♀ NMB); Mecklenburg (22°10'S, 17°39'E), iv.1977, E. Temesvary (3♂♂ 7♀♀ ZSM); Namibgrens Farm, 1820m (23°37'S, 16°14'E), 4-5.ii.2010, R. Müller (1♂ TMSA); 4km NE Nauchas (23°37'S, 16°20'E), 6.ii.1974, Davis & Kirsten (1♂ SANC); 30km N Rehoboth (23°03'S, 17°05'E), 13.ii.1974, Davis & Kirsten (1♂ SANC); Windhoek (22°34'S, 17°04'E) (1♂ IRSNB); Windhoek (22°34'S, 17°04'E) (1♂ 1♀ NMPC); Windhoek (22°34'S, 17°04'E), ii.1997 (1♂ 1♀ PMOC); Windhoek (22°34'S, 17°04'E), Dr. Burckel (1♀ ZSM); Windhoek (22°34'S, 17°04'E), Hartmann (3♂♂ 4♀♀ NMB); Windhoek (22°34'S, 17°04'E), iii.1974, Sander (1♀ ZSM); Windhoek (22°34'S, 17°04'E), 11.ii.2004, P. Leonard (1♀ PMOC); 20km S Windhoek, Leutwein (22°45'S, 17°04'E), 12.iv.1974, H.H. Aschenborn (1♂ 1♀ SANC); 51km W Windhoek (22°34'S, 16°35'E), 31.iii.1973, Davis & Sorutton (1♂ MNHN); Windhoek Airport (22°19'S, 17°29'E), 6.iv.1993, M. Uhlig (2♂♂ 4♀♀ ZMHB); **KUNENE**: Fransfontein (20°13'S, 15°01'E), 14.v.1948, C. Koch (4♀♀ NMB); 25km N Outjo (19°53'S, 16°09'E), 11.ii.1974, Davis & Kirsten (1♂ 2♀♀ SANC; 1♂ MNHN); Outjo (20°06'S, 16°09'E), 10.iii.1979, V.B. Whitehead (1♀ SAMC); **OMAHEKE**: Gobabis (22°27'S, 18°58'E) (1♀ ZSM); Gobabis (22°27'S, 18°58'E), 10.vi.1973, B.E. Frey (2♂♂ 3♀♀ NMB); Gobabis (22°27'S, 18°58'E), 18.iv.1981, V.B. Whitehead (1♀ SAMC); Gobabis (22°27'S, 18°58'E), 29.i.1982, Watt (1♂ NMB); 16km SW of Gobabis, 965m (20°32'S, 19°04'E), 4.iii.2014, M.A. Hielkema (2♀♀ MHPC); 32km W Gobabis (22°27'S, 18°39'E), 8.iv.1973, A.L.V. Davis (2♀♀ SANC); 30km W Witvlei (22°25'S, 18°12'E), 23.xii.1975, H.H. Aschenborn (1♀ SANC); 61km W Witveli (22°25'S, 17°54'E), 8.iv.1973, A.L.V. Davis (1♂ SANC); **OTJOZONDJUPA**: Abachaus, Otjiwarongo District (20°26'S, 16°39'E), ii.1953, G. Hobohm (1♂ 3♀♀ ZSM); Grootfontein (19°34'S, 18°06'E) (1♂ TMSA); Grootfontein (19°34'S, 18°06'E), 15.i.1978, W. Fourie (1♂ TMSA); Grootfontein (19°34'S, 18°06'E), i.1992, Rautenstrauch (1♂ 2♀♀ ZSM; 1♂ 1♀ MHNL); 23mi. SW of Grootfontein (19°47'S, 17°51'E), 3.iv.1972, Southern African Expedition (1♀ BMNH); 23km W Grootfontein (19°34'S, 17°53'E), 2.iv.1974, H. Sievers (1♂ 1♀ SANC); Hochfeld (21°29'S, 17°51'E), 20.v.1973, R. Kluge (2♂♂ 2♀♀ SANC); Neudamm (22°30'S, 17°22'E), 24.i.1972, Southern African Expedition (1♀ BMNH); Okahandja (21°59'S, 16°59'E) (1♂ MTD); Okahandja (21°59'S, 16°59'E), viii.1956, W. Hoesch (1♀ TMSA); 48km N Okahandja (21°33'S, 16°55'E), 2.ii.1976, Culligan & van der Vegte (1♀ SANC); 42km NW of Osire, 1640m (20°55'S, 17°06'E), 20.iii.2014, M.A. Hielkema (1♂

2♀♀ MHPC); 46km SW Otavi (19°56'S, 17°01'E), 12.ii.1974, Davis & Kirsten (2♂♂ 5♀♀ SANC); Otjiwarongo (20°27'S, 16°40'E), ii.1978, S.J. van Tonder (6♂♂ 4♀♀ SANC); 9km S Otjiwarongo (20°33'S, 16°40'E), 1.i.1976, Culligan & van der Vegte (1♂ SANC); 16km S Otjiwarongo (20°36'S, 16°40'E), 12.ii.1974, Davis & Kirsten (1♂ 1♀ SANC); 22km S Otjiwarongo (20°39'S, 16°40'E), 7.iv.1973, A.L.V. Davis (1♂ SANC); 22km S Otjiwarongo (20°39'S, 16°40'E), 12.ii.1974, Davis & Kirsten (1♂ SANC); 35km SE of Otjiwarongo, 1640m (20°41'S, 16°50'E), 18.iii.2014, M.A. Hielkema (1♂ 1♀ MHPC); **SOUTH AFRICA**: [no precise locality] (3♂♂ 1♀ MTD); [no precise locality], E. Holub (1♂ 1♀ NMPC); Caffraria (2♂♂ 1♀ MNHN); Caffraria (1♀ BMNH); Caffraria (2♂ IRSNB); Transvaal (1♂ 1♀ BMNH); **FREE STATE**: Bloemfontein (29°07'S, 26°12'E), 9.i.1951, W.F. van Ee (2♂♂ 2♀♀ RMNH); bei Bloemfontein (29°07'S, 26°12'E), F. Neubecker (1♀ NMPC); near Bothaville (27°23'S, 26°37'E), iv-vi.1902, E.N. Bennett (2♂♂ OUMNH); Lemoen Farm, 1250m (28°15'S, 25°00'E), 29-31.xii.1997, R. Stals (1♂ 2♀♀ SANC); 7mi N Theunissen (28°19'S, 26°42'E), 12.iii.1971, H.H. Aschenborn (1♂ 3♀♀ SANC; 1♂ BMNH); Vredefort Dom, 1388m (26°50'S, 28°38'E), 19-20.ii.2012, R. Müller (2♂♂ TMSA); **GAUTENG**: Bordeaux (26°06'S, 28°01'E), 22.ii.1980, Whitehead (1♀ SAMC); 10km SE Buffersdrift Gate (25°16'S, 28°35'E), 5.i.1974, A.L.V. Davis (2♂♂ SANC); Magdaliessburg (25°59'S, 27°32'E) (1♂ MTD); Pretoria (25°45'S, 28°14'E), W.L. Distant (1♂ BMNH); Pretoria (25°45'S, 28°14'E), xii.1900, Dr. Breyer (1♀ IRSNB); Pretoria (25°45'S, 28°14'E), xii.1900, Dr. Breyer (1♂ TMSA); Pretoria (25°45'S, 28°14'E), i.1919, C.J. Swierstra (1♀ IRSNB); Pretoria (25°45'S, 28°14'E) (1♂ ZMHB); Pretoria (25°45'S, 28°14'E), 10.ii.1948 (1♀ TMSA); Pretoria North (25°41'S, 28°11'E), i.1917, C.J. Swierstra (1♂ 1♀ TMSA); **KWAZULU-NATAL**: Natal, Dr. Martin (1♂ 1♀ NMPC); **LIMPOPO**: Bela-Bela (24°49'S, 28°23'E), 30.xii.2007, C.J. van Niekerk (1♀ SANC); 60km NW Buffelsdoorn (24°59'S, 27°30'E), 13.i.1974, L. Pitsi (5♂♂ 2♀♀ SANC); 75km W Ellisras [=Lephalale] (23°40'S, 27°01'E), 22.xi.1974, A.L.V. Davis (2♂♂ 1♀ SANC); Grootpan Farm, 930m (24°01'S, 27°06'E), 12.ii.1987, R. Stals (1♂ 1♀ SANC); Grootpan Farm, 930m (24°01'S, 27°06'E), 9-10.i.1988, R. Stals (1♂ 1♀ SANC); Luipershoek Farm (25°07'S, 29°50'E), 8.vii.1990, L.G. le Roux (1♀ SANC); Moorddrift (24°14'S, 28°58'E), i.1925, G. van Dam (1♀ IRSNB); Moorddrift (24°14'S, 28°58'E), v.1925, G. van Dam (1♂ TMSA); 1km NW Northam (24°56'S, 27°16'E), 5.i.1974, A.L.V. Davis (1♂ 3♀♀ SANC; 1♀ MNHN); Nylsvley Nature Reserve (24°39'S, 28°42'E), 28.xi.1979, E. Grey (1♀ SANC); Pienaars River (25°13'S, 28°18'E), iii.1932, G. Kobrow (1♂ TMSA); 37km SW Rooibokraal (24°46'S, 26°34'E), 5.i.1974, A.L.V. Davis (1♂ SANC); Vivo, Soutpansberg (23°04'S, 29°38'E), 10.iv.2004, B. van Rooyen (1♂ SANC); Warmbaths [=Bela-Bela] (24°53'S, 28°20'E), xii.1976, G.L. Prinsloo (1♂ SANC); **MPUMALANGA**: Lydenburg (25°05'S, 30°27'E), 1879, T. Ayres (1♂ SAMC); Lydenburg district (25°05'S, 30°27'E), 1896, Krantz (2♀♀ TMSA); Pietersburg [=Polokwane] (23°54'S, 29°27'E), 23.iii.1961, A. Spies (1♂ TMSA); Pietersburg [=Polokwane] (23°54'S, 29°27'E), 22.iv.1961, A. Spies (1♀ TMSA); **NORTH WEST**: Bloemhof (27°39'S, 25°36'E), xii.1956, Zumpt (2♂♂ NMB); Broedersput (26°49'S, 25°07'E), J.S. Braom (1♂ 1♀ SAMC); 16mi SW Mafeking (26°02'S, 25°27'E), 22.v.1972, A.L.V. Davis (1♀ SANC); 44km SW Mafeking (26°09'S, 25°20'E), 21-22.i.1976, Culligan & van der Vegte (1♂ SANC); Maquassie [=Makwassie] (27°19'S, 26°00'E), R. Broom (4♂♂ BMNH); Maquassie [=Makwassie] (27°19'S, 26°00'E), iii.1933, R. Broom (1♂ SAMC); Potchefstroom (26°43'S, 27°06'E), 15.i.1910, L. Gunning (1♀ TMSA); Potchefstroom (26°43'S, 27°06'E), i.1952, Frey (1♂ 1♀ NMB); Potchefstroom (26°43'S, 27°06'E), 14.ii.1953 (1♀ NMB); Potchefstroom Cantonments (26°43'S, 27°06'E), 10.iii.1904, E.E. Hamm (1♂ OUMNH); 12km NE Stella (26°29'S, 24°57'E), 27.i.1974, Davis & Kirsten (1♂ SANC); 20km N Stella (26°23'S, 24°52'E), 25.iii.1974, I.D. Temby (1♂ SANC); Upington (28°27'S, 21°15'E), iv.1933, H. Lang (1♂ TMSA); Vierboslaagte (25°20'S, 28°01'E), 27-28.iii.1976, L. Pitsi (1♂ SANC); Vryburg (26°57'S, 24°44'E), J.M. Bain (1♀ SAMC); Vryburg (26°57'S, 24°44'E), i.1904 (1♀ SAMC); Vryburg (26°57'S, 24°44'E), 27.ii.1973, Bornemissza & Temby (1♀ SANC); 20km N Vryburg (26°47'S, 24°44'E), 6.iv.1974, H.H. Aschenborn (1♂ SANC); 61km SW Vryburg (27°21'S, 24°17'E), 25.iii.1973, A.L.V. Davis (1♀ SANC); 11km NE Wolmaransstad (27°08'S, 26°04'E), 24.iii.1973, A.L.V. Davis (1♂ SANC); **NORTHERN CAPE**: Benfontein Nature Reserve (28°49'S, 24°49'E), 15.ii.2010, E. Holm (1♀ SANC); Dronfield Nature Reserve, 1220m (28°37'S, 24°48'E), 10-12.ii.2012, R. Müller (2♂♂ TMSA); Green Kalahari, Olifantshoek (27°42'S, 22°39'E), 20-22.iii.2017, M. Ströhle & Schaarschmidt (4♂♂ 2♀♀ PMOC); 30km N Hopetown (29°22'S, 24°04'E), 2.iii.1973, Bornemissza & Temby (1♀ BMNH); 62km SW of Hotazel (27°31'S, 22°19'E), 26.iii.1974, I.D. Temby (2♂♂ 1♀ SANC); Kimberley (28°44'S, 24°45'E), Rombach (1♂ IRSNB); Kimberley (28°44'S, 24°45'E), 1893, E. Simon (1♂ NMPC); Kimberley (28°44'S, 24°45'E), 1967, Zumpt (1♀ NMB); 32km SW Kuruman (27°40'S, 23°12'E), 30.i.1976, P.D. & A.D. Stickler (1♀ SANC); Olifantshoek (27°56'S, 22°44'E), 27.ii.1973, Bornemissza & Temby (1♂ 2♀♀ SANC); 2km SW Olifantshoek (27°58'S, 22°43'E), 25.iii.1973, A.L.V. Davis (3♂♂ 1♀ SANC; 1♀ MNHN); 47km SW Olifantshoek, 1150m (28°11'S, 22°21'E), 24.iv.1976, Davis & Aschenborn (1♀ SANC); 29km SW Sishen (27°57'S, 22°44'E), 30.i.1976, P.D. & P.A. Stickler (1♂ 1♀ BMNH; 1♂ SANC); Smythe Farm, 1200m (27°53'S, 22°55'E), ii.1992, H. Steenkamp (5♀♀ SANC).

**Diagnosis:** Males of this species are easily identified by the distinctive pronotal carina along which there are four sharp protrusions. Females are very similar in appearance to *C. telemachus* sp. nov., but in *C. ulyssees*, only the extreme basal region of the elytra has alutaceous microsculpture and the epipleural carina extends two-thirds of the length of the elytra. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** this species has a disjointed distribution in open grassland and savanna habitats at higher elevations in southern Africa. This species has been attracted to cattle dung baited pitfall traps and to light. Specimens have been caught between November and August.

**Distribution** (Pl. 15: fig. 8): Namibia, Botswana, South Africa.

## 16. *Catharsius telemachus* sp. nov.

(Pl. 16: figs. 1-8; Pl. 30: fig.16)

**HOLOTYPE** ♂ (ZMHB):

“// D. Ost-Afrika / Dar es Salaam //”

**Description:** Holotype ♂ (Pl. 16: figs. 1, 2, 5): Colour: Black, pubescence reddish-brown. Length: 24mm.

**Head:** anterior clypeal edge unevenly arcuate, rounded laterally and very slightly concave centrally; clypeal margin continuous; clypeal surface granulose except for some minimal transverse rugulae at the very extreme anterior edge; Genal edge rounded and obtusely angled, the surface covered evenly with ovaline granules becoming finer towards the eyes; clypeogenal suture well defined to base of an incomplete clypeal carina. A laterally flattened, narrow, parallel-sided and apically pointed cephalic horn positioned anteriorly on clypeus; horn slanted forward, slightly curved back apically in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin rounded, lateral margin arcuate. Pronotal disc with an angular transverse carina anteriorly, emarginate medially with short angular projections at each end of the emargination; situated two thirds of the way along carina from the midline to the edge is a second angular projection, positioned slightly to the posterior of the medial projections, the carina in between bowed slightly; the carina in the final third is bowed and terminates posteriorly to the lateral projections; the carina is no wider than the widest point of the lateral margin in dorsal view and forms just above the fovea in lateral view; anterior surface of pronotal disc with an ovaline smooth region on each side of the midline, extending laterally just beyond the lateral projections and at its longest nearly two thirds the distance from the carina to the posterior pronotal margin. The posterior and lateral surface covered evenly in circular granules; lateral declivity with fovea; lateral portion of anterior declivity with a smooth region extending from just under the carina to the lateroanterior margin; central portion of anterior declivity granulose except for a “M” shaped smooth region basally as wide as the distance between the eyes extending half way up the anterior declivity. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae deep with inconsistent and weak punctures. Interstriae with fine punctures and some alutaceous microsculpture; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with

reddish-brown pubescence. **Aedeagus** (Pl. 16: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 16).

**FEMALE PARATYPE** (Pl. 16: figs. 3, 4, 6): **Head**: anterior clypeal edge broadly arcuate with continuous clypeal margin; clypeal surface transversely rugulate posterior portion behind clypeal carina granulose; genal edge rounded and acutely angled, surface covered with ovaline granules becoming finer towards the eyes; clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central tubercle being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum**: anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin obtusely angled, lateral margin arcuate. Margin weakly emarginate centrally. Pronotal disc with short transverse carina anteriorly; carina arcuate, shorter than the distance between the eyes; a very short carina runs posteriorly along the midline from the carina. Posterior surface of pronotal disc with well-defined circular granules, with a circular area on each side of the midline where the granules are poorly-defined; the distinct boundary between these two areas forming a concave arc on each side of the midline, starting near the carina and terminating on the posterior margin. The rest of the pronotal disc is covered in granules arranged circularly towards the lateral and anterior edges from the region of poorly-defined granules. Lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra**: carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae deep with inconsistent and weak punctures. Interstriae with fine punctures and some alutaceous microsculpture; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternite with long pubescence. **Legs**: protibia tridentate; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length**: male 17-25mm; female 20-23mm.

**Variation**: in smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the pronotal carina is reduced to a short interrupted carina. In smaller females, the tridentate clypeal carina is reduced.

**PARATYPES** (56♂♂ 49♀♀):

**KENYA**: **MAKUENI**: Emali Range, Sultan Hamud (2°01'S, 37°22'E), 4900-5900ft., iii.1940 (2♂♂ NMK); Mito Andei (2°41'S, 38°10'E), xii.1991, Werner (1♂ PMOC); 7km SE Sultan Hamud, Nzai Farm, ca 1300m (2°03'S, 37°25'E), 30.v.1975, Davis & Dewhurst (3♂♂ 5♀♀ SANC); 16km NW Sultan Hamud, Konza Ranch, ca 1300m (1°55'S, 37°16'E), 6.v.1975, Davis & Dewhurst (2♂♂ SANC); Tsavo West National Park, near Headquarters, 850m (2°42'S, 38°10'E), 4.v.1975, Davis & Dewhurst (1♀ SANC); **MERU**: Meru National Park (0°13'N, 38°10'E), 8.xii.1978, K. Stemmler (1♀ NMB); Meru National Park (0°13'N, 38°10'E), 9.xi.1983, R. Mourglia (1♂ 1♀ PMOC; 1♂ NMPC); Meru National Park, 600m (0°12'N, 38°12'E), 13.iv.1981, J. Krikken (2♀♀ RMNH); Meru National Park, 650m (0°13'N, 38°10'E), 13.iv.1981, J. Krikken (1♀ RMNH); Meru National Park, campsite near post 12 (0°10'N, 38°13'E), 1-3.xii.1975, C.F. Dewhurst (1♀

SANC); Meru National Park, 17km SW Headquarters, 600m (0°04'N, 38°05'E), 30.xi.1975, C.F. Dewhurst (1♂ 1♀ SANC); Meru National Park, Leopard Rock Swamp, post 12-33, ca 600m (0°12'N, 38°13'E), 14.xi.1975, C.F. Dewhurst (1♀ SANC); Meru National Park, Mulika Lodge, 700m (0°13'N, 38°10'E), 9.iv.1981, J. Krikken (1♀ RMNH); Meru National Park, Mulika Lodge, 650m (0°13'N, 38°10'E), 13.iv.1981, J. Krikken (3♀ RMNH); Meru National Park, Mururi Swamp area, ca 650m (0°13'N, 38°06'E), 12.v.1975, Davis & Dewhurst (8♂♂ 8♀♀ SANC); Meru National Park, Mururi Swamp, post 48-46, ca 680m (0°13'N, 38°06'E), 1.xii.1975, C.F. Dewhurst (1♂ 1♀ SANC); Meru National Park, Mururi Swamp, post 46-45, ca 760m (0°13'N, 38°04'E), 1.xii.1975, C.F. Dewhurst (1♀ SANC); **TAITA-TAVETA**: Kilaguni, Tsavo West National Park (2°54'S, 38°04'E), F. Vieuxgué (12♂♂ 7♀♀ MHNH; 6♂♂ MDCL); Tsavo (3°00'S, 38°28'E), Vieuxgué (2♀♀ MDCL); Tsavo National Park, near Mtito Andei, 850m (2°47'S, 38°07'E), 5.i.1973, J. Krikken (1♀ RMNH); **MOZAMBIQUE**: Nyassa (1♂ IRSNB); **CABO DELGADO**: Ravia (site 1), Parque Nacional das Quirimbas, 380m (12°40'S, 39°25'E), 2.i.2013, F. & S. Génier & M. Denja (1♂ FGIC); Ravia (site 1), Parque Nacional das Quirimbas, 380m (12°40'S, 39°25'E), 3.i.2013, F. & S. Génier (1♀ FGIC); Ravia (site 3), Parque Nacional das Quirimbas, 380m (12°40'S, 39°26'E), 3.i.2013, F. & S. Génier (1♀ FGIC); Ravia (site 4), Parque Nacional das Quirimbas, 380m (12°40'S, 39°27'E), 3.i.2013, F. & S. Génier (1♀ FGIC); Ravia (site 6), Parque Nacional das Quirimbas, 380m (12°31'S, 39°19'E), 3.i.2013, F. & S. Génier & M. Denja (1♀ FGIC); Ravia (site 6), Parque Nacional das Quirimbas, 380m (12°31'S, 39°19'E), 4.i.2013, F. & S. Génier (1♀ FGIC); **TANZANIA**: **DAR ES SALAAM**: Dar es Salaam (6°49'S, 39°17'E) (1♂ ZMHB); **LINDI**: Lindi (10°00'S, 39°42'E), 1903 (1♂ MTD); **MOROGORO**: Mikumi National Park (7°19'S, 37°07'E), 17.iii.1996, J. Roggeman (1♂ IRSNB); Uluguru Mountains (7°01'S, 37°44'E), iv.1992, K. Werner (1♂ PMOC); **MTWARA**: Lukuledi (10°34'S, 38°48'E) (1♂ ZMHB; 1♂ MTD); Lukuledi (10°34'S, 38°48'E), 1903 (3♂♂ 3♀♀ ZSM); Lukuledi (10°34'S, 38°48'E), 1903, Ertl (1♂ ZMHB); **MWANZA**: Nyegezi (2°36'S, 32°54'E), 8.v.1986, P.C. Goudswaard (1♀ RMNH); **PWANI**: Ubenazomzi, 380m (6°38'S, 38°10'E), 27.ii.2004, R. Minetti (1♂ PMOC); **RUUVUMA**: Nyassa-see, Mango (11°15'S, 34°47'E), Sr. Fischer (2♂♂ 2♀♀ ZSM); **ZAMBIA**: **CENTRAL**: Chingombe (14°25'S, 29°58'E) (1♂ MRAC; 1♂ NMB); **LUSAKA**: Lusaka (15°23'S, 28°19'E), 30.xii.2008 (1♂ JFJC).

**Diagnosis:** this species and the subsequent species have previously been confused with *C. polynices*, based on the shape of the clypeal carina. *C. polynices* is a larger insect and can be distinguished by the obtusely-angled lateroanterior margin. *C. telemachus* sp. nov. and *C. thersander* sp. nov. are very similar in appearance but males can easily be separated by the “M” shaped smooth region on the anterior declivity in *C. telemachus* sp. nov.. The female is very similar to *C. ulysses* from which it can be separated by the shorter length of the epipleural carina and the greater extent of alutaceous microsculpture at the base of the elytra. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** this species is widely distributed in open grassland and woodland habitats of East Africa from Kenya to Mozambique. It has been collected in elephant dung and the species is readily attracted to light. Specimens have been caught between November and May.

**Derivation nominis:** this species is named after Telemachus, son of Ulysses, a figure in Greek Mythology; in reference to the similarity, especially in the females, between this species and *C. ulysses*.

**Distribution** (Pl. 16: fig. 8): Kenya, Tanzania, Mozambique, Malawi (?), Zambia.

## 17 *Catharsius thersander* sp. nov.

(Pl. 17: figs. 1-8; Pl. 30: fig. 17)

*Catharsius polynices* sensu Gillet, 1901 (*nec* Kolbe): 595.

*Catharsius polynices* sensu Ferreira, 1960a (*nec* Kolbe): 33.

**HOLOTYPE** ♂ (BMNH):

“// Entebbe, Uganda. / (F.J. Jackson) // Brit. Mus. / 1929-606. //”

**Description:** Holotype ♂ (Pl. 17: figs. 1, 2, 5): Colour: Black, pubescence reddish-brown. Length: 24mm.

**Head:** anterior clypeal edge unevenly arcuate, rounded laterally and very slightly concave centrally; clypeal margin continuous; clypeal surface granulose except for some minimal transverse rugulae at the very extreme anterior edge; Genal edge rounded and obtusely angled, the surface covered evenly with ovaline granules becoming finer towards the eyes; clypeogenal suture well defined to base of an incomplete clypeal carina. A laterally flattened, narrow, parallel-sided and apically pointed cephalic horn positioned anteriorly on clypeus; horn slanted forward, slightly curved back apically in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin weakly emarginate centrally. Lateroanterior margin rounded, lateral margin arcuate. Pronotal disc with an angular transverse carina anteriorly, emarginate medially with short angular projections at each end of the emargination; situated two thirds of the way along carina from the midline to the edge is a second angular projection, positioned slightly to the posterior of the medial projections, the carina in between bowed slightly; the carina in the final third is bowed and terminates posteriorly to the lateral projections; the carina is no wider than the widest point of the lateral margin in dorsal view and forms just above the fovea in lateral view; anterior surface of pronotal disc with an ovaline smooth region on each side of the midline, extending laterally as far as the edge of the carina and at its longest nearly two thirds the distance from the carina to the posterior pronotal margin. The posterior and surface covered evenly in circular granules; lateral declivity with fovea; lateral portion of anterior declivity with a smooth region extending from just under the carina to the lateroanterior margin; central portion of anterior declivity completely granulose, with “V” shaped shallow depression medially. **Elytra:** carinate basally; basal portion of elytra with some fine alutaceous microsculpture and slight rugosity; elytral striae with weak punctures. Interstriae with fine punctures and some alutaceous microsculpture centrally; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 17: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 17).

**FEMALE PARATYPE** (Pl. 17: figs. 3, 4, 6): **Head:** anterior clypeal edge broadly arcuate with continuous clypeal margin; clypeal surface transversely rugulate posterior portion behind clypeal carina granulose; genal edge rounded and acutely angled, surface covered with ovaline granules becoming finer towards the eyes; clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central tubercle being positioned slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with

transverse arcuate carina anteriorly, with the width greater than the distance between the eyes; the carina bowed from the midline to its terminal point positioned to the posterior of the medial point of the carina; a very short carina runs posteriorly along the midline from the carina. Surface of pronotal disc granulose except for a small ovaline smooth region on each side of the midline; the granules circular posteriorly turning more elongate anteriorly and laterally. Lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra**: carinate basally; basal portion of elytra with some fine alutaceous microsculpture and slight rugosity; elytral striae with weak punctures. Interstriae with fine punctures and some alutaceous microsculpture centrally; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs**: protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length**: male 19-27mm; female 18-25mm.

**Variation**: in smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the pronotal carina is reduced to a short interrupted carina. In smaller females, the tridentate clypeal carina is reduced and the smooth ovaline regions on the pronotal disc more indistinct.

**PARATYPES** (286♂♂ 301♀♀):

**BENIN**: DONGA: Goutansoukpa (9°13'N, 1°50'E), 21.x.2011, B. Rainon (2♂♂ 1♀ MDCL); Goutansoukpa (9°13'N, 1°50'E), 29.x.2011, B. Rainon (1♂ 1♀ MDCL); Penelan (9°15'N, 1°31'E), viii.2013, B. Rainon (1♂ 1♀ MDCL); **CENTRAL AFRICAN REPUBLIC**: HAUT-MBOMOU: Semnio [=Zemio] (5°02'N, 25°08'E), Bohndorff (2♂♂ 1♀ ZMHB; 1♂ 1♀ MNHN); KEMO: Fort Sibut (5°44'N, 19°05'E) (3♂♂ 1♀ ZMHB; 1♂ 1♀ BMNH; 1♂ 1♀ MTD; 1♂ NMB); Fort Sibut (5°44'N, 19°05'E), G. Favarel (1♂ 1♀ MHNL); OUAKA: Bambari (5°46'N, 20°40'E), 8.viii.1970, J. Poulard (2♂♂ 10♀♀ MHNL); OUHAM: Bouca (6°30'N, 18°17'E), 1909, Lefebvre (2♂♂ 1♀ MNHN); **D.R. CONGO**: HAUT-UELE: Dungu (3°36'N, 28°34'E), De Greef (2♂♂ MRAC); Dungu (3°36'N, 28°34'E), x.1912, Mme. Hutereau (1♂ 1♀ MRAC); Dungu (3°36'N, 28°34'E), vi.1922, D.J. Bussey (1♀ BMNH); Dungu (3°36'N, 28°34'E), vii.1922, D.J. Bussey (1♂ BMNH); Dungu (3°36'N, 28°34'E), viii.1922, D.J. Bussey (3♂♂ BMNH); Faradje (3°44'N, 29°43'E), vi.1915, Blommaert (1♀ MRAC); Gangala na Bodio (3°42'N, 29°17'E), 7.v.1928, H.J. Bredo (1♂ MRAC); Gangala na Bodio (3°42'N, 29°17'E), 30.viii.1931, H.J. Bredo (35♂♂ 62♀♀ MRAC; 1♂ BMNH); Gangala na Bodio (3°42'N, 29°17'E), x.1956, Dr. M. Poll (1♂ NMPC); Nyangara [=Niangara] (3°41'N, 27°54'E), v.1912, Mme. Hutereau (1♀ MRAC); Parc National de la Garamba (4°11'N, 29°30'E), 1949-1950, Mission H. de Saeger (1♂ TMSA); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 18.iv.1951, J. Verschuren (1♂ NMB); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 4.v.1951, H. de Saeger (8♂♂ 6♀♀ MRAC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 7.vi.1951, H. de Saeger (8♂♂ 5♀♀ MRAC; 1♀ JFJC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 17.vii.1951, H. de Saeger (3♂♂ JFJC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 28.vii.1951, H. de Saeger (20♂♂ 30♀♀ MRAC; 2♂♂ ZMHB); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 19.ix.1951, H. de Saeger (1♀ JFJC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 25.ix.1951, H. de Saeger (2♂♂ 4♀♀ MRAC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 28.iv.1952, H. de Saeger (1♂ TMSA); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 29.v.1952, H. de Saeger (54♂♂ 53♀♀ MRAC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 24.vi.1952, H. de Saeger (19♂♂ 12♀♀ MRAC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 2.vii.1952, H. de Saeger (37♂♂ 51♀♀ MRAC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 16.viii.1952, H. de Saeger (9♂♂ MRAC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 22.viii.1952, H. de Saeger (15♂♂ 4♀♀ MRAC); Parc National de la Garamba, Cellule II (4°11'N, 29°30'E), 5.ix.1952, H. de Saeger (1♂ MRAC); Van Kerkhovenville [=Nzoro] (3°20'N, 29°30'E), De Greef (3♀♀ MRAC); Yebo Moto (2°54'N, 29°25'E), v.1926, L. Burgeon (1♂ 2♀♀ MRAC); Yebo Moto (2°54'N, 29°25'E), 26.vii.1926, L. Burgeon (5♂♂ 2♀♀ MRAC); Yebo Moto (2°54'N, 29°25'E), x.1926, L. Burgeon (3♂♂ 7♀♀ MRAC); **ITURI**: Aru (2°52'N, 30°50'E), Mme. Hutereau (1♀ MRAC); Aru (2°52'N, 30°50'E), 1953, M. Winand (2♀♀ MRAC); **SUD-UBANGI**: M'Paka, Libenge (3°39'N, 18°38'E), x.1959, M. Pecheur (2♂♂ 1♀ MRAC); **GUINEA**: CONAKRY: Camayenne (9°32'N, 13°41'W), 1909, Duport (1♂ MNHN); FARANAH: Kisidougou (9°11'N, 10°06'W), Dr. E. Krysa (1♂ NMPC); KINDIA: Mont Gangan, 700m (10°05'N, 12°54'W), 26.v.1951, Bechyne (1♂ NMB); Kolanguelle (10°49'N, 13°01'W), 11.vi.1951, Bechyne (1♂

3♀♀ NMB); **LABÉ**: Labé (11°19'N, 12°17'W), iv.1964, J. Dedycker (1♀ MRAC); **MAMOU**: Dalaba, (10°41'N, 12°15'W), 10-14.xi.2008, M. & J. Bouletreau (1♂ MDCL); Dalaba, 1200m (10°41'N, 12°15'W), 13.vi.1951, Bechyne (2♂♂ 2♀♀ NMB); Dalaba, 1200m (10°41'N, 12°15'W), 16.vi.1951, Bechyne (5♂♂ 5♀♀ NMB); Dalaba, 1200m (10°41'N, 12°15'W), 18.vi.1951, Bechyne (1♀ NMB); Dalaba, 1200m (10°41'N, 12°15'W), 19.vi.1951, Bechyne (6♂♂ 5♀♀ NMB); Dalaba, 1200m (10°41'N, 12°15'W), 23.vi.1951, Bechyne (1♂ 1♀ NMB); Dalaba, 1200m (10°41'N, 12°15'W), 26.vi.1951, Bechyne (1♀ NMB); Dalaba, 1200m (10°41'N, 12°15'W), 27.vi.1951, Bechyne (1♀ NMB); Ditinn (10°53'N, 12°11'E), 21.x.1945, P. Clement (1♂ SANC); Ditinn (10°53'N, 12°11'E), 28.x.1945, P. Clement (1♀ SANC); **GUINEA-BISSAU**: **BAFATA**: Chime [=Xime] (11°58'N, 14°56'W), 1906, G. Favarel (1♂ MNHN); **BOLAMA**: Bolama (11°35'N, 15°29'W), vi-xii.1899, L. Fea (45♂♂ 29♀♀ MCG; 4♂♂ 5♀♀ IRSNB); **IVORY COAST**: **DENGUÉLÉ**: Niamasso, 475m (9°29'N, 7°41'W), 9-10.vii.2013, P. Moretto (3♂♂ PMOC); **SAVANES**: M'banto, 395m (9°34'N, 6°41'W), 6-8.vii.2013, P. Moretto (1♂ 3♀♀ PMOC); M'banto, 395m (9°34'N, 6°41'W), 13-15.vii.2013, P. Moretto (2♀♀ PMOC); **NIGERIA**: **FEDERAL CAPITAL TERRITORY**: Abuja (9°04'N, 7°27'E), 1.viii.2006 (1♀ JFJC); 20km N Abuja (9°16'N, 7°23'E), 1.viii.2006 (2♂♂ JFJC); **KADUNA**: 6km N Kaduna (10°34'N, 7°26'E), 20.vii.1974, G.F. Bornemissza (1♂ 1♀ SANC); 15km W Kafanchan, 180m (9°05'N, 8°37'E), 19.vii.2006, Leonard & Vingerhoedt (1♂ 1♀ PMOC); Samaru (11°10'N, 7°38'E), 7.ix.1969, P.H. Ward (1♀ BMNH); Samaru (11°10'N, 7°38'E), 15-18.ix.1970, P.H. Ward (1♀ BMNH); Samaru cattle market (11°10'N, 7°38'E), 20.vii.1974, G.F. Bornemissza (3♂♂ 6♀♀ SANC); **KANO**: Lama-Bura [=Lame-Burra] Game Reserve, 630m (11°05'N, 8°37'E), 21-25.vii.2006, Leonard & Vingerhoedt (1♂ 1♀ PMOC); **NIGER**: 75km S Kontagora (9°44'N, 5°28'E), 19.vii.1974, G.F. Bornemissza (1♂ SANC); Zungeru (9°49'N, 6°09'E), Dr. W.B. Johnson (1♂ 1♀ BMNH); **PLATEAU**: Jos (9°56'N, 8°53'E), 24.vi.1977, M.J. Roberts (1♂ BMNH); 16km S Jos (9°46'N, 8°53'E), 28.vii.1974, G.F. Bornemissza (1♂ SANC); Mangu, 1200m (9°23'N, 9°09'E), 1.vi.1976, C. Smeenk (1♂ 2♀♀ RMNH); **SENEGAL**: **SÉDHIQU**: Sédhiou (12°42'N, 15°34'W), 1891, E. Laglaize (3♂♂ 1♀ MNHN); **ZIGUINCHOR**: Ziguinchor (12°35'N, 16°16'W), x.1966, P.J.J.H. Kuijten (4♀♀ RMNH); Ziguinchor (12°35'N, 16°16'W), 8.x.1966, P.J.J.H. Kuijten (3♂♂ RMNH); **TOGO**: [no precise locality] (2♂♂ ZMHB; 1♀ NMB; 1♀ RMNH; 2♀♀ IRSNB); **UGANDA**: [no precise locality], Dr. Sells (1♂ BMNH); **CENTRAL**: Nakajongola [=Nakasongola] (1°19'N, 32°28'E), iv.2013, local collector (5♂♂ 2♀♀ PMOC); **EASTERN**: Serere (1°30'N, 33°34'E), J. Ford (2♂♂ BMNH); **NORTHERN**: Chobe Lodge (2°15'N, 32°08'E), 13.i.1966, A.W.R. McCrae (1♂ OUMNH); Murchison Falls National Park, Paraa (2°17'N, 31°34'E), 27.vii.1971, N. Sanfilippo (1♀ MCG); Ochodri [=Ocodri] (3°04'N, 31°05'E), 1927, G. Babault (4♂♂ 10♀♀ MNHN); **WESTERN**: Murchison Falls National Park, Chobe (2°14'N, 32°08'E), 27.vii.1971, N. Sanfilippo (1♀ MCG).

**Diagnosis**: see under *C. telemachus* sp. nov. and *C. achates*. This species is most similar in appearance to *C. telemachus* sp. nov. but can be distinguished by the completely granulose anterior declivity. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance. This species is found together with *C. achates* in the western part of its range but can be separated by the shape of the central portion of the carina which is bowed on each side of the midline and the greater extent of the smooth regions on the pronotal disc. In the female, the pronotal carina is much wider in *C. achates*.

**Biology**: this species is found in the Sudanian savanna belt from Senegal to Uganda. This species has been found in cattle dung in Senegal and has been caught in human dung baited pitfall traps as well as at light in the Ivory Coast. Specimens have been caught between April and January.

**Derivation nominis**: This species is named after Thersander, King of Thebes and son of Polynices in Greek Mythology. In reference to the confusion between this species and *C. polynices*.

**Distribution** (Pl. 17: fig. 8): Senegal, Gambia (?), Guinea-Bissau, Guinea, Mali (?), Ivory Coast, Burkina Faso (?), Ghana (?), Togo, Benin, Nigeria, Cameroon (?), Central African Republic, D.R. Congo, South Sudan (?), Uganda.

## 18. *Catharsius bradshawi* Lansberge, 1887

(Pl. 18: figs. 1-8; Pl. 30: fig. 18)

*Catharsius bradshawi* Lansberge, 1887: 107; Péringuey, 1901: 327; Ferreira, 1960a: 12; Ferreira, 1967: 230;

*Catharsius insignis* Péringuey, 1892: 27; Felsche, 1901: 154;

**Type localities:**

*Catharsius bradshawi* Lansberge, 1887: “Zambesi”

*Catharsius insignis* Péringuey, 1892: “Northern Ovampoland”

**Name-bearing types:**

*Catharsius bradshawi* Lansberge, 1887: 11 syntypes (6♂♂ 5♀♀) in RMNH, 2 syntypes (2♂♂) in BMNH, 2 syntypes (1♂ 1♀) in MNHN and 1♀ syntype in NMB. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series in the RMNH is here **designated as the lectotype**:

“// N.A.M. / Zambesi [circle; handwritten] // Bradshaw / Zambesi / 1878. // Catharsius / Bradshawi / Lansbge [handwritten] // Bradshawi / n.sp. Lansb. [brown paper with black border; handwritten] // LECTOTYPE / CATHARSIUS / bradshawi / Lansberge / det. H Takano 2017 [white card with red border; partially handwritten] //”

*Catharsius insignis* Péringuey, 1892: 5 syntypes (4♂♂ 1♀) in SAMC, 4 syntypes (2♂♂ 2♀♀) in SANC and 1♂ syntype in TMSA from three localities (Evari River, Omrora and Okovango River). In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series is here **designated as the lectotype**:

“//Evari R. / “Nov. 97.” / Eriksson [handwritten] // SAM-COL- / A032814 [partially handwritten] // LECTOTYPE / CATHARSIUS / insignis / Péringuey / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black, pubescence reddish-brown. **Male** (Pl. 18: figs. 1, 2, 5): **Head:** anterior clypeal edge broadly arcuate, with a very slight arcuate extension centrally; clypeal margin continuous; clypeal surface transversely regulate. Genal edge rounded and obtusely angled, surface covered evenly with granules laterally becoming more rugulate towards the cephalic horn; suture well defined to base of clypeal carina. A laterally flattened, gently tapering, parallel-sided and apically arcuate cephalic horn positioned anteriorly on clypeus; horn slanted forward in lateral view; cephalic horn carinate laterally as continuation of clypeal carina. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin weakly emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate with an obtuse angle one third of the way along. Pronotal disc with a wide angular transverse carina anteriorly; carina interrupted centrally and rounded at its inner termination; carina bowed on each side of the midline, the lateral portions angled backwards with the carina forming a sharp projection at the angle; the carina extends far beyond the widest point of the lateral margin in dorsal view and forms just above the fovea in lateral view; anterior surface of pronotal disc with a weakly punctate ovaline smooth region on each side of the midline tapering towards the edge, terminating laterally before the carinal projection and extending longitudinally just over half the distance from the carina to the posterior pronotal margin at

its longest. The posterior and lateral surface covered evenly in circular granules, with alutaceous microsculpture in between; lateral declivity with fovea, the surface granulose with the exception of a very small area surrounding the fovea which is smooth; anterior declivity completely granulose with alutaceous microsculpture throughout. **Elytra**: carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae well-defined with inconsistent and weak punctures. Interstriae with fine punctures and some alutaceous microsculpture centrally; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs**: protibia tridentate; mesa- and metatibia with an undulating apical margin. The first mesa- and metatarsomeres very broad apically, gently arcuate laterally; tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 18: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 18).

**Female** (Pl. 18: figs. 1, 2, 5): **Head**: anterior clypeal edge evenly arcuate with continuous clypeal margin; clypeal surface transversely rugulate; genal edge rounded and acutely angled, surface covered with ovaline granules disappearing towards the eyes; clypeogenal suture to base of clypeal carina; clypeal carina raised and broad, the central point flattened and only slightly higher than the lateral edge of the clypeus. **Pronotum**: anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin weakly emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with a short indistinct transverse carina anteriorly shorter than the distance between the eyes; anterior surface of pronotal disc with a large, broadly ovaline smooth region on each side of the midline tapering towards the edge, each covering at least half of the distance between the midline and the lateral margin. The posterior and lateral surface covered evenly in circular granules, with alutaceous microsculpture in between; lateral declivity with fovea, the surface granulose; anterior declivity completely granulose with some alutaceous microsculpture. **Elytra**: carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae well-defined with inconsistent and weak punctures. Interstriae with fine punctures; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs**: protibia tridentate; mesa- and metatibia with an undulating apical margin. The first three mesa- and metatarsomeres very broad apically, gently arcuate laterally and wider than they are long; tarsomeres with reddish-brown pubescence.

**Length**: male 25-31mm; female 25-30mm.

**Variation**: in smaller males, the cephalic horn is reduced to a short sharp point on the clypeal carina; the pronotal carina extends beyond the lateral margin in even the smaller male specimens.

**Other material examined** (17♂♂ 12♀♀):

**ANGOLA:** [no precise locality], Gleim (1♂ ZMHB); **BOTSWANA:** Zambesi (1♂ ZMHB; 2♂♂ 1♀ MTD; 1♂ 1♀ IRSNB); Zambesi (2♂♂ 2♀♀ MNHN); **ZAMBIA:** WESTERN: piste de Ndanda (15°07'S, 23°41'E), 10.xii.2008, J.-F. Josso & R. Minetti (1♂ 1♀ PMOC); Ndanda, 1090m (15°05'S, 23°46'E), 10-11.xi.2013, R. Smith, H. Takano & D. Oram (4♂♂ 5♀♀ BMNH); Sefula (15°26'S, 23°15'E), 10-11.xii.2008, J.-F. Josso & R. Minetti (1♂ PMOC); **ZIMBABWE:** MATABELELAND NORTH: 7mi W Victoria Falls National Park (17°58'S, 25°45'E), 11.ii.1972, Bornemissza & Kirk (1♀ SANC); Victoria Falls National Park, Chamabondo (17°56'S, 25°49'E), 24.xi.1972, A.L.V. Davis (4♂♂ 1♀ SANC).

**Notes:** Benjamin Frederick Bradshaw (d. 1883) was a physician and amateur naturalist who gained employment in Africa under the British ivory trader George Cobb Westbeeche. Bradshaw was stationed for six years from 1872 at Westbeeche's main trading station at Pandamatenga (18°33'S, 25°39'E) and returned to England in 1879 (Jamieson, 1959). It is possible that the type locality of *C. bradshawi* is in the vicinity of Pandamatenga or somewhere on the route to Sesheke on the Zambezi River. It is unlikely to be in Mozambique as stated by Ferreira (1967). Westbeeche had opened up a trade route from South Africa to the Zambezi River and further north into Barotseland (an area in modern day western Zambia). This had been the ambition of explorer David Livingstone who, in the early 1860's, had taken a different route from the mouth of the Zambezi at Chinde in Mozambique to access the mid-Zambezi valley and Victoria Falls. The expedition failed due to the steamers being unable to navigate past the rapids at Cahora Bassa. The lower-Zambezi in Mozambique had been explored more thoroughly with a number of mission stations having been set up along its course at Caia and Tete. The specimens from this area collected in the period 1850 to 1900 often have labels with the names of the mission stations or with "Mozamb., Nyassa", rather than Zambezi.

The type specimens of *C. insignis* were all collected by Axel Eriksson during his expedition to Ovampoland and Damaraland. The type series is from three different localities of Evari River, Omrora and Okovango. Although there is no published map of Eriksson's route, some information is provided about the expedition in the introduction to Roland Trimen's publication (1891) on the butterflies collected by Eriksson. Evari River [=Evale] (16°33'S, 15°45'E) is located in the Cunene Province of Angola. Omrora is stated as being between Ovaquenyama and Ombuela which cross-referenced against a map in Andersson (1872) gives a rough locality of 17°00'S, 16°00'E in the Cunene Province of Angola. This is contrary to the belief of Mendes et al (2013) that Omrora is in Damaraland, Namibia. The locality of Okovango River is likely to be near the confluence of the Omatako tributary (17°51'S, 19°15'E), in the Kavango West Region of Namibia.

**Diagnosis:** An unmistakable species, the male having a very wide, angled pronotal carina extending far beyond the widest point of the lateral margin. The first three meso- and metatarsomeres are very broad apically in both sexes.

**Biology:** This species is rare in collections and appears to be restricted to the Zambezian Baikiea woodlands and flooded grasslands on Kalahari sands. Contrary to the belief of Ferreira (1967) and Davis (2013), this species is unlikely to be found in Mozambique and is not solely an elephant dung

specialist with the author having caught a number of individuals in human dung baited pitfall traps. Specimens have been caught between November and January.

**Distribution** (Pl. 18: fig. 8): Angola, Namibia, Botswana, Zambia, Zimbabwe.

### 19. *Catharsius achates* (Olivier, 1789)

(Pl. 19: figs. 1-8; Pl. 30: fig. 19)

*Scarabaeus achates* Olivier, 1789: 133.

*Copris achates* (Olivier, 1789): Schönherr, 1806: 34; Castelnau, 1840: 77.

*Catharsius achates* (Olivier, 1789): Gemminger & Harold, 1869: 1012; Ferreira, 1960a: 8.

**Type locality:** “Sénégal”

**Name-bearing type:** 1♂ syntype in MNHN. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, this specimen is here **designated as the lectotype**:

“// COLLECTION / OLIVIER / TYPE [green disc with black border] // *Catharsius / achates* Oliv. [orange paper; handwritten] // LECTOTYPE / SCARABAEUS / *achates* / Olivier / det. H Takano 2018 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black, pubescence reddish-brown. **Male** (Pl. 19: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and very slightly concave centrally; clypeal margin continuous; clypeal surface granulose with some transverse rugulae centrally; Genal edge rounded and obtusely angled, surface covered evenly with ovaline granules becoming finer towards the eyes; suture well defined to base of cephalic horn, the suture raised into a sharp projection at its inner-most end; central portion of the clypeus between the two points raised forming the posterior base to the cephalic horn; cephalic horn stout and straight, wide on basal third with edges converging evenly; horn perpendicular to clypeus in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with an angular transverse carina anteriorly that is weakly emarginate centrally; carina straight with a slight bow for three quarters of its length from the midline, the final quarter angled sharply backwards and bowed; the carina on each side terminates in dorsal view with a sharp projection; the carina is very as wide as the widest point of the lateral margin in dorsal view and forms just above the fovea in lateral view; anterior surface of pronotal disc with an posteriorly rounded smooth region on each side of the midline, extending laterally for half the length of the carina and just under half the distance from the carina to the posterior pronotal margin. The posterior and lateral surface covered evenly in circular granules; lateral declivity with fovea, the surface granulose with the exception of a small area surrounding the fovea; anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral

striae deep with inconsistent and weak punctures. Interstriae with uneven punctures and some alutaceous microsculpture; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs**: protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 19: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 19).

**Female** (Pl. 19: figs. 3, 4, 6): **Head**: anterior clypeal edge evenly arcuate with continuous clypeal margin; clypeal surface transversely rugulate posterior portion behind clypeal carina granulose; genal edge rounded and acutely angled, surface covered with ovaline granules; clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central tubercle being positioned very slightly to the posterior of and higher than the tubercles on either side. **Pronotum**: anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin gently emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with transverse carina anteriorly; carina gently arcuate and slightly angled medially, with the width almost as wide as the width of the head. Surface of pronotal disc covered in circular granules, except for a very small circular region on each side of the midline where the granules are poorly-defined; lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra**: carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae deep with weak punctures. Interstriae smooth with well-spaced fine punctures with some indistinct alutaceous microsculpture centrally; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence. **Legs**: protibia tridentate; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length**: male 19-29mm; female 19-26mm.

**Variation**: in smaller males, the cephalic horn is positioned further to the posterior, often reduced to a short point on the clypeal carina. In smaller females, the tridentate clypeal carina is reduced.

**Other material examined** (149♂♂ 123♀♀):

**BENIN**: **BORGOU**: Borgou (9°32'N, 2°47'E), viii-x.1984, I. van Woersem (2♂♂ 3♀♀ RMNH); **ALIBORI**: Mammasi Gourma (12°03'N, 3°08'E), 29.ix.2015, B. Rainon (1♂ 1♀ MDCL); **BURKINA FASO**: **CENTRE-EST**: Koupela (12°11'N, 0°21'W), 1922, Regnier (1♀ MNHN); **CENTRE**: Ouagadougou (12°22'N, 1°31'W), x.1970, P.C. Fernandez (4♂♂ 8♀♀ MRAC); Ouagadougou (12°22'N, 1°31'W), i.1971, P.C. Fernandez (2♀♀ MRAC); Ouagadougou (12°22'N, 1°31'W), 1976, M. Delpont (5♂♂ 1♀ MHNH); Ouagadougou (12°22'N, 1°31'W), 1977, J. Remy (1♂ 1♀ PMOC); **CENTRE-SUD**: Pô, (11°09'N, 1°09'W), vii.2005, P. Moretto (1♂ 1♀ OUMNH); **HAUTS-BASSINS**: 20km W of Bobo-Dioulasso (11°11'N, 4°29'W), 23.vii.2009, M.A. Hielkema (2♂♂ 1♀ MHPC); **CAMEROON**: **FAR NORTH**: Waza National Park (11°20'N, 14°40'E), 18.vii.2006, C. Vanderbergh (1♂ PMOC); **CHAD**: [no precise locality] autumn, 1969 (1♂ RMNH); **CHARI-**

**BAGUIRMI:** 30km S N'Djamena (11°52'N, 15°11'E), 2.viii.2006, C. Vanderbergh (1♀ PMOC); **LAC:** Ngouri (13°38'N, 15°22'E), viii.1958, P. Renaud (1♂ 1♀ MRAC); Ngouri (13°38'N, 15°22'E), x-xi.1958, P. Renaud (2♂♂ 18♀♀ MRAC; 1♂ 1♀ NMPC); **LOGONE OREINTAL:** Bebedija (8°40'N, 16°34'E), 28.vii.1964, L. Brader (2♂♂ 2♀♀ RMNH); Bebedija (8°40'N, 16°34'E), 21.i.1978, G. Ruella (1♂ 3♀♀ MRAC); Komé (8°28'N, 16°42'E), 1904, J. Decorse (1♂ MNHN); **MOYEN-CHARI:** Est de Fort Archambault [=Sarh] (9°09'N, 18°23'E), vi.1904, Dr. J. Decorse (1♂ MNHN); **N'DJAMENA:** Fort Lamy [=N'Djamena] (12°07'N, 15°03'E) (2♂♂ 1♀ NMB); Fort Lamy [=N'Djamena] (12°07'N, 15°03'E), M. André (1♂ MHNL); **OUADDAI:** Abeche (13°50'N, 20°50'E), vii.1971, M. André (1♂ PMOC); **D.R. CONGO:** **BAS-UELE:** Region de Sassa (5°05'N, 25°30'E), 1895-96, Colmant (1♂ 1♀ MRAC); **GAMBIA:** [no precise locality] (1♀ MNHN); [no precise locality] (1♂ 1♀ OUMNH); **BANJUL:** umgebung Fajara (13°28'N, 16°41'E), 2-10.viii.1989, T. & H.J. Bremer (1♂ ZSM); **CENTRAL RIVER:** Ballanghar (13°40'N, 15°24'W), 23.viii.1997, D.J. Mann (1♂ 3♀♀ OUMNH); McCarthy Island (13°32'N, 14°46'W), G. Svensson (1♂ 1♀ NHRS); **WEST COAST:** Tanji (13°21'N, 16°47'W), 22.xi.2002, Roggeman (1♂ 1♀ IRSNB); Tanji (13°21'N, 16°47'W), 3.xii.2002, M.A. Hielkema (5♂♂ 1♀ MHPC); Yundum Agricultural Station (13°20'N, 16°40'W), 18.viii.1997, D.J. Mann (1♂ OUMNH); **GUINEA-BISSAU:** [no precise locality] (1♂ 1♀ RMNH); [no precise locality] 1904, Lucas (1♂ 1♀ MTD; 14♂♂ 8♀♀ IRSNB); **CACHEU:** Bambora [=Barraca Bambore] (12°27'N, 16°13'W), 1904, Lucas (1♀ RMNH); Calikis [=Calequisse] (12°04'N, 16°13'W), 1904, Lucas (1♂ 1♀ IRSNB); **MALI:** **KAYES:** Kayes (14°26'N, 11°27'W) (1♂ 1♀ ZSM); Kita (13°02'N, 9°29'W) (2♂♂ MNHN); **SÉGOU:** Segou (13°26'N, 6°15'W), viii.2008, E. Bonnard (2♂♂ 2♀♀ PMOC); **SIKASSO:** Sikasso (11°19'N, 5°41'W) (1♂ 1♀ NMPC); **NIGER:** [no precise locality], vii.1980, P. Leblanc (3♂♂ 1♀ MHNL); **MARADI:** Maradi (13°30'N, 7°06'E), 22.vii.1965 (1♀ ZSM); Maradi environs (13°30'N, 7°06'E), viii.1981 (2♂♂ NMPC); **NIAMEY:** Niamey (13°32'N, 2°07'E), 7.viii.1980, P. Leblanc (2♀♀ MHNL); **ZINDER:** Dungass [=Dengas] (13°04'N, 9°21'E), Mission Tilho (1♂ MNHN); **NIGERIA:** **BAUCHI:** Yankari Game Reserve (9°51'N, 10°18'E), 23-25.vii.1974, G.F. Bornemissza (3♀♀ SANC); **BORNO:** Maiduguri (11°50'N, 13°07'E), 1948-1949, Mrs Newman (1♂ BMNH); **JIGAWA:** Birnin Kudu (11°27'N, 9°29'E), 23.vii.1974, G.F. Bornemissza (2♂♂ SANC); **KATSINA:** Katsina (12°59'N, 7°36'E), 16.vii.1965, L. Segers (2♂♂ 3♀♀ ZSM); **NIGER:** Mokwa (9°18'N, 5°03'E), 15.ii.1969 (1♂ BMNH); **SOKOTO:** Boka (12°35'N, 5°19'E) (1♀ ZSM); **SENEGAL:** Casamance, vii.1985 (1♂ 1♀ RMNH); [no precise locality] (1♂ 1♀ RMNH); [no precise locality] (1♂ SAMC); [no precise locality] 1849, Boccande (1♂ MNHN); [no precise locality] (15♂♂ 7♀♀ MNHN); [no precise locality] (8♂♂ 3♀♀ IRSNB); [no precise locality] (1♂ 2♀♀ ZSM); [no precise data], 1880, J.W. Miers (1♂ OUMNH); [no precise locality] (1♂ OUMNH); [no precise locality] (2♂♂ 1♀ NHRS); [no precise locality] (6♂♂ MTD); [no precise locality] M. Kirsch (1♂ 1♀ MTD); [no precise locality] (6♂♂ 5♀♀ BMNH); **DAKAR:** Cap-Vert (14°44'N, 17°27'W) (1♂ 2♀♀ MNHN); Dakar (14°46'N, 17°22'W) (1♂ MNHN); Dakar (14°46'N, 17°22'W) (1♂ 1♀ NMPC; 1♂ NMB); Dakar (14°46'N, 17°22'W), M. André (1♂ MHNL); Rufisque (14°43'N, 17°16'W) (2♀♀ SAMC); Rufisque (14°43'N, 17°16'W), G. Favarel (2♂♂ ZMHB); **DIOURBEL:** Bambey (14°42'N, 16°27'W), viii.1939, J. Risbec (5♂♂ 5♀♀ BMNH); Bambey (14°42'N, 16°27'W), ix.1939, J. Risbec (1♀ BMNH); Bambey (14°42'N, 16°27'W), 1949, J. Risbec (1♂ BMNH); M'Bambey [=Bambey] (14°42'N, 16°27'W), 12.viii.1939, J. Risbec (2♂♂ 1♀ MRAC); **FATICK:** Diouroup, 2m (14°22'N, 16°32'W), 14-18.viii.2007, P. Moretto (2♂♂ 2♀♀ PMOC); **KAOLAK:** Kaolak (14°10'N, 16°04'W) (4♂♂ 4♀♀ IRSNB); Niore du Rip (13°45'N, 15°46'W), vii.2009, P. Moretto (8♂♂ 5♀♀ BMNH); **SAINT-LOUIS:** Saint-Louis (16°02'N, 16°29'W) (2♂♂ MTD); Saint-Louis (16°02'N, 16°29'W), 1896, Delestre (1♂ MNHN); Saint-Louis (16°02'N, 16°29'W), xii.1896 (1♂ MNHN); Saint-Louis (16°02'N, 16°29'W), 1899, V. Planchat (15♂♂ 14♀♀ MNHN); **SÉDHIQU:** Sédhiou (12°42'N, 15°34'W), 13.vii.1947 (1♂ MNHN); **TAMBACOUNDA:** Parc National Niokolo-Koba, Dienoundialla (13°13'N, 13°07'W), viii.1995, local collector (3♂♂ 3♀♀ PMOC); Parc National Niokolo-Koba, Dienoundialla (13°13'N, 13°07'W), 29.vii.2015, P. Moretto (1♂ 1♀ PMOC); **THIÈS:** Mbour (14°25'N, 16°58'W), 3-10.ix.1991, J.L. Moreno & T. Mestre (4♂♂ 6♀♀ JLMC); **ZIGUINCHOR:** Boukitimgo, 18m (12°28'N, 16°34'W), 29-30.vii.2008, P. Moretto (2♂♂ PMOC).

**Diagnosis:** this medium-bodied species may be confused with *C. thersander* sp. nov., which has a similar distribution but can be identified by the shape of the cephalic horn and the pronotal carina as well as the sculpture of the pronotal disc. In *C. achates*, the cephalic horn is conical and placed just to the posterior of the clypeal carina whereas in *C. thersander* sp. nov. it is laterally flattened and positioned near the anterior margin of the clypeus. The central portion of the pronotal carina in *C. achates* is much straighter with only a small emargination medially, whereas the carina is bowed on either side of the midline with a distinct emargination medially in *C. thersander* sp. nov.. The extent of the smooth regions on the pronotal disc of *C. achates* is much less than in *C. thersander* sp. nov.. In females, the pronotal carina is wider, angled back and quite straight from the midline to termination point in *C. achates*, whereas it is shorter and bowed in *C. thersander* sp. nov..

**Biology:** this is a species of the West Sudanian savannas from Senegal to Chad. Specimens have been caught in pitfall traps baited with human and cattle dung and are often attracted to light. Specimens have been caught between July and January.

**Distribution** (Pl. 19: fig. 8): Senegal, Gambia, Guinea-Bissau, Mali, Burkina Faso, Benin, Niger, Nigeria, Cameroon, Chad.

## 20. *Catharsius polynices* Kolbe, 1893

(Pl. 20: figs. 1-8; Pl. 30: fig. 20)

*Catharsius polynices* Kolbe, 1893: 135.

*Catharsius oedipus* Felsche, 1907: 282; Ferreira, 1960a: 31. **syn. nov.**

*Catharsius simillimus* Ferreira, 1960a: 42; 1967: 255. **syn. nov.**

### Type localities:

*Catharsius polynices* Kolbe, 1893: “Nyassa-See” [=Lake Malawi]

*Catharsius oedipus* Felsche, 1907: “Zomba, Ob. Schire” [=Zomba (15°23’S, 35°19’E), upper Shire River, Malawi]

*Catharsius simillimus* Ferreira, 1960: “Norte do Lago Niasso” [=North of Lake Malawi]

### Name-bearing types:

*Catharsius polynices* Kolbe, 1893: 3 syntypes (2♂♂ 1♀) in ZMHB. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series is here **designated as the lectotype**:

“// Type [orange card] // Nyassa-S. / (Heyne) [green card] // 64841 // LECTOTYPE / CATHARSIUS / polynices / Kolbe / det. H Takano 2015 [white card with red border; partially handwritten] //”

*Catharsius oedipus* Felsche, 1907: 3 syntypes (2♂♂ 1♀) in MTD. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series is here **designated as the lectotype**:

“// Zomba, / Upp. Shire R. / 3000 ft. x-xii.95 / Dr.P.Rendall. // Oedipus / Felsche / Mossambik [cream paper with green border, handwritten] // Typus. [orange card] // Coll. C. Felsche / Kauf 20, 1918 [blue card] // Staatl. Museum für / Tierkunde Dresden // Senckenberg Natur- / hist. Sammlungen / Dresden, Museum / für Tierkunde (MTD) // LECTOTYPE / CATHARSIUS / oedipus / Felsche / det. H Takano 2015 [white card with red border; partially handwritten] //”

*Catharsius simillimus* Ferreira, 1960: Holotype ♂ in BMNH:

“// Holo- / type [white disc with red border] // N.L.Nyassa / B.C.A. / 96,51. [brown paper with blue horizontal line; handwritten] // HOLOTYPE ♂ / Catharsius simillimus / FERREIRA / M.C.Ferreira det., 1960 [partially handwritten] // NHMUK010367764 [QR code] //”

**Redescription:** Colour: Black, pubescence reddish-brown. **Male** (Pl. 20: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and very slightly concave centrally; clypeal margin continuous; clypeal surface granulate except for a very small region of transverse rugulae in the

region between the cephalic horn and anterior margin; posterior portion with fine granule. Genal edge rounded and obtusely angled, surface covered evenly with ovaline granules becoming finer towards the eyes; clypeogenal suture well defined to base of an incomplete clypeal carina. A laterally flattened, gently tapering, parallel-sided and apically arcuate cephalic horn positioned anteriorly on clypeus; horn slanted forward in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin sharply emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with an angular transverse carina anteriorly; the central portion straight and weakly emarginate centrally; the lateral portions angled backwards with the carina forming a sharp projection at the angle; the carina is very slightly wider than the widest point of the lateral margin in dorsal view and forms just above the fovea in lateral view; anterior surface of pronotal disc with an ovaline smooth region on each side of the midline, extending laterally as far as the projection and just over half the distance from the carina to the posterior pronotal margin. The posterior and lateral surface covered evenly in circular granules; lateral declivity with fovea, the surface granulose with the exception of a small area surrounding the fovea; anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae deep with inconsistent and weak punctures. Interstriae with fine punctures and some alutaceous microsculpture; epipleural carina well-developed, extending half of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 20: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 20).

**Female** (Pl. 20: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate with continuous clypeal margin; clypeal surface transversely rugulate posterior portion behind clypeal carina granulose; genal edge rounded and acutely angled, surface covered with ovaline granules; clypeogenal suture to base of clypeal carina; clypeal carina raised and tridentate, the central tubercle being positioned very slightly to the posterior of and higher than the tubercles on either side. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin gently emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with transverse carina anteriorly; carina gently arcuate and emarginate centrally, with the width greater than the distance between the eyes. Surface of pronotal disc covered in circular granules; lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae deep with weak punctures. Interstriae smooth with well-spaced fine punctures with some indistinct alutaceous microsculpture centrally; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:**

covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence. **Legs:** protibia tridentate; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 24-30mm; female 22-29mm.

**Variation:** in smaller males, the cephalic horn is reduced to a short point on the clypeal carina. In smaller females, the tridentate clypeal carina is reduced.

**Other material examined (30♂♂ 30♀♀):**

**D.R. CONGO:** TANGANYIKA: Moliro (8°13'S, 30°34'E), J. Duvivier (1♀ IRSNB) **MALAWI:** NORTHERN: Vwaza Game Reserve, Kazuni Camp (11°08'S, 33°39'E), i.1993, C. Dudley (1♀ MHNL); **MOZAMBIQUE:** mittel-Sambesi [mid-Zambezi River] (3♂♂ 3♀♀ ZMHB); mittel-Zambezi [mid-Zambezi River], W. Tiesler (1♂ 1♀ RMNH); Nyassa (1♂ MTD); Nyassa, F.A.A. Simons (*allotype* ♀ of *C. simillimus* Ferreira, 2♂♂ BMNH); Nyassa (4♂♂ 1♀ MNHN); CABO DELGADO: Taratibu (site 4), Parque Nacional das Quirimbas, 340m (12°48'S, 39°42'E), 10.i.2013, F. & S. Génier (1♂ FGIC); MANICA: Chimoio (19°08'S, 33°28'E), G.A.K. Marshall (1♀ BMNH); TETE: Chifumbasi (14°22'S, 32°56'E), xii.1904-i.1905, W. Tiesler (1♀ ZMHB); N Lake Nyassa, H. Crawford Angus (1♂ 1♀ BMNH); **TANZANIA:** MOROGORO: Mikumi (7°24'S, 36°59'E), iii.2002 (1♀ MDCL); MTWARA: Lukuledi (10°34'S, 38°48'E), 1903, Ertl (1♀ ZMHB); RUKWA: Katisunga (6°51'S, 31°06'E), 1949, Petre & Brédo (2♂♂ IRSNB); Lake Rukwa area (8°20'S, 32°15'E), 3700ft., iv.1938, D.G.M. MacInnes (1♂ NMK); RUVUMA: Kigonsera (10°48'S, 35°04'E), P.C. Hartl (1♂ ZSM); Kigonsera (10°48'S, 35°04'E), 1949, Hartl (5♂♂ 2♀♀ NMB); Kigonsera (10°48'S, 35°04'E), 1950, Hartl (1♂ NMB); Kigonsera (10°48'S, 35°04'E), i.1950, Hartl (1♀ NMB); Kigonsera (10°48'S, 35°04'E), 1952, Hartl (1♂ 1♀ NMB); Kigonsera (10°48'S, 35°04'E), 1954, Hartl (1♀ NMB); Neu-Helgoland [=Liuli] (11°06'S, 34°39'E), xii.1899, Fülleborne (1♂ ZMHB); Ruvuma (1♂ IRSNB); Wandonde-Gebiet am Ruvuma, P. Kammerer (1♂ ZMHB); **ZAMBIA:** CENTRAL: Chisanga (13°50'S, 27°50'E), v.1915, H.C. Dollman (1♂ 8♀♀ BMNH); Kafue National Park, Kacheleko Wildlife Outpost (15°01'S, 26°25'E), 12.xii.2012, Josso, Juhel & Minetti (1♂ JFJC); COPPERBELT: Kashitu (13°44'S, 28°39'E), xi.1914, H.C. Dollman (2♀♀ BMNH); Kashitu (13°44'S, 28°39'E), xii.1914, H.C. Dollman (1♂ 1♀ BMNH); Kashitu (13°44'S, 28°39'E), iii.1915, H.C. Dollman (1♀ BMNH); Kashitu (13°44'S, 28°39'E), 26.iii.1915, H.C. Dollman (2♂♂ 2♀♀ BMNH); Kashitu (13°44'S, 28°39'E), iv.1915, H.C. Dollman (2♀♀ BMNH); Mwendwa (13°00'S, 27°40'E), iv.1914, H.C. Dollman (1♀ BMNH); Mwendwa (13°00'S, 27°40'E), xii.1913, H.C. Dollman (1♂ BMNH); MUCHINGA: Upper Luangwa, xii.1904, R.L. Harger (1♂ BMNH); NORTHERN: Kambole (8°47'S, 30°46'E), x-1894-x.1895, W.H. Nutt (1♀ BMNH); **ZIMBABWE:** MANICALAND: Chirinda (20°25'S, 32°42'E), x.1905, G.A.K. Marshall (1♂ BMNH); Christmas Pass (18°57'S, 32°38'E), 1892, F.C. Selous (2♂♂ 1♀ SAMC; 1♂ TMSA; 1♀ SANC); Mpudzi River (19°23'S, 32°34'E), xii.1901, G.A.K. Marshall (1♂ BMNH); Umtali [=Mutare] (18°59'S, 32°39'E), xi.1895, G.A.K. Marshall (1♀ *paratype* of *C. simillimus* Ferreira, BMNH); MASHONALAND WEST: Gadzema (18°02'S, 30°09'E), xii.1895, G.A.K. Marshall (1♂ BMNH).

**Notes:** The type locality of *C. simillimus* Ferreira, collected by H. Crawford Angus is likely to be in the Tete Province of Mozambique rather than the north of Lake Nyassa. The specimens were accessioned in the BMNH register in 1896, a year after Crawford Angus had undertaken a twelve month journey exploring an area “as far as Angoniland in the north and in the south as far as Tete on the River Zambizi...” (Crawford Angus, 1898: 316). It appears the registrar who would have made the accession entry may have made an error with the provenance of the specimens.

**Diagnosis:** this species is similar in appearance to *C. telemachus* sp. nov. or *C. thersander* sp. nov. but can be distinguished by the obtusely angled lateroanterior margin of the pronotum in *C. polynices*. The central portion of the pronotal carina in *C. polynices* is much straighter with only a small emargination medially, whereas the carina is bowed on either side of the midline with a distinct emargination medially in the other two species. In females, the pronotal carina is gently arcuate in *C. polynices*, whereas it is bowed from the midline to the termination point in *C. thersander* sp. nov. and short in *C. telemachus* sp. nov..

**Biology:** a widely distributed but sporadically encountered species in Miombo woodland habitats of central and south-eastern Africa. One specimen collected by H.C. Dollman in Zambia was found in Zebra dung and the only recent specimens with collecting data show this species is attracted to light. Specimens have been caught between October and April.

**Distribution** (Pl. 20: fig. 8): Mozambique, Zimbabwe, Zambia, Malawi, Tanzania.

## 21. *Catharsius juheli* Josso, 2011

(Pl. 21: figs. 1-8; Pl. 30: fig. 21)

*Catharsius juheli* Josso, 2011: 3.

**Type locality:** “Zambie, 18km Ouest Kaoma”

**Name bearing type:** Holotype ♂ in JFJC:

“// ZAMBIE / 18km W KAOMA / 14°52'00.3”S / 24°38'29.4”E / 09-XII-2008 / JF Josso R Minetti leg // Exc. / HUMAINS // HOLOTYPE / *Catharsius* / *juheli* n.sp. / J-F Josso det 2010 [red card; partially handwritten] //”

**Redescription:** Colour: Black, pubescence reddish-brown. **Male** (Pl. 21: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and slightly concave centrally; clypeal margin continuous; clypeal surface transversely rugulate anteriorly becoming more granulose laterally and posteriorly; Genal edge rounded and acutely angled, surface covered with ovaline granules arranged circularly from a point along the lateroposterior edge, turning finer posteriorly. Clypeogenal suture well defined to base of an incomplete clypeal carina. Cephalic horn conical and apically sharp, wide on the basal third with edges converging evenly; horn placed anteriorly to the clypeal carina; horn almost perpendicular to clypeus in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin almost straight centrally. Lateroanterior margin almost at right angles, lateral margin arcuate. Pronotal disc with a broadly arcuate transverse carina anteriorly, weakly interrupted medially; carina with an obtuse angle just above its termination point in lateral view. Pronotal disc granulate, the granules ovaline anteriorly becoming circular posteriorly. Posterior portion of pronotal disc with some alutaceous microsculpture. Lateral declivity with fovea and surface fully granulose; anterior declivity granulose with alutaceous microsculpture throughout. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture; elytral striae well defined with evenly-spaced weak punctures. Interstriae rugose with some alutaceous microsculpture; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick coppery pubescence; metasternum with long well-developed sulcus; the first sternite heavily

punctured with some pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 21: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 21).

**Female** (Pl. 21: figs, 3, 4, 6): **Head:** anterior clypeal edge arcuate and the very central portion straight; clypeal margin continuous; clypeal surface transversely rugulate turning more granulose towards the clypeogenal suture. Genal edge rounded and acutely angled, surface covered with ovaline granules, disappearing posteriorly. Clypeogenal suture to base of clypeal carina; clypeal carina raised and weakly tridentate, the central point being positioned slightly to the posterior of and higher than the edges of the carina. **Pronotum:** anterior margin obliquely orientated anteriorly on each side of eyes. Margin very weakly emarginate centrally. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with a short, slightly arcuate transverse carina anteriorly, interrupted medially; carina length shorter than the distance between the eyes; Surface of pronotal disc covered in circular granules, except for a very small circular region on each side of the midline where the granules are poorly-defined; posterior portion of disc with some alutaceous microsculpture; Lateral declivity with fovea and surface fully granulose; anterior declivity granulose with alutaceous microsculpture throughout. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and some rugosity; elytral striae well defined with evenly-spaced weak punctures. Interstriae smooth, with some rugosity and alutaceous microsculpture, particularly on the third and fourth interstriae; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick coppery pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with some pubescence. **Legs:** protibia tridentate; mesa- and metatibia with an undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 19-24mm; female 20-23mm.

**Variation:** in smaller males, the cephalic horn is reduced to a short point on the clypeal carina and the pronotal carina is reduced to a gently arcuate carina.

**Other material examined** (21♂♂ 11♀♀):

**D.R. CONGO:** LUALABA: Tshipaza (8°34'S, 22°24'E), iv.1934, F.G. Overlaet (1♂ MRAC); **ZAMBIA:** NORTH-WESTERN: Chavuma Forest Reserve, 1080m (13°04'S, 92°56'E), 25-27.iv.2014, R. Smith, H. Takano, L. Chmurova & L. Smith (1♂ 1♀ BMNH); Hillwood, Ikelenge, 1400m (11°16'S, 24°19'E), 17-24.iii.2013, R. Smith & H. Takano (2♀♀ BMNH); Hillwood, Ikelenge, 1400m (11°16'S, 24°19'E), 21-28.x.2013, R. Smith, H. Takano, L. Chmurova & L. Smith (5♂♂ 2♀♀ BMNH); Lukwakwa, West Lunga National Park, 1147m (12°40'S, 24°26'E), 4-8.xi.2013, R. Smith, H. Takano & D. Oram (7♂♂ BMNH); WESTERN: 15km W Kaoma (14°52'S, 24°38'E), 10.xii.2008, J. Touroult (1♂ MDCL); 18km W Kaoma (14°52'S, 24°38'E), 9.xii.2008, J-F. Josso & R. Minetti (*allotype* ♀ JFJC; 3♂ 3♀ *paratypes* PMOC); 18km W Kaoma (14°52'S, 24°38'E), 14-15.xii.2009, Josso, Juhel & Minetti (2♂♂ *paratypes* IRSNB; 1♂ 1♀ *paratypes* MRAC; 1♂ 1♀ *paratypes* PMOC); Ndanda, 1090m (15°05'S, 23°46'E), 10-11.xi.2013, R. Smith, H. Takano & D. Oram (1♂ 1♀ BMNH); Ndanda, 1090m (15°05'S, 23°46'E), 21-23.iv.2011, R. Smith, H. Takano, L. Chmurova & L. Smith (1♀ BMNH); piste de Ndanda (15°05'S, 23°46'E), 13.xii.2008, J-F. Josso & R. Minetti (1♂ *paratype* PMOC).

**Diagnosis:** Superficially similar in appearance to *C. achates* but the shape of the pronotal carina is evenly arcuate in *C. juheli* but angled in *C. achates*. In females, the pronotal carina is much shorter in *C. juheli*. The distribution alone should separate specimens with provenance.

**Biology:** this recently described species is rare in collections and restricted to areas of *Cryptosepalum* dry evergreen forests on Kalahari sands in south-central Africa. It is regularly attracted to light and has been collected in human dung-baited pitfall traps. Specimens have been caught between November and July.

**Distribution** (Pl. 21: fig. 8): Zambia, Angola (?), D.R. Congo.

## 22. *Catharsius mirabilis* Felsche, 1901

(Pl. 22: figs. 1-8; Pl. 30: fig. 22)

*Catharsius mirabilis* Felsche, 1901: 147; Ferreira, 1960b: 203.

**Type locality:** “Africa Centr.”

**Name-bearing type:** 1♂ syntype in MTD. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, this specimen is here **designated as the lectotype:**

“// Mombasa [handwritten] // mirabilis / Felsche / Equator. Africa [cream paper with green border, handwritten] // Typus. [orange card] // Coll. C. Felsche / Kauf 20, 1918 [blue card] // Staatl. Museum für / Tierkunde Dresden // Senckenberg Natur- / hist. Sammlungen / Dresden, Museum / für Tierkunde (MTD) // LECTOTYPE / CATHARSIUS / mirabilis / Felsche / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black, pubescence brown. **Male** (Pl. 22: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and straight centrally; clypeal margin continuous; clypeal surface transversely rugulate centrally and only in the very anterior portion, turning into scale-like granules laterally; posterior portion behind cephalic horn smooth; genal edge rounded and acutely angled, the margin with a clear emargination at the clypeogenal suture. Suture well defined to base of cephalic horn; genal surface covered with scale-like granules anteriorly, disappearing towards the posterior. Cephalic horn long, conical and stout, bifid at apex; rising at the perpendicular to the clypeus in lateral view, before curving back on itself; in frontal view, wide on the basal third with edges converging evenly, the horn tapering in the middle third and swelling towards the bifidation at the apex. The length of the horn is higher than the highest point on the pronotum in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin strongly emarginate, the basal area of the emargination rounded; the lateral margin gently arcuate. Pronotal disc with two conical horns extending forwards, tapering to a sharp point at the apex, extending beyond the anterior margin of the pronotum in dorsal view; the distance

between the horns at the apex, no wider than the distance between the eyes; in lateral view, the apex of the horn is the highest point on the pronotum, sloping down to the posterior margin of the pronotal disc; anterior slope of the horns sloping backwards with a sharp projection about a third of the way down. Surface of pronotal disc covered evenly in circular granules; lateral declivity with an excavation underneath the horns with surface completely smooth. Anterior declivity with a transverse region of well-spaced punctures with the occasional, fine long brown hair. **Elytra**: quite straight, giving a triangular aspect to the body in rear view; carinate basally; basolateral portion distinctly bulbous; elytral striae well developed without punctures; the basal section being wide and evenly tapering towards the apex. First elytral interstriae punctured, the second to the fifth interstriae finely rugose, the other interstriae smooth with some puncture are alutaceous microsculpture. Epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventrites**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs**: protibia tridentate; mesa- and metatibia with undulating apical margin. Tarsomeres with reddish-brown pubescence; **Aedeagus** (Pl. 22: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 22).

**Female** (Pl. 22: figs. 3, 4, 6): **Head**: anterior clypeal edge unevenly arcuate, rounded laterally and almost straight laterally; clypeal margin continuous; clypeal surface transversely regulate anteriorly, turning into ovaline granules laterally; posterior portion behind cephalic horn smooth; genal edge rounded and acutely angled, the margin with a clear emargination at the clypeogenal suture. Suture well defined to base of cephalic horn; genal surface covered with scale-like granules anteriorly, disappearing towards the posterior. Cephalic horn long, flattened and tapers to a rounded point, sloping backwards in lateral view. In frontal view, wide on the basal third, the apicolateral angles produced into a fine denticle. Surface of horn completely granulose. **Pronotum**: anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin obtusely angled, lateral margin arcuate. Pronotal disc with an “M” shaped process centrally, flanked by short, slightly inward curving horns on either side. The central process with short denticles at each of the angles of the “M”. Surface of pronotal disc covered evenly in circular granules; lateral declivity with fovea and surface completely granulose. Anterior declivity granulose under the central process, with the occasional, fine long brown hair; in frontal view, the basal portion of the declivity completely smooth. **Elytra**: quite straight, giving a triangular aspect to the body in rear view; carinate basally; basolateral portion distinctly bulbous; elytral striae well developed with very weak punctures; the basal section being wide and evenly tapering towards the apex. First elytral interstriae punctured, the second to the fifth interstriae finely rugose, the other interstriae smooth with some puncture are alutaceous microsculpture. Epipleural carina well-developed, extending two-thirds of the length of the

elytra. **Legs:** protibia tridentate; mesa- and metatibia with undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 26-35mm; female 21-34mm.

**Variation:** in smaller males the pronotal horns have an extra lateral projection on the outer edge of the pronotal horns. In smaller females, the clypeal horn is reduced into a backward-sloping tridentate equilateral triangle; the anterior declivity of both minor males and females has a great deal more pubescence than the well-developed males.

**Other material examined (69♂♂ 76♀♀):**

**KENYA:** ISIOLO: Archers Post (0°38'N, 37°40'E), 1920, Toncker (1♂ NMB); KAJIADO: Amboseli National Park, Headquarters area, 1050m (2°44'S, 37°22'E), 5.v.1975, Davis & Dewhurst (1♀ SANC); KILIFI: Kilifi (3°30'S, 39°55'E), 1987, Rautenstrauch (1♀ PMOC); Malindi (3°13'S, 40°07'E), v.1976 (1♂ 1♀ ZMHB); Malindi (3°13'S, 40°07'E), 20.v.1976 (1♂ 2♀♀ RMNH); Malindi (3°13'S, 40°07'E), 23.v.1977 (1♂ RMNH); KWALE: Mackinnon Road (3°43'S, 39°02'E), vii.1973 (1♂ RMNH); Mbungu (4°05'S, 39°23'E), G. Hauser (1♂ 1♀ ZMHB); MARSABIT: Marsabit National Reserve, near Gof Bongole, 1010m (2°12'N, 37°56'E), 18.v.1975, Davis & Dewhurst (1♀ SANC); MERU: Meru National Park (0°13'N, 38°10'E), 29.xii.1977, J.L. Nicolas (1♂ 2♀♀ MHNL); Meru National Park (0°13'N, 38°10'E), 30.xii.1977, J.L. Nicolas (1♂ MHNL; 1♂ PMOC); Meru National Park, campsite near post 12 (0°10'N, 38°13'E), 1-3.xii.1975, C.F. Dewhurst (1♂ 1♀ SANC); Meru National Park, near Headquarters, 610m (0°10'N, 38°12'E), 30.xi.1975, C.F. Dewhurst (5♂♂ 2♀♀ SANC; 1♀ BMNH); Meru National Park, Headquarters/Leopard Rock, ca 650m (0°12'N, 38°12'E), 12.v.1975, Davis & Dewhurst (1♂ SANC); Meru National Park, Leopard Rock Swamp, ca 610m (0°12'N, 38°12'E), 2.xii.1975, C.F. Dewhurst (8♂♂ 9♀♀ SANC); Meru National Park, Mulika Lodge, 700m (0°13'N, 38°10'E), 9.iv.1981, J. Krikken (2♂♂ 1♀ RMNH); Meru National Park, Mulika Lodge, 650m (0°13'N, 38°10'E), 13.iv.1981, J. Krikken (2♀♀ RMNH); Meru National Park, Mulika Plains, 600m (0°10'N, 38°12'E), 19.xi.1975, C.F. Dewhurst (1♀ MNHN); Meru National Park, Mulika Plains, post 10-9, ca 600m (0°11'N, 38°13'E), 13.xi.1975, C.F. Dewhurst (1♂ 2♀♀ SANC); Meru National Park, Mulika Plains, 650m (0°10'N, 38°12'E), 25.xii.1978, J. Krikken (1♀ RMNH); Meru National Park, Rogewero Plains, post 48-30, ca 650m (0°12'N, 38°09'E), 1.xii.1975, C.F. Dewhurst (1♂ 1♀ SANC); Meru National Park, Tana River area, 300-450m (0°04'S, 38°23'E), 13.v.1975, Davis & Dewhurst (1♂ 1♀ SANC; 1♀ BMNH); Meru National Park, 6km NW Ura Gate, 650m (0°04'N, 38°02'E), 30.xi.1975, C.F. Dewhurst (5♂♂ 2♀♀ SANC; 1♂ BMNH); MOMBASA: Mombasa (4°03'S, 39°40'E), 14.vi.1916, Slaty (1♂ BMNH); Mtwapa (3°57'S, 39°45'E), 25.v.1987, B.L. Parker (2♀♀ NMK); SAMBURU: Samburu (0°37'N, 37°32'E), 6.iv.1988, P. Dauguet (1♀ PMOC); Samburu Game Reserve (0°37'N, 37°32'E), 16.xi.1975, C.F. Dewhurst (2♂♂ SANC); TAITA-TAVETA: Kilaguni Lodge (2°54'S, 38°04'E), 7.v.1976, J. Krikken (1♂ RMNH); Lion Hill near Voi, 500-600m (3°21'S, 38°25'E), 9.xii.1974, J. Krikken & A. van Berge Henegouwen (1♂ RMNH); Ngulia Lodge (3°01'S, 38°13'E), i.1977, D.J. Peason (1♂ 1♀ NMK); Sagala Hills (3°28'S, 38°35'E), 23.xi-4.xii.2000, I.Martinů (1♂ 1♀ PMOC); Taveta (3°24'S, 37°40'E), 19.xi.1973, Y. Jongema (1♀ RMNH); Tsavo National Park (2°45'S, 38°49'E), 26.xi.1973, T.J. Kingston (1♀ OUMNH); Tsavo National Park, Aruba Lodge, 450m (3°21'S, 38°47'E), 21.xii.1972, J. Krikken (1♀ RMNH); Tsavo National Park, near Aruba Lodge, 550m (3°21'S, 38°47'E), 28.xii.1972, J. Krikken (1♂ RMNH); Tsavo East National Park, Mzinga, 600m (3°21'S, 38°37'E), 19-31.xii.1972, J. Krikken & C. Smeenk (1♂ 1♀ RMNH); Tsavo East National Park, Ndara, 550m (3°42'S, 38°43'E), 31.xii.1972, J. Krikken (1♀ RMNH); Tsavo East National Park, 2.5km from Voi, 487m (3°23'S, 38°35'E), x.1972, M. Coe (1♀ OUMNH); Tsavo East National Park, 2.5km from Voi, 487m (3°23'S, 38°35'E), xi.1973, T.J. Kingston (2♂♂ OUMNH); Tsavo East National Park, Voi Safari Lodge, 600m (3°21'S, 38°35'E), 1-6.i.1973, J. Krikken (16♂♂ 10♀♀ RMNH); Voi (3°24'S, 38°33'E), 8.i.1972, C. Smeenk (1♀ RMNH); Voi (3°24'S, 38°33'E), xii.1980 (1♂ 1♀ RMNH); Voi (3°24'S, 38°33'E), 23.xi.1997, M. Snížek (1♂ NMPC); TANA RIVER: Galana Game Ranch, Lali Hills area, 250m (3°01'S, 39°16'E), 2-3.vi.1975, Davis & Dewhurst (7♂♂ 13♀♀ SANC; 1♂ MNHN); **SOMALIA:** LOWER SHEBELLE: Genale [=Janale] (1°48'N, 44°42'E), 6.vi-13.vii.1980 (1♀ BMNH); **TANZANIA:** ARUSHA: Serena Lodge (3°22'S, 35°50'E), iv.2002, D. Moore (1♀ PMOC); 10km E Sinya Mine (2°45'S, 37°07'E), 18.xii.2009, J.L. Moreno (1♀ JLMC); MOROGORO: Morogoro (6°50'S, 37°40'E) (1♀ ZMHB); Morogoro (6°50'S, 37°40'E), P. Ringler (3♀♀ IRSNB); MARA: Serengeti National Park, Seronera Lodge (2°27'S, 34°48'E), 8.xii.1969, L.B. Holthuis (1♀ RMNH).

**Diagnosis:** both sexes can easily be distinguished by the presence of well-developed clypeal and pronotal armature. The males possess a long clypeal horn and two forwarding pointing pronotal horns, whilst the females possess a backward-sloping clypeal horn with an “M-shaped” central pronotal process. The unique combination of the clypeal and pronotal armature of both sexes makes this one of the most extraordinary dung beetles in the world.

**Biology:** this species is found in open bushlands and deciduous savannas of East Africa and appears to be associated solely with elephant dung. It is also commonly attracted to light. Specimens have been caught between November and June. P. Moretto and M. Dierkens have communicated to the author reports of this species being found in northern Cameroon. Although it is a large range extension, the habitat is a similar dry, open savanna and it is just possible that there is an isolated population found there. The specimens of Cameroonian origin will need to be studied in order to conclude whether it is the same taxon as the true *C. mirabilis* of East Africa.

**Distribution** (Pl. 22: fig. 8): Tanzania, Kenya, Somalia, Cameroon (?).

### 23. *Catharsius princeps* Kolbe, 1893 **stat. res.**

(Pl. 23: figs. 1-8; Pl. 30: fig. 23)

*Catharsius princeps* Kolbe, 1893: 136; Felsche, 1901: 149.

*Catharsius pseudoedipus* Ferreira, 1960a: 35. **syn. nov.**

#### **Type localities:**

*Catharsius princeps* Kolbe, 1893: “Stanley Pool” [= Pool Malebo (4°17’S, 12°29’E), D.R. Congo]

*Catharsius pseudoedipus* Ferreira, 1960: “Tshuapa (Boende)” [(0°17’S, 20°53’E), D.R. Congo]

#### **Name-bearing Types:**

*Catharsius princeps* Kolbe, 1893: 4 syntypes (2♂♂ 2♀♀) in ZMHB. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series is here **designated as the lectotype**:

“// Type [orange card] // Stanley Pool / Tseuz [green card; handwritten] // 64840 // LECTOTYPE / CATHARSIUS / princeps / Kolbe / det. H Takano 2015 [white card with red border; partially handwritten] //”

*Catharsius pseudoedipus* Ferreira, 1960: Holotype ♂ in MRAC.

“// HOLOTYPUS [orange card with black border] // COLL. MUS. CONGO / Tshuapa : Boende / 1940/46 / R. P. Wynants // HOLOTIPO / Catharsius pseudoedipus / mihi / M.C. Ferreira det., 1960 [partially handwritten] //”

**Redescription:** Colour: Black, with a reddish undertone; pubescence reddish-brown. **Male** (Pl. 23: figs. 1, 2, 5): **Head:** anterior clypeal edge unevenly arcuate, rounded laterally and very slightly concave centrally; clypeal margin continuous; clypeal surface transversely rugulate anteriorly, turning more granulose towards the clypeogenal suture; central portion with fine granulations and posterior portion with transverse rugulae. Genal edge rounded and obtusely angled, surface covered evenly with longitudinal granules turning more ovaline posteriorly; the genal margin with an emargination at the clypeogenal suture. In dorsal view, the lateral sides of genae parallel-sided. Suture well defined to

base of an incomplete clypeal carina. A laterally flattened, gently tapering, rectangular and slightly apically bifidate cephalic horn positioned anteriorly on clypeus; horn slanted forward in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin sharply emarginate centrally. Lateroanterior margin obtusely angled, lateral margin very slightly arcuate. Pronotal disc with a continuous evenly arcuate, transverse carina anteriorly and depressed strongly on each side of the midline; carina forms just above the fovea in lateral view; surface of pronotal disc covered evenly in circular granules, becoming smaller and closer together anteriorly towards the midline; lateral declivity with fovea and surface completely granulose, central portion of anterior declivity completely granulose, with a short depression in the basal third the length of the emargination of the margin; in frontal view, a narrow smooth region extends from the fovea to the anterior margin of pronotum. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; basolateral portion very slightly bulbous; elytral striae deep with weak punctures. Interstriae smooth with the occasional fine puncture; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia with three external rounded projections; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 23: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 23).

**Female** (Pl. 23: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate with continuous clypeal margin; clypeal surface transversely rugulate posterior portion behind clypeal carina granulose; genal edge rounded and acutely angled, surface covered with longitudinal, granules turning more ovaline posteriorly; clypeogenal suture to base of clypeal carina; clypeal carina raised, with four well defined tubercles, the two central tubercles raised higher, being placed close together and posteriorly to the lateral tubercles. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin gently emarginate centrally. Lateroanterior margin weakly angled, lateral margin gently arcuate. Pronotal disc with a short indistinct transverse carina anteriorly; carina as wide as the distance between the eyes. Surface of pronotal disc covered in circular granules; lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; basolateral portion very slightly bulbous; elytral striae deep with weak punctures. Interstriae smooth with the occasional fine puncture; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence. **Legs:** protibia with three external rounded projections; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 29-36mm; female 29-35mm.

**Variation:** in smaller males, the cephalic horn is positioned further to the posterior, often reduced to a short point on the clypeal carina. In smaller females, the clypeal carina is reduced.

**Other material examined (67♂♂ 56♀♀):**

**CAMEROON:** [no precise locality] Sjoestedt (1♀ NHRS); [no precise locality] (4♂♂ 1♀ MTD); **LITTORAL:** Babimbi (4°14'N, 10°37'E) (1♂ MNHN); Ndom (4°23'N, 10°49'E), iv.1993, J.C. Thibaud (1♀ PMOC); **NORTHWEST:** Baliland [=Bali] (5°53'N, 10°00'E), Museum Lübeck (1♀ ZMHB); **SOUTH:** Akonangi (2°12'N, 11°21'E), iii-iv.1909, Tessmann (1♂ ZMHB); Lolodorf (3°14'N, 10°44'E), Jacob (1♀ ZMHB); **CENTRAL AFRICAN REPUBLIC:** Ubangi, Lameere (1♂ MNHN); **SANGHA-MBAËRÉ:** Parc National Ndoki, Lac 1, 392m (2°29'N, 19°13'E), 28.xi.2010 (1♀ PMOC); Sangha (3°30'N, 16°05'E), 1977, Heck (1♀ MRAC); **CONGO:** [no precise locality] (2♂ IRSNB); [no precise locality] 1893, Thollon (2♂♂ 2♀♀ MNHN); **CUVETTE:** Diele (1°41'S, 14°45'E), 1890, Dolisie & Uzac (1♂ MNHN); **CUVETTE-QUEST:** Diba (0°20'N, 14°47'E), ii.1991, Camiade (1♂ PMOC); **PLATEAUX:** Lefinie Reservation, Nambouli River (2°30'S, 15°29'E), 11.i.1964, S. Endrödy-Younga (1♂ 1♀ NMPC); **D.R. CONGO:** [no precise locality] (1♂ NMPC); Region des Lacs [=between Lake Edward and Lake Kivu], Dr. Sagona (1♀ MRAC); **BAS-UELE:** Bambesa (3°27'N, 25°41'E), 1937, J. Vrydagh (1♂ BMNH, 2♂♂ IRSNB); Bambesa (3°27'N, 25°41'E), 16.vi.1937, J. Vrydagh (1♂ 1♀ MRAC); Bambesa (3°27'N, 25°41'E), 8.x.1937, J. Vrydagh (1♂ 2♀♀ MRAC); Bambesa (3°27'N, 25°41'E), 28.x-3.xi.1937, J. Vrydagh (2♂♂ 4♀♀ IRSNB); Bambesa (3°27'N, 25°41'E), 2.xii.1937, J. Vrydagh (2♂♂ MRAC); Bambesa (3°27'N, 25°41'E), 6-16.v.1938, J. Vrydagh (2♂♂ 1♀ IRSNB); Bambesa (3°27'N, 25°41'E), 4.vi.1939, J. Vrydagh (1♀ IRSNB); Bambesa (3°27'N, 25°41'E), 19-23.vii.1938, J. Vrydagh (1♂ IRSNB); Bambesa (3°27'N, 25°41'E), 3.ix.1938, J. Vrydagh (4♂♂ 1♀ MRAC); Bambesa (3°27'N, 25°41'E), 3-5.x.1938, J. Vrydagh (1♂ 3♀♀ IRSNB); Bambesa (3°27'N, 25°41'E), 6.x.1938, J. Vrydagh (2♂♂ 2♀♀ MRAC); Bambesa (3°27'N, 25°41'E), 3.xi.1938, J. Vrydagh (1♂ 3♀♀ MRAC); Bambesa (3°27'N, 25°41'E), 4.vi.1939, J. Vrydagh (1♀ paratype of *C. pseudoedipus* Ferreira, NMB); Bambesa (3°27'N, 25°41'E), 16.xii.1939, J. Vrydagh (1♂ paratype of *C. pseudoedipus* Ferreira, NMB); Bambesa (3°27'N, 25°41'E), 15-16.i.1940, J. Vrydagh (allotype ♀ of *C. pseudoedipus* Ferreira, MRAC); Buta (2°48'N, 24°45'E) (1♀ NMPC); Ibembo (2°38'N, 23°37'E), ix.1949, Fr. Hutsebaut (1♀ MRAC); Ibembo (2°38'N, 23°37'E), ix.1951, Fr. Hutsebaut (1♂ BMNH); **ÉQUATEUR:** Busira (0°15'N, 18°59'E) (1♂ ZMHB); Eala (0°03'N, 18°19'E), ix-x.1930, Dr. P. Staner (1♂ MRAC); Flandria (0°21'S, 19°00'E), 1932, P. Hulstaert (1♂ MRAC); Flandria (0°21'N, 19°00'E), 25.xi.1947, P. Hulstaert (1♂ 1♀ MRAC); Lukolela (1°04'S, 17°11'E), ix.1923, Lt. J. Ghesquiere (1♂ MRAC); **HAUT-UELE:** Arebi (2°49'N, 29°34'E), 1922, D.J. Bussey (1♂ BMNH); Moto (2°54'N, 29°25'E), 1920, L. Burgeon (1♂ MRAC); Moto (2°54'N, 29°25'E), 1926, L. Burgeon (1♂ BMNH); Moto (2°54'N, 29°25'E), 26.vii.1926, L. Burgeon (1♂ MRAC); **ITURI:** Mawambi (1°04'N, 28°34'E), 1911, Grauer (1♀ IRSNB); **KASAI OCCIDENTAL:** Katoka (5°40'S, 22°24'E), 1939, Vankerckhoven (1♂ paratype of *C. pseudoedipus* Ferreira, TMSA); **LOMAMI:** 30km NE Gandajika (6°32'S, 24°09'E), 24.v.1959, J. Decelle (1♂ MRAC); Mwene-Ditu (7°01'N, 23°27'E), Doutrelepont (1♀ paratype of *C. pseudoedipus* Ferreira, 2♀♀ MRAC); **MAI-NDOMBE:** Bokoro (2°48'S, 18°14'E), 20.iii.1915, R. Mayne (1♀ MRAC); Galli - Koko (2°14'S, 19°10'E), R. Carlier (1♂ 1♀ MRAC); **MANIEMA:** Kasongo (4°26'S, 26°40'E), viii-ix.1959, L.G. Benoit (1♂ 1♀ MRAC); **MONGALA:** Bopoto (2°08'N, 21°30'E), F. Oram (2♂♂ MTD); Bopoto (2°08'N, 21°30'E), W. Forfeitt (2♂ MTD); **NORD-KIVU:** Beni (0°30'N, 29°27'E), Lt. Borgenhoff (1♀ MRAC); Beni (0°30'N, 29°27'E), i.1895, L. Cloetens (1♂ IRSNB); Beni (0°30'N, 29°27'E), ix-x.1910, Grauer (1♀ MRAC); Beni (0°30'N, 29°27'E), x.1910, Grauer (1♀ IRSNB); Beni (0°30'N, 29°27'E), x-xi.1931, L. Lelun (1♀ MRAC); **SUD-UBANGI:** Molanda (2°29'N, 20°48'E), xii-1951 (3♂♂ 1♀ MNHN); **TSHOPO:** Banalia (1°33'N, 25°19'E) (1♂ 1♀ MRAC); Barumbu (1°15'N, 23°29'E), viii.1925, Lt. J. Ghesquiere (1♀ MRAC); Kisangani (0°31'N, 25°11'E), xii.1973, M. Bokdam-Koek (1♂ RMNH); Stanleyville [=Kisangani] (0°31'N, 25°11'E), 18.xi.1954, P. Saussus (1♂ MRAC); Yangambi (0°48'N, 24°27'E), ii.1939, M. Brouwers (1♀ BMNH); Yangambi (0°48'N, 24°27'E), 1946, R. Mayne (1♀ MRAC); Yangambi (0°48'N, 24°27'E), 11.vi.1949, Raignier & Van Boven (1♀ MRAC); Yangambi (0°48'N, 24°27'E), xii.1959, J. Decelle (1♀ NMPC); Yangambi (0°48'N, 24°27'E), i.1974, M. Bokdam-Koek (1♂ RMNH); **TSHUAPA:** Bosekele (1°18'N, 22°32'E), vi.1952, J. van Vynckt (1♀ MRAC); Bosekele (1°18'N, 22°32'E), xii.1952, J. van Vynckt (1♀ MRAC); Etata (0°14'S, 20°42'E), iii-iv.1970, J. Hauwaerts (1♂ MRAC); Etata (0°14'S, 20°42'E), ix.1971, J. Hauwaerts (1♂ NMB); Ikela (1°03'S, 23°22'E), 1956, R. Deguide (1♂ MRAC); Ikela (1°03'S, 23°22'E), 1957, R. Deguide (2♂♂ NMPC); **GABON:** **NGOUNIE:** Koumba (1°48'S, 11°59'E), 1.v.1992, Pageix (1♀ PMOC); **OGOUE-IVINDO:** Makokou (0°34'N, 12°51'E), 21.xi.1973, Mission Balachowsky & Menier (1♂ MNHN); **OGOUE-MARITIME:** Bongo (2°10' S, 10°12'E), 22.vii.1974, Poulard (1♀ MHNL); near Ndougou (1°39'S, 9°40'E), 1-12.xii.1982, H.W. Hielkma (6♂♂ 4♀♀ RMNH).

**Diagnosis:** this is one of three superficially similar species, with a bifid clypeal horn and an arcuate pronotal carina in the males. *C. princeps* has an angled lateroanterior margin of the pronotum whilst *C. obtusicornis* and *C. genieri* have rounder lateroanterior margins. The females of the three species can also easily be distinguished. In *C. princeps*, the carina is indistinct and almost absent in

some specimens. In *C. obtusicornis*, the carina is short and straight, with a slight emargination centrally. In *C. genieri*, the carina is wide, bowed from the midpoint to the edge and slightly arcuate centrally. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance.

**Biology:** this large-bodied species is restricted to the lowland forests of Central Africa where elephants are found. Specimens are regularly attracted to light and in the Central African Republic one female specimen was collected at a light trap set in the canopy in Ndoki National Park. Specimens have been caught throughout the year.

**Distribution** (Pl. 23: fig. 8): Cameroon, Gabon, Equatorial Guinea (?), Congo, Central African Republic, Democratic Republic of the Congo.

## 24. *Catharsius obtusicornis* Boheman, 1857 **stat. res.**

(Pl. 24: figs. 1-8; Pl. 30: fig. 24)

*Copris platycera* Klug, 1855: 655; Peters, 1862: 240. **junior primary homonym**

*Catharsius platycerus* (Klug, 1855): Gemminger & Harold, 1869: 1013; Péringuey, 1901: 326; Moretto, 2014: 62.

*Catharsius obtusicornis* Boheman, 1857: 217.

### **Type localities:**

*Catharsius obtusicornis* **Boheman, 1857:** “Caffraria interior”

*Copris platycera* **Klug, 1855:** “Sena” [(17°27’S, 35°02’E), Mozambique]

### **Name-bearing types:**

*Catharsius obtusicornis* **Boheman, 1857:** 5 syntypes (4♂♂ 1♀) in NHRS. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, the largest male specimen from the series is here **designated as the lectotype:**

“// Caffra / ria. // J. Wahlb. // obtusicornis Bhm [handwritten] // Typus [red card with black border] // 265 / 60 [pink paper; partially handwritten] // 4939 / E92 + [light blue paper] // NHRS-JONI / 000000253 // LECTOTYPE / CATHARSIUS / obtusicornis / Boheman / det. H Takano 2015 [white card with red border; partially handwritten] //”

*Copris platycera* **Klug, 1855:** 1♂ syntype in ZMHB. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, this specimen is here **designated as the lectotype:**

“// Type [orange card] // 9347 // platycerus / Klug\* / Mozmb., Natal. [turquoise card with black border; handwritten] // bison / Kl. / Sinna Peters [turquoise card with black border; handwritten] // LECTOTYPE / COPRIS / platycera / Klug / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black, with a reddish undertone; pubescence reddish-brown. **Male** (Pl. 24: figs. 1, 2, 5): **Head:** anterior clypeal edge broadly arcuate, with a very slight concavity centrally; clypeal margin continuous; clypeal surface transversely rugulate anteriorly, turning more granulose towards the clypeogenal suture; central portion with fine granulations and posterior portion with transverse rugulae. Genal edge rounded and obtusely angled, surface covered evenly with longitudinal granules turning more ovaline posteriorly; the genal margin with a clear emargination at the clypeogenal suture. In dorsal view, the lateral sides of genae parallel-sided. Suture well defined to base of an incomplete clypeal carina. A laterally flattened, rectangular and slightly apically bifid cephalic horn position anteriorly on clypeus; horn slanted forward in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin sharply emarginate centrally. Lateroanterior margin rounded, lateral margin very slightly arcuate. Pronotal disc with a continuous evenly arcuate, transverse carina anteriorly and depressed strongly on each side of the midline; carina forms just above the fovea in lateral view; surface of pronotal disc covered evenly in circular granules, becoming smaller and closer together anteriorly towards the midline; lateral declivity with fovea and surface completely granulose, central portion of anterior declivity completely granulose, with a short depression in the basal third the length of the emargination of the margin; in frontal view, the lateral basal portion of the anterior declivity smooth, from the fovea to the anterior margin of the pronotum. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; basolateral portion very slightly bulbous; elytral striae deep with weak punctures. Interstriae smooth with well-spaced fine punctures; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 24: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 24).

**Female** (Pl. 24: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate with continuous clypeal margin; clypeal surface transversely rugulate posterior portion behind clypeal carina granulose; genal edge rounded and acutely angled, surface covered with longitudinal, granules turning more ovaline posteriorly; clypeogenal suture to base of clypeal carina; clypeal carina raised, with four well defined tubercles, the two central tubercles raised higher, being placed close together and posteriorly to the lateral tubercles. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin gently emarginate centrally. Lateroanterior margin rounded, lateral margin gently arcuate. Pronotal disc with transverse carina anteriorly; carina almost straight and with width no wider than the distance between the eyes. Surface of pronotal disc covered evenly in circular granules; lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and

slight rugosity; basolateral portion very slightly bulbous; elytral striae deep with weak punctures. Interstriae smooth with well-spaced fine punctures; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout. **Ventriles**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence. **Legs**: protibia tridentate; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence.

**Length**: male 18-32mm; female 19-30mm.

**Variation**: in smaller males, the cephalic horn is positioned further to the posterior, often reduced to a short triangular peak on the clypeal carina. In smaller females, the clypeal carina is reduced with the quadridentate carina becoming tridentate.

#### Other material examined (210♂♂ 159♀♀):

**D.R. CONGO**: **ITURI**: Lac Albert, Kasenyi (1°24'N, 30°26'E), vii.1934, J.V. Leroy (1♀ MRAC); Lac Albert, Kasenyi (1°24'N, 30°26'E), 15.v.1935, H.J. Brédo (1♂ 3♀ MRAC; 1♂ NMB); **KENYA**: **KAJIADO**: Amboseli (2°40'S, 37°17'E), R. Minetti (1♂ 1♀ PMOC); Amboseli Game Reserve, campsites near Ol Tukai, 1000m (2°41'S, 37°16'E), 4-5.xii.1974, J. Krikken & A. van Berge Henegouwen (1♀ RMNH); Mara area (1°24'S, 36°26'E), 31.vii.1977, C.F. Dewhurst (1♂ 1♀ NMK); **KILIFI**: Mbuyuni (3°24'S, 37°53'E), 1100m, iii.1912 (1♂ MNHN); **KITUI**: E of Mwingi, W of Nguni (1°31'S, 37°56'E), 1.xii.2010, Snížek (1♀ PMOC); **MAKUENI**: Emali Range, Sultan Hamud (2°01'S, 37°22'E), 4900-5900ft., iii.1940 (1♀ NMK); **MERU**: Meru National Park (0°13'N, 38°10'E), 29.xii.1977, J.L. Nicolas (1♀ MHNL); Meru National Park, Mulika Lodge, 650m (0°13'N, 38°10'E), 13.iv.1981 (1♀ RMNH); Meru National Park, 6km NW Ura Gate, 650m (0°04'N, 38°02'E), 30.xi.1975, C.F. Dewhurst (1♂ SANC); **NAROK**: Masai Mara Game Reserve, Keekorok, 1625m (1°35'S, 35°14'E), 26.iv.1975, Davis & Dewhurst (3♂♂ 2♀♀ SANC); **SAMBURU**: Samburu Lodge (00°34'N, 37°34'E), E.J. Fittkan (1♀ ZSM); **TAITA-TAVETA**: Bungule (3°51'S, 38°40'E), 1.xii.2005, E. Vingerhoedt (1♂ 1♀ PMOC); Bura (3°27'S, 38°19'E), i.1991, K. Werner (1♀ PMOC); Kilaguni Lodge (2°54'S, 38°04'E), 7.v.1976, J. Krikken (2♀♀ RMNH); Kilaguni, Tsavo West National Park (2°54'S, 38°04'E), F. Vieuxgué (11♂♂ 1♀ MHNL; 5♂♂ MDCL); Kilaguni Lodge (2°54'S, 38°04'E), Tsavo West National Park, xi.1974, Hüdepohl (1♀ ZSM); 260km E Nairobi-Mombassa Road (3°00'S, 38°28'E), 21.iv.1974 (1♀ SANC); Ngulia Lodge (3°01'S, 38°13'E), 28.ii.1972, L. Gangloff (1♂ MHNL); Ngulia Lodge (3°01'S, 38°13'E), i.1977, D.A. Peason (1♂ NMK); Sagala Hills (3°28'S, 38°35'E), xii.1993, Werner (4♂♂ 1♀ MDCL; 1♂ 1♀ PMOC); Taveta (3°25'S, 38°00'E), 19.xi.1973, Y. Jongema (1♂ 1♀ RMNH); Tsavo (3°00'S, 38°28'E), iv.1994, Champanhet (1♂ PMOC); Tsavo (3°00'S, 38°28'E), Vieuxgué (1♂ 1♀ MDCL); Tsavo (3°00'S, 38°28'E), 15.ii.1972, M. Delpont (4♂♂ 4♀♀ MHNL; 1♂ MNHN); Tsavo East National Park (2°45'S, 38°49'E), iv.1987, G. Lecourt (1♀ MHNL); Tsavo National Park (2°45'S, 38°49'E), 26.ii.1972, H. & J. Hazewinkel (3♀♀ RMNH); Tsavo National Park (2°45'S, 38°49'E), 16.xi.1973, T.J. Kingston (1♂ OUMNH); Tsavo National Park, Mzinga, 600m (3°21'S, 38°39'E), 27.xii.1972, J. Krikken (2♂♂ 1♀ RMNH); Tsavo East National Park, 15km W of Buchuma (3°36'S, 38°49'E), 1.ii.1981-15.iii.1981, Dr. A. Rasa (1♂ NMK); Tsavo East National Park, Dida Harea, 450m (3°35'S, 38°50'E), 25.xii.1972, J. Krikken (1♂ RMNH); Tsavo East National Park, Mzinga, 600m (3°21'S, 38°37'E), 19-31.xii.1972, J. Krikken & C. Smeenk (1♂ RMNH); Tsavo East National Park, 2.5km from Voi, 487m (3°23'S, 38°35'E), xi.1973, T.J. Kingston (2♀♀ OUMNH); Tsavo East National Park, Voi Safari Lodge, 600m (3°21'S, 38°35'E), 1-6.i.1973, J. Krikken (7♂♂ 8♀♀ RMNH); Tsavo West National Park, Kilaguni, 800m (2°54'S, 38°04'E), 8.xii.1975, C.F. Dewhurst (1♀ SANC); Tsavo West National Park, Ngulia (3°01'S, 38°13'E), i.1987, Ongango (1♂ 1♀ NMK); Tsavo West National Park, Ngulia Circuit (3°01'S, 38°13'E), 7.xii.1978, C.F. Dewhurst (4♂♂ 1♀ NMK); Voi (3°24'S, 38°33'E), iv.1967, E. Carcasson (1♂ NMK); Voi (3°24'S, 38°33'E), 29.v.1971, C. Smeenk (1♀ RMNH); Voi (3°24'S, 38°33'E), 27.viii.1972, C. Smeenk (1♂ RMNH); Voi (3°24'S, 38°33'E), 30.xi.1972, C. Smeenk (3♂ RMNH); Voi (3°24'S, 38°33'E), 13.iv.1988, P. Dauguet (2♂♂ PMOC); Voi environs (3°24'S, 38°33'E), 13-19.xi.2011, Snížek (1♀ PMOC); Voi (3°24'S, 38°33'E), xii.1991, Werner (1♂ JLMC; 1♀ MDCL); ENE of Voi, 500-600m (3°21'S, 38°39'E), 21.xii.1972, J. Krikken (1♂ RMNH); **TANA RIVER**: Galana Game Ranch, Lali Hills area, 250m (3°01'S, 39°16'E), 2-3.vi.1975, Davis & Dewhurst (1♀ SANC); **MOZAMBIQUE**: **CABO DELGADO**: Namaluco (site 4), Parque Nacional das Quirimbas, 180m (12°19'S, 40°15'E), 29.xii.2012, F. & S. Génier (1♂ 1♀ FGIC); Ravia (site 1), Parque Nacional das Quirimbas, 380m (12°40'S, 39°25'E), 1.i.2013, F. & S. Génier & M. Denja (7♂♂ 10♀♀ FGIC); Ravia (site 1), Parque Nacional das Quirimbas, 380m (12°40'S, 39°25'E), 2.i.2013, F. & S. Génier & M. Denja (5♂♂ 1♀ FGIC); Ravia (site 1), Parque Nacional das Quirimbas, 380m (12°40'S, 39°25'E), 3.i.2013, F. & S. Génier & M. Denja (1♀ FGIC); Ravia (site 6), Parque Nacional das Quirimbas, 380m (12°31'S, 39°19'E), 3.i.2013, F. & S. Génier & M. Denja (3♀♀ FGIC); Taratibu (site 1), Parque Nacional das Quirimbas, 320m (12°49'S, 39°42'E), 7.i.2013, F. & S. Génier & M. Denja (4♀♀ FGIC); Taratibu (site 2), Parque Nacional das Quirimbas, 350m (12°49'S, 39°42'E), 8.i.2013, F. & S. Génier (1♀ FGIC); Taratibu (site 3), Parque Nacional das Quirimbas, 340m (12°48'S, 39°42'E), 9.i.2013, F. & S. Génier (1♀ FGIC); Taratibu (site 4), Parque Nacional das Quirimbas, 340m (12°48'S, 39°42'E), 7.i.2013, F. & S. Génier & M. Denja (26♂♂

8♀♀ FGIC); Taratibu (site 4), Parque Nacional das Quirimbas, 340m (12°48'S, 39°42'E), 9.i.2013, F. & S. Génier (1♀ FGIC); Taratibu (site 5), Parque Nacional das Quirimbas, 340m (12°47'S, 39°42'E), 8.i.2013, F. & S. Génier & M. Denja (17♂♂ 13♀♀ FGIC); Taratibu (site 5), Parque Nacional das Quirimbas, 340m (12°47'S, 39°42'E), 8.i.2013, F. & S. Génier (1♂ 2♀♀ FGIC); Taratibu (site 7), Parque Nacional das Quirimbas, 310m (12°48'S, 39°42'E), 10.i.2013, F. & S. & M. Denja (2♂♂ FGIC); **MANICA**: Bandula (19°02'S, 33°09'E), 28.xi.2005, A. Littel (1♂ HPC); environs de Tambara (16°44'S, 34°15'E), 1926, J. Surcoff (1♂ MNHN); **SOFALA**: Gorongosa National Park (18°49'S, 34°30'E), 11-28.i.1972, Bornemissza & Kirk (1♂ 1♀ SANC); **SOUTH AFRICA**: Caffraria (1♂ IRSNB); [no precise locality] J. Burke (1♀ BMNH); **LIMPOPO**: Kruger National Park, near Phalaborwa (24°01'S, 31°13'E), 25.i.2012, Davis, Tshikae & Deschodt (1♂ UPSA); **TANZANIA**: **ARUSHA**: W shore of Lake Manyara (3°36'S, 35°44'E), ii-v.1935, B. Cooper (1♀ BMNH); **IRINGA**: Mgololo (8°43'S, 35°19'E), iv.2012, local collector (3♂♂ BMNH); Ruaha National Park, Tandala Camp, 912m (7°46'S, 35°00'E), 6.xii.2006, P. Darge (18♂♂ 17♀♀ MHNL; 5♂♂ 2♀♀ PMOC; 1♂ 1♀ MDCL); **KILIMANJARO**: Moshi (3°21'S, 37°20'E), 24.iv.1963, B. Salwegter (2♀♀ NMK); **LINDI**: Lindi (10°00'S, 39°42'E) (1♂ 2♀♀ ZMHB); **MANYARA**: Babati district (4°13'S, 35°45'E), 8.xii.2011 (2♂♂ 1♀ MDCL); **MARA**: near Klein's Camp, 1700m (1°42'S, 35°11'E), 13.i.1973, J. Krikken (1♀ RMNH); Lobo environs (2°00'S, 35°10'E), 18.xi-4.xii.1994, M. Homolac (1♂ NMPC); Lobo Lodge, Serengeti National Park (2°00'S, 35°10'E), i.1987, Burmeister (1♀ ZSM); **MBEYA**: Rungwe (9°10'S, 33°33'E), xii.2012, local collector (1♂ BMNH); **MOROGORO**: Kihonda (6°46'S, 37°39'E), iii.1963, E. Haaf (1♀ NMB); Mikumi (7°24'S, 36°59'E), iii.2012, R. Minetti (1♂ 1♀ PMOC); Mikumi National Park (7°24'S, 36°59'E), 14.i.1994, Curletti (1♂ JLMC); Morogoro (6°50'S, 37°40'E), Gommenginger (1♂ MNHN); Hondo Hondo, Udzungwa Mountains, 300m (7°50'S, 36°54'E), 14-19.iii.2012, D.A. Oram (1♂ BMNH); **PWANI**: Selous Game Reserve, 400m (7°48'S, 38°15'E), xii.2012, local collector (2♂♂ 1♀ BMNH); **RUKWA**: Katusunga (6°51'S, 31°06'E), 1949, Petre & Brédo (7♂♂ 3♀♀ IRSNB); Lac Rukwa (8°20'S, 32°15'E), i.1945, H.J. Brédo (1♂ IRSNB); **RUUVUMA**: Wandonde-Gebiet am Ruvuma, P. Kammerer (3♂♂ 3♀♀ ZMHB); **ZAMBIA**: **CENTRAL**: Kafue National Park, Chunga Camp (14°57'S, 25°49'E), xi.1989, L. Williense (2♀♀ RMNH); **EASTERN**: Mfuwe, South Luangwa National Park (13°05'S, 31°47'E), 8.ii.1984 (1♀ RMNH); Nkwali, South Luangwa Game Management Area, 529m (13°23'S, 29°33'E), 10-18.xi.2012, R. Smith & H. Takano (42♂♂ 34♀♀ BMNH); South Luangwa National Park, 525m (13°05'S, 31°47'E), 9.xi.2005, S. Beynon & M. Jubb (1♂ OUMNH); **NORTHERN**: Abercorn [=Mbala] (8°51'S, 31°22'E), 13.xii.1941, H.J. Brédo (1♂ IRSNB); Kabwe (8°34'S, 29°33'E), 26.ii.1943, H.J. Brédo (1♂ IRSNB); entre Kalaba et Seranani, 7.iii.1943, H.J. Brédo (2♀♀ IRSNB); Kalundu (10°18'S, 29°23'E), 23.ii.1943, H.J. Brédo (3♂♂ IRSNB); Mporokoso (9°23'S, 30°08'E), i.1945, H.J. Brédo (5♂♂ 7♀♀ IRSNB); Mweru-Wantipa (8°46'S, 29°32'E), i.1945, H.J. Brédo (51♂♂ 31♀♀ IRSNB); Nkamba Bay, Sumbu National Park, 873m (8°36'S, 30°33'E), 23-25.xi.2012, R. Smith & H. Takano (1♀ BMNH); **SOUTHERN**: Victoria Falls, Livingstone (17°55'S, 25°52'E), 10.ii.1984 (1♂ RMNH); **ZIMBABWE**: **MANICALAND**: Mount Chirinda (20°25'S, 32°42'E), 1906, Swynnerton (1♂ BMNH); **MASHONALAND WEST**: Kariba (16°31'S, 28°51'E), 10.ii.1973, N.J. Duke (1♂ 1♀ TMSA); Marongora, 550m (16°13'S, 29°10'E), 6-9.ii.1987, W. Wittmer (2♂♂ NMB); Rekometjie (16°08'S, 29°24'E), 8-9.i.1982, Doube & Macqueen (12♂♂ 11♀♀ SANC); **MASVINGO**: Kyle Game Reserve (20°11'S, 31°00'E), 22.iv.1971, Bornemissza & Aschenborn (1♂ SANC); Kyle National Park (20°11'S, 31°00'E), 17-18.xi.1973, Tribe & Aschenborn (1♀ SANC); Kyle Recreational Park at Lake Mutirikwi (20°10'S, 31°01'E), 1-5.xii.1993, M. Uhlig (1♂ ZMHB); **MATABELELAND NORTH**: 96km NW Bulawayo (19°33'S, 27°56'E), 20.xi.1973, Tribe & Aschenborn (1♀ SANC); Victoria Falls, Zambezi National Park camp (17°54'S, 25°48'E), 11.xii.1993, K. Ebert (1♀ ZMHB); Victoria Falls (17°54'S, 25°48'E), 18.xii.1974, Kirsten & Scholtz (1♀ TMSA); Wankie [=Hwange] National Park (18°43'S, 26°57'E), 21-23.xi.1973, Tribe & Aschenborn (2♂♂ SANC).

**Notes:** There has been a great deal of confusion over the true identity of *C. obtusicornis*. At one time or another, at least four taxa have been identified under this name: *C. genieri*, *C. gibbicollis*, *C. platycerus* and *C. princeps*. Klug described *Copris platycera* on a series of specimens collected by Carl Peters at Sena in Mozambique. *Copris platycera* is however a junior primary homonym (*C. platycera* Wiedemann, 1823, is a junior subjective synonym of *Onthophagus giraffa* (Hausmann, 1807)), which went unnoticed by Harold (1869) who correctly identified that *C. platycerus* and *C. obtusicornis* were the same species. Kolbe (1893) described *C. princeps* from the Congo but this taxon was incorrectly synonymised by Felsche (1901) under *C. obtusicornis*. Gillet (1907) added to the confusion by synonymising *C. gibbicollis* with *C. platycerus* and stated that *C. obtusicornis* was a different taxon. Gillet published the following synonymies in his catalogue of 1911: *C. obtusicornis* = *C. princeps* and *C. platycerus* = *C. gibbicollis*. Ferreira (1960a) synonymised all of the names under *C. obtusicornis* but the male and female she figures in the redescription is *C. genieri*. The final change she made (1960b) was to raise *C. platycerus* to species level with the other three names as synonyms

and subsequent works dealing with this species have used the name *C. platycerus* (Ferreira, 1967; 1972; Moretto, 2014).

**Diagnosis:** see under *C. princeps*. Although similar to *C. princeps*, it is closest to *C. genieri* from which it can be separated by the arcuate aspect of the body in rear view. In *C. genieri*, the body has a triangular aspect.

**Biology:** a widespread East African species found in open savanna and woodland habitats but restricted to areas where elephants are present. The author has collected the species under elephant dung and at light in Zambia but only in areas with healthy elephant populations. Elephant populations have decreased significantly in north-east Zambia over the past century (M.T. Harvey, pers. comm., 2015) and having revisited areas where H.J. Brédo had collected the species in the 1940's, 75 years on, the species was not present. Specimens have been caught between November and July.

**Distribution** (Pl. 24: fig. 8): South Africa, Mozambique, Zimbabwe, Zambia, D.R. Congo, Burundi (?), Rwanda (?), Uganda (?), Tanzania, Kenya.

## 25. *Catharsius genieri* Moretto, 2014

(Pl. 25: figs. 1-8; Pl. 30: fig. 25)

*Catharsius obtusicornis* sensu Ferreira, 1960a (nec Boheman): 29.

*Catharsius platycerus* sensu Ferreira, 1967 (nec Klug): 244.

*Catharsius genieri* Moretto, 2014: 59.

**Type locality:** “Burkina Faso, Nahouri, Forêt de Nazinga, Akwazena”

**Name-bearing type:** Holotype ♂ in CMNC:

“// BURKINA FASO: NAHOURI / Forêt de Nazinga, Akwazena / 275m, 11°09'24"N 001°36'44"O / 26.VII.2006, zone soudanienne / savane boisée, piège lumineux / F. & S. Génier, 2006-76 // HOLOTYPE / *Catharsius / genieri* n.sp. / dés.: P. Moretto, 2014 [red card with black border] // COLÉOPTÈRES / DU / BURKINA FASO / BF005619 [QR Code; white card with black border] // [aedeagus glued onto triangular card] //”

**Redescription:** Colour: Black, with a reddish undertone; pubescence reddish-brown. **Male** (Pl. 25: figs. 1, 2, 5): **Head:** anterior clypeal edge broadly arcuate, with a very slight concavity centrally; clypeal margin continuous; clypeal surface transversely rugulate anteriorly, turning more granulose towards the clypeogenal suture; central portion with fine granulations and posterior portion with transverse rugulae. Genal edge rounded and obtusely angled, surface covered evenly with longitudinal granules turning more ovaline posteriorly; the genal margin with an emargination at the clypeogenal suture. Suture well defined to base of an incomplete clypeal carina. A laterally flattened, rectangular and slightly apically bifid cephalic horn position anteriorly on clypeus; horn slanted forward in

lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin sharply emarginate centrally. Lateroanterior margin rounded, lateral margin very slightly arcuate. Pronotal disc with a continuous evenly arcuate, transverse carina anteriorly and depressed strongly on each side of the midline; carina forms just above the fovea in lateral view; surface of pronotal disc covered evenly in circular granules, becoming smaller and closer together anteriorly towards the midline; lateral declivity with fovea and surface completely granulate, central portion of anterior declivity completely granulate, with a short depression in the basal third the length of the emargination of the margin; in frontal view, the lateral basal portion of the anterior declivity smooth, from the fovea to the anterior margin of the pronotum. **Elytra:** quite straight, giving a triangular aspect to the body in rear view; carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; basolateral portion distinctly bulbous; elytral striae deep with weak punctures. Interstriae smooth with well-spaced fine punctures; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventriles:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 25: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 25).

**Female** (Pl. 25: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate with continuous clypeal margin; clypeal surface transversely rugulate posterior portion behind clypeal carina granulate; genal edge rounded and acutely angled, surface covered with longitudinal, granules turning more ovaline posteriorly; clypeogenal suture to base of clypeal carina; clypeal carina raised, with an upright bifidate horn centrally; in frontal view, wide on the basal third, the apicolateral angles produced into a fine denticle. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin gently emarginate centrally. Lateroanterior margin rounded, lateral margin gently arcuate. Pronotal disc with transverse carina anteriorly; carina deeply bowed at lateral edges, gently arcuate anteriorly centrally and notched medially. Carina much wider than the distance between the eyes. Surface of pronotal disc covered evenly in circular granules; lateral declivity with fovea and surface completely granulate. Anterior declivity completely granulate. **Elytra:** quite straight, giving a triangular aspect to the body in rear view; carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; basolateral portion distinctly bulbous; elytral striae deep with weak punctures. Interstriae smooth with well-spaced fine punctures; epipleural carina well-developed, extending two-thirds of the length of the elytra; **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout; **Ventriles:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence.

**Length:** male 26-35mm; female 26-32mm.

**Variation:** in smaller males, the cephalic horn is positioned further to the posterior, often reduced to a short triangular peak on the clypeal carina. In smaller females, the clypeal horn is reduced into a quadridentate carina.

**Other material examined** (35♂♂ 32♀♀):

**BURKINA FASO:** CENTRE: Ouagadougou (12°22'N, 1°31'W), M. Delpont (1♀ MHNL); environs de Ouagadougou (12°22'N, 1°31'W), vii-viii.1987, M. Delpont (2♀♀ MHNL); CENTRE-SUD: Forêt de Nazinga, Akwazena, 275m (11°09'N, 1°37'W), 21.vii.2006, F. & S. Genier (1♂ 1♀ *paratypes*, IRSNB); Forêt de Nazinga, Akwazena, 275m (11°09'N, 1°37'W), 21.vii.2006, F. & S. Genier (*allotype* ♀, CNC); Forêt de Nazinga, Akwazena, 275m (11°09'N, 1°37'W), 21.vii.2006, F. & S. Genier (1♂ *paratype*, PMOC); Forêt de Nazinga, Naguio, 275m (11°08'N, 1°35'W), 24.vii.2006, F. & S. Genier (1♂ 2♀♀ *paratypes*, PMOC); Pama, 232m (11°05'N, 1°18'W), 24-28.viii.2005, P. Moretto (1♂ PMOC); Pô (11°09'N, 1°09'W), ix.2005, A.R. Ouedraogo (3♂♂ 3♀♀ PMOC); Pô (11°09'N, 1°09'W), viii-ix.2005, local collector (1♂ PMOC); Reserve de Nazinga (11°09'N, 1°37'W), 9-12.vi.2005, S. Rojkoff (1♂ MDCL); **D.R. CONGO:** **BAS-UELE:** Bambesa (3°27'N, 25°41'E), 6.x.1938, P. Lefevre (1♂ TMSA); **HAUT-UELE:** Parc National de la Garamba, Cellule II (3°53'N, 29°24'E), 29.iii.1951, J. Verschuren (6♂♂ 1♀ MRAC); Parc National de la Garamba, Cellule II (3°53'N, 29°24'E), 4.vi.1952, H. de Saeger (1♂ 2♀♀ NMB); Parc National de la Garamba, Cellule II (3°53'N, 29°24'E), 28.iv.1952, H. de Saeger (1♀ NMB); Parc National de la Garamba, Cellule II (3°53'N, 29°24'E), 29.v.1952, H. de Saeger (20♂♂ 23♀♀ MRAC); **SOUTH SUDAN:** **IMATONG:** Assua River (3°43'N, 31°55'E), 11.iv.1912, Lady Jackson (1♀ BMNH); Nimule (3°35'N, 32°04'E), 1900ft., 3.v.1912, Lady Jackson (1♂ BMNH).

**Diagnosis:** see under *C. princeps*. Males very similar to *C. obtusicornis* but can be differentiated by the triangular aspect of the body. The females are easily distinguished by the length and shape of the pronotal carina as well as the clypeal horn.

**Biology:** a widespread species found in the Sudanian Savanna belt which appears to be strictly restricted to areas where elephants are found. Individuals are readily attracted to light. The distribution of the specimens studied is disjointed but this is most likely down to under-collecting. The elephant populations within this region are very fragmented but *C. genieri* is likely to be found in areas with healthy elephant populations such as Zakouma National Park in Chad, Bamingui-Bangoran National Park in Central African Republic and Bouba Ndjida National Park in Cameroon. Specimens have been caught between March and October.

**Distribution** (Pl. 25: fig. 8): Burkina Faso, Ghana (?), Benin (?), Nigeria (?), Cameroon (?), Chad (?), Central African Republic (?), D.R. Congo, South Sudan, Uganda (?).

## 26. *Catharsius severini* Gillet, 1907

(Pl. 26: figs. 1-8; Pl. 30: fig. 26)

*Catharsius severini* Gillet, 1907: 183; Ferreira, 1960a: 41; 1967: 253.

**Type locality:** "Chinde" [(18°35'S, 36°28'E), Mozambique]

**Name-bearing type:** Holotype ♂ in IRSNB (by original monotypy):

"// Type [grey card with black border; red print] // Tschinde / Fruhstorfer. [yellow card; partially handwritten] // Cath. ♂ / Severini Gillet / (type) [handwritten] // Catharsius / Severini / n.sp. Gillet

[handwritten] // HOLOTYPE / CATHARSIUS / severini / Gillet / det. H Takano 2018 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black, with a reddish undertone; pubescence reddish-brown. **Male** (Pl. 26: figs. 1, 2, 5): **Head:** anterior clypeal edge broadly arcuate, with a very slight concavity centrally; clypeal margin continuous; clypeal surface granulose except for a very small region of transverse rugulae in the region between the cephalic horn and anterior margin; posterior portion with fine granules and rugulae. Genal edge rounded and acutely angled, surface covered evenly with longitudinal granules turning more ovaline and finer towards the eye; genal suture well defined to base of an incomplete clypeal carina. A laterally flattened, spade-shaped cephalic horn positioned anteriorly on clypeus; horn gently slanted forward in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin sharply emarginate centrally. Lateroanterior margin rounded, lateral margin very slightly arcuate. Pronotal disc with an interrupted carina anteriorly, curving back on each side following the slope of the anterior declivity; the central portion widely emarginate with the carina raised into two upward pointing projections either side of the midline; carina forms above the fovea in lateral view; surface of pronotal disc covered evenly in circular granules, becoming smaller and disappearing around the central projections; lateral declivity with fovea and surface completely granulose; anterior declivity completely granulose. **Elytra:** carinate basally; basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae deep with weak punctures. Interstriae with some alutaceous microsculpture and rugosity; epipleural carina well-developed, extending two-thirds of the length of the elytra. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in light brown pubescence; metasternum with long well-developed sulcus; the first sternite heavily punctured with pubescence. **Legs:** protibia tridentate; mesa- and metatibia with a weakly undulating apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 26: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 26).

**Female** (Pl. 26: figs. 3, 4, 6): **Head:** anterior clypeal edge gently arcuate with continuous clypeal margin; clypeal surface transversely rugulate posterior portion behind clypeal carina granulose; genal edge rounded and acutely angled, surface covered with longitudinal granules turning more ovaline posteriorly; clypeogenal suture to base of clypeal carina; clypeal carina slightly raised, with two small tubercles positioned anteriorly either side of a central longitudinally elongate tubercle; **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Margin gently emarginate centrally. Lateroanterior margin rounded, lateral margin gently arcuate. Pronotal disc with a short indistinct transverse carina anteriorly; carina emarginate centrally and shorter than the distance between the eyes. Surface of pronotal disc covered in circular granules; lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose; **Elytra:** carinate basally;

basal portion of elytra with fine alutaceous microsculpture and slight rugosity; elytral striae deep with weak punctures. Interstriae with some alutaceous microsculpture and rugosity; epipleural carina well-developed, extending two-thirds of the length of the elytra; **Pygidium**: transverse, fully margined, with fine ovaline punctures throughout; **Ventrites**: covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternite with long pubescence; **Legs**: protibia tridentate; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence.

**Length**: male 29-30mm; female 30-31mm.

**Variation**: all the specimens studied are well developed males and females with little variation. It is likely that smaller males will have a reduced cephalic horn positioned further to the posterior.

**Other material examined** (4♂♂ 3♀♀):

**KENYA**: KAJIADO: Suswa (1°11'S, 36°22'E), xi.1997, local collector (1♂ PMOC); **MOZAMBIQUE**: [no precise locality] (1♂ 1♀ BMNH); SOBALA: Chironde Camp, Inhamitanga (18°23'S, 35°33'E), xii.2005-i.2006, D. Camiade (1♂ JFJC); Marromeu (18°18'S, 35°56'E), van Eldik (1♂ RMNH); **TANZANIA**: MOROGORO: Ngerengere (6°45'S, 38°07'E), S. Schauer (1♀ ZMHB); PWANI: Selous Game Reserve (7°49'S, 38°20'E), xii.2004, local collector (1♀ PMOC);

**Diagnosis**: the male is unmistakable with its curved pronotal carina and the arcuate margin of the clypeus. The female is similar in appearance to *C. obtusicornis*, a species with a similar distribution, but the indistinct pronotal carina as well as the evenly arcuate shape of the clypeus should allow for easy identification.

**Biology**: although widely distributed from Kenya to Mozambique, this is a very rare species in collections. The biology is unknown, although it is likely this large-bodied species has a preference for elephant dung like other member of this clade. The few specimens in collections with data have been caught between November and January.

**Distribution** (Pl. 26: fig. 8): Kenya, Tanzania, Mozambique.

## 27. *Catharsius heros* Boheman, 1860

(Pl. 27: figs. 1-8; Pl. 30: fig. 27)

*Catharsius heros* Boheman, 1860: 109; Péringuey, 1901: 329; Ferreira, 1960a: 27; 1967: 237; 1968: 270; Moretto, 2008: 38.

**Type locality**: “juxta lacum N’Gami” [=near Lake Ngami (20°28’S, 22°42’E), Botswana]

**Name-bearing type**: 1♂ syntype in NHRS. In order to preserve the stability of nomenclature by fixing the published name to a single specimen, this specimen is here **designated as the lectotype**:

“// N’Gami / Africae // J. Wahlb. // Type. // Heros Bhm. [handwritten] // Typus [red card with black border] // 4825 / E92 + [light blue paper] // NHRS-JONI / 000000251 // LECTOTYPE /

CATHARSIUS / heros Boheman / det. H Takano 2015 [white card with red border; partially handwritten] //”

**Redescription:** Colour: Black, pubescence brown. **Male** (Pl. 27: figs. 1, 2, 5): **Head:** anterior clypeal edge broadly arcuate, with a very slight concavity centrally; clypeal margin continuous; clypeal surface transversely rugulate centrally, turning more granulose towards the clypeogenal suture; posterior portion behind cephalic horn granulose; genal edge rounded and obtusely angled, surface covered evenly with poorly-formed longitudinal, granules; lateral edge of clypeogenal suture raised into an apical projection at the junction with the margin; suture well defined to base of cephalic horn; cephalic horn stout and straight, wide on basal third with edges converging evenly; horn perpendicular to clypeus in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin rounded, lateral margin almost straight. Pronotal disc with transverse carina anteriorly and depressed strongly on each side of the midline; carina forms just above the fovea in lateral view; carina angled obliquely forward to a sharp forward and upward-pointing projection on each side of the midline, the lateral portion of carina gently sinuous; central portion between the two projections almost straight and strongly serrated, with a very slight forward expansion centrally. Surface of pronotal disc covered evenly in circular granules; lateral declivity with fovea and surface completely granulose; anterior declivity granulose centrally, the lateral portions with a broad excavation, its surface smooth, extending from the edges of the carina towards the anterior margin but stopped by an area of granulation surrounding the excavation. **Elytra:** quite straight, giving a triangular aspect to the body in rear view; carinate basally; basal portion of elytra with fine alutaceous microsculpture; basolateral portion distinctly bulbous; elytral striae well developed with weak punctures. First elytral interstriae punctured, the other interstriae with fine diagonal wrinkles; epipleural carina well-developed, extending almost the whole length of the elytra, with a slight notch near the base. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence. **Legs:** protibia tridentate; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 27: fig. 7): parameres as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 27).

**Female** (Pl. 27: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate with continuous clypeal margin; clypeal surface transversely rugulate centrally, turning more granulose towards the clypeogenal suture; posterior portion behind cephalic carina granulose; genal edge rounded and almost at right angles, surface covered evenly with poorly-formed longitudinal, granules; clypeogenal suture to base of cephalic carina; clypeal carina raised, with four well defined tubercles, the two central tubercles being placed posteriorly to the lateral tubercles; a suture joins the four tubercles together. From the carina extends anteriorly a raised shield-shaped region with well-defined lateral

margins. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin rounded, lateral margin gently arcuate. Pronotal disc with transverse carina anteriorly; carina arcuate and emarginate centrally, its total length wider than the distance between the eyes. Surface of pronotal disc covered evenly in circular granules; lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** quite straight, giving a triangular aspect to the body in rear view; carinate basally; basal portion of elytra with fine alutaceous microsculpture; baso-lateral portion distinctly bulbous; elytral striae well developed with weak punctures. First elytral interstriae punctured, the other interstriae with fine diagonal wrinkles; epipleural carina well-developed, extending almost the whole length of the elytra, with a slight notch near the base. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence; **Legs:** protibia tridentate; meso- and metatibia with a smooth apical margin. First metatarsomere very broad apically, gently arcuate laterally.

**Length:** male 26-42mm; female 33-39mm.

**Variation:** in smaller males the anterior declivity is completely granulose, the cephalic horn is reduced to a short point or in some cases slightly bifid and the pronotal carina is reduced becoming slightly sinuous lacking the projections or any serrations.

#### **Other material examined (89♂♂ 73♀♀):**

**ANGOLA:** CUNENE: Evari River [=Evale] (16°33'S, 15°45'E), xi.1897, Eriksson (1♂ SAMC); HUILA: Bicuar National Park, 8km E Camp (15°06'S, 14°55'E), 19.xii.1974, Davis & Temby (1♂ SANC); **BOTSWANA:** Bechuanaland (1♀ BMNH); CENTRAL: Khumaga (20°28'S, 24°31'E), ii.2017, B.O. Sands (1♂ 3♀♀ BMNH); 120km N Nata (19°14'S, 25°48'E), 20.xi.2001, K. Werner & R. Lizler (1♂ 1♀ PMOC); 120km N Nata (19°14'S, 25°48'E), 29-30.xi.2001, K. Werner & R. Lizler (1♂ 1♀ PMOC); north of Planet Baobab Camp (20°11'S, 25°18'E), 25.ii.2017, T. Lackner (1♂ BMNH); NORTH-WEST: Chobe Game Reserve, Caprivi Gate (17°56'S, 24°44'E), 28-29.xi.1973, Tribe & Aschenborn (4♂♂ 2♀♀ SANC; 1♂ BMNH); near Kasane (17°48'S, 25°10'E), 29.xi.2003, K. Werner & P. Smrž (1♂ PMOC); Moremi Game Reserve (19°22'S, 23°03'E), 11.iv.1973, A.L.V. Davis (1♂ SANC); Moremi Game Reserve (19°22'S, 23°03'E), 30.xi.1973, Tribe & Aschenborn (6♂♂ 5♀♀ SANC); Senyati Safari Camp (17°52'S, 25°14'E), 28.ii.2017, T. Lackner (5♂♂ 3♀♀ BMNH); Zambesi, Bradshaw (1♂ NMB; 1♀ BMNH); Zambesi, 1878, Bradshaw (1♂ 3♀♀ RMNH; 1♀ SAMC); **MOZAMBIQUE:** MAPUTO: Maputo Special Reserve, West Gate, 22m (26°30'S, 32°43'E), 21-30.xi.2016, M. Aristophanous, J. Cristóvão, G. László & W. Miles (1♂ 1♀ BMNH); **NAMIBIA:** Damara (2♂♂ 1♀ BMNH); Damaraland (1♂ NHRS); Ovampoland (1♀ MNHN); Ovampoland, G.A.K. Marshall (1♂ BMNH); HARDAP: 32km S of Gochas, 1100m (25°08'S, 18°57'E), 2.iii.2014, M.A. Hielkema (1♂ MHPC); KARAS: Kleinbegin (27°58'S, 19°01'E), 20.xii.1968, R.C. Biggs (1♂ TMSA); KAVANGO: Kaudom Game Reserve, N of Soncana (18°56'S, 20°43'E), 2.i.1999, Mann & Marais (5♂♂ 3♀♀ OUMNH); Nawasha Pan (19°10'S, 20°54'E), 27.xii.1998, D.J. Mann & E. Marais (1♀ OUMNH); West Caprivi Park, 5km N of Nova (18°10'S, 21°44'E), 16.xii.1999, Mann & Marais (4♂♂ 2♀♀ OUMNH); West Caprivi Park, 4km W Immelman runway (17°47'S, 23°16'E), 15.xii.1999, Mann & Marais (4♂♂ 1♀ OUMNH); KUNENE: Sesfontein, Khowarib Schlucht (19°16'S, 13°53'E), 18.v.1978, V.B. Whitehead (1♂ SAMC); OSHANA: Oshakati (17°47'S, 15°42'E), 5.v.1977, N.J. Duke (1♀ TMSA); OSHIKOTO: Etosha National Park, Mushara area (18°36'S, 16°53'E), 21.xii.1999, Mann & Marais (1♂ 3♀♀ OUMNH); Etosha National Park, Mushara Waterhole (18°35'S, 16°55'E), 22.xii.1999, Mann & Marais (1♂ OUMNH); 32mi. SE Ondangua (18°10'S, 16°21'E), 1.iv.1972, Southern African Expedition (1♂ BMNH); 105km W Tsumeb (19°15'S, 16°35'E), 8.viii.1998, G. Betti (1♂ PMOC); OTJOZONDJUPA: Hochfeld (21°29'S, 17°51'E), 20.v.1973, R. Kluge (1♂ SANC); Klein Karas, 3578ft. (27°34'S, 18°05'E), I. Örtendahl (1♀ NHRS); ZAMBEZI: Bande de Caprivi, Kwando (18°02'S, 23°20'E), 28.xii.2007, P. Tauzin (1♀ PMOC); Caprivi Strip, Kongola (17°49'S, 23°23'E), 7.i.2015, S. Prepsl (1♂ PMOC); Caprivi Strip, B8 Road (17°46'S, 23°19'E), 29.iii.2002, Mann, Marais & Karsch (1♂ OUMNH); **SOUTH AFRICA:** [no precise locality], W.A. Bullen (1♀ BMNH); GAUTENG: Andalucia (26°01'S, 28°04'E), i.1943 (1♂ RMNH); KWAZULU-NATAL: False Bay (27°58'S, 32°22'E), 16-17.xii.2006, R. Perissinotto & L. Clennell (1♀ PMOC); 17km W Muzi (26°52'S, 32°31'E), xii.1980, H.H. Aschenborn (1♂ 1♀ SANC); NE Ndumo, W border Tembe Elephant Park, 80m (26°57'S, 32°23'E), 29.xii.2007-9.i.2008, M. Snižek (1♂ PMOC); Ndumo Game Reserve (26°53'S,

32°16'E), 25.x.1973, Tribe & Temby (1♀ SANC); Ndumo Game Reserve (26°53'S, 32°16'E), 23.xi.2001, P. Schüle (1♀ PMOC); Tembe Elephant Park (27°01'S, 32°24'E), 17.iii.1996, B.J. van Rensburg (1♀ SANC); Tembe Elephant Park (27°01'S, 32°24'E), xii.1998, B.J. van Rensburg (1♀ SANC); Tembe Elephant Park (27°01'S, 32°24'E), 14.v.1995, B.J. van Rensburg (1♂ SANC); **LIMPOPO**: 24km S Pafuri, Machai Pan, Kruger National Park (23°10'S, 31°23'E), 25.iii.1973, I.D. Temby (2♂♂ 2♀♀ SANC; 1♀ MNHN); Little Muck, 512m (22°15'S, 29°16'E), 12.xii.2009, D. MacFadyen (1♀ TMSA); Mokopane, Shikwaru Lodge, 1395m (24°14'S, 28°54'E), 1-8.ii.2014, M. Strohle & Schaarschmidt (1♂ PMOC); **NORTH WEST**: Maquassie [=Makwassie] (27°19'S, 26°00'E), Dr. R. Broom (1♂ 1♀ BMNH); Maquassie [=Makwassie] (27°19'S, 26°00'E), i.1934, Dr. R. Broom (1♂ 1♀ TMSA); **NORTHERN CAPE**: 7km W Dibeng (27°36'S, 22°48'E), 2.v.1974, Temby & Pitsei (1♂ SANC); Dronfield Nature Reserve, 1220m (28°37'S, 24°48'E), 10-12.ii.2012, R. Müller (1♂ TMSA); Kimberley (28°44'S, 24°45'E), 1889, M. Wilman (1♀ SAMC); 26km NE Kuruman (27°19'S, 23°37'E), 28-29.i.1974, Davis & Kirsten (1♂ 1♀ SANC); 40km NE Kuruman (27°16'S, 23°45'E), 28.i.1074, Davis & Kirsten (1♂ BMNH); Schmidtsdrift (28°42'S, 24°03'E), xi.1950, E. Parker (1♀ TMSA); Upington (28°27'S, 21°15'E), 1922, A. White (4♂♂ SAMC); 65km E Upington (28°20'S, 21°54'E), 19.xii.1975, H.H. Aschenborn (1♂ MNHN); 34km SE Van Zylsrus, Sonstraal (27°02'S, 22°21'E), 30.i.1974, Davis & Kirsten (2♂♂ BMNH); Warrenton (28°08'S, 24°51'E), 8.xii.1977, F. de Moor (1♂ TMSA); **ZAMBIA**: **SOUTHERN**: Highlands, Livingstone (17°49'S, 25°52'E), 2.xii.2010, T. Johnson (2♂♂ LMRZ); 20mi E Kazangula (17°47'S, 25°35'E), 11.ii.1972, Bornemissza & Kirk (1♂ 2♀♀ SANC); Victoria Falls environs (17°55'S, 25°52'E), xii.1993, J. Moravec (1♂ NMPC); **ZIMBABWE**: between Limpopo and Zambezi Rivers, 1879, T. Ayers (1♂ 1♀ SAMC); **MATABELELAND NORTH**: Hwange National Reserve (18°43'S, 26°57'E), 11.iii.1991, R. Minetti (1♂ PMOC); Victoria Falls (17°56'S, 25°51'E), 22.i.1974, H.H. Aschenborn (1♂ MNHN); Victoria Falls (17°56'S, 25°51'E), 27.i.1974, H.H. Aschenborn (1♂ 1♀ SANC); Victoria Falls (17°56'S, 25°51'E), 18.xii.1974, Kirsten & Scholtz (1♂ 2♀♀ TMSA); 7mi W Victoria Falls National Park (17°58'S, 25°45'E), 11.ii.1972, Bornemissza & Kirk (2♂♂ 1♀ SANC); Wankie [=Hwange] National Park (18°43'S, 26°57'E), 14.i.1960, J.S. Weir (1♀ BMNH); Wankie [=Hwange] National Park (18°43'S, 26°57'E), 15.ii.1972, Bornemissza & Kirk (7♀♀ SANC); Wankie [=Hwange] National Park (18°43'S, 26°57'E), 21-23.xii.1973, Tribe & Aschenborn (2♂♂ 5♀♀ SANC); Wankie [=Hwange] National Park (18°43'S, 26°57'E), 30.i.1974, H.H. Aschenborn (1♂ SANC).

**Diagnosis:** this species, together with the subsequent two species, are unmistakable. All three species are large-bodied and have a serrated central portion of the pronotal carina as well as a distinct upward pointing tooth at the juncture of the clypeogenal suture and the clypeal margin. In *C. heros* the pronotal carina is almost straight either side of the midline, whilst in *C. karlwerner* it is bowed either side of the midline. In *C. lepineyi*, a short horn is present at both ends of the pronotal carina, which is not present in either of the other two species. As these species are distributed allopatrically, there is unlikely to be any confusion in specimens with provenance. *C. heros* is the largest of all *Catharsius* species, with the largest males exceeding 40mm in length.

**Biology:** this large-bodied species is widely distributed in open areas with sandy soils in southern Africa, from near sea level to 2000m. It has been collected in elephant dung, and often attracted to light. In a recent study in Botswana, a few individuals were caught in cattle dung baited pitfall traps, in an area with a large population of elephants (pers. comm. B.O. Sands, 2017). Specimens have been caught between October and May.

**Distribution** (Pl. 27: fig. 8): Namibia, Angola, Botswana, Zambia, Zimbabwe, Mozambique, South Africa.

## 28. *Catharsius lepineyi* Boucomont, 1934

(Pl. 28: figs. 1-8; Pl. 30: fig. 28)

*Catharsius heros* var. *lepineyi* Boucomont, 1934: 25.

*Catharsius heros* var. *lepineyi* Boucomont, 1934: Ferreira, 1960a: 27.

*Catharsius lepineyi* Boucomont, 1934: Moretto, 2008: 39.

**Type locality:** “Moninpe” [= Manimpé (14°09'N, 5°31'W), Mali]

**Name-bearing type:**

The ♂ holotype specimen was collected by Jacques de Lépiney (1896-1941) on his expedition to the French Sudan and could not be located in the Boucomont collection (MNHN). Lépiney spent the last years of his life in Rabat, Morocco and his collection may reside in the Institut Scientifique de Rabat. Due to its unmistakable shape and size, the designation of a neotype is deemed unnecessary.

**Redescription:** Colour: Black, pubescence brown. **Male** (Pl. 28: figs. 1, 2, 5): **Head:** anterior clypeal edge broadly arcuate, with a very slight concavity centrally; clypeal margin continuous; clypeal surface transversely rugulate centrally, turning more granulose towards the clypeogenal suture; posterior portion behind cephalic horn granulose; genal edge rounded and obtusely angled, surface covered evenly with poorly-formed longitudinal, granules; lateral edge of clypeogenal suture raised into an apical projection at the junction with the margin; suture well defined to base of cephalic horn; cephalic horn stout and straight, wide on basal third with edges converging evenly; horn perpendicular to clypeus in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin rounded, lateral margin almost straight. Pronotal disc with transverse carina anteriorly and depressed strongly on each side of the midline; carina forms just above the fovea in lateral view; carina with sharp forward-pointing projection at each end of the carina; the central portion between the two projections almost straight and serrated, with a very slight depression centrally. Surface of pronotal disc covered evenly in circular granules; lateral declivity with fovea and surface completely granulose. Anterior declivity granulose centrally; lateral portions with a deep rounded excavation; its surface smooth, extending from the edges of the carina towards the anterior margin but stopped by an area of granulation surrounding the excavation. **Elytra:** quite straight, giving a triangular aspect to the body in rear view; carinate basally; basal portion of elytra with fine alutaceous microsculpture; basolateral portion distinctly bulbous; elytral striae well developed with weak punctures. First elytral interstriae punctured, the other interstriae with fine diagonal wrinkles; epipleural carina well-developed, extending almost the whole length of the elytra, with a slight notch near the base. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence. **Legs:** protibia tridentate; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence; **Aedeagus** (Pl. 28: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 28).

**Female** (Pl. 28: figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate with continuous clypeal margin; clypeal surface transversely rugulate centrally, turning more granulose towards the clypeogenal suture; posterior portion behind cephalic carina granulose; genal edge rounded and almost at right angles, surface covered evenly with poorly-formed longitudinal, granules; clypeogenal

suture to base of cephalic carina; clypeal carina raised, with four well defined tubercles, the two central tubercles being placed posteriorly to the lateral tubercles; a suture joins the four tubercles together. From the carina extends anteriorly a raised shield-shaped region with well-defined lateral margins. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin rounded, lateral margin gently arcuate. Pronotal disc with transverse carina anteriorly; carina straight and emarginate centrally, its total length wider than the distance between the eyes. Surface of pronotal disc covered evenly in circular granules; lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** quite straight, giving a triangular aspect to the body in rear view; carinate basally; basal portion of elytra with fine alutaceous microsculpture; basolateral portion distinctly bulbous; elytral striae well developed with weak punctures. First elytral interstriae punctured, the other interstriae with fine diagonal wrinkles; epipleural carina well-developed, extending almost the whole length of the elytra, with a slight notch near the base; **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout; **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence; **Legs:** protibia tridentate; mesa- and metatibia with a smooth apical margin. First metatarsomere very broad apically, gently arcuate laterally.

**Length:** male 26-35mm; female 26-37mm.

**Variation:** in smaller males the anterior declivity is completely granulose, the cephalic horn is reduced to a short point or in some cases slightly bifid and the pronotal carina is reduced becoming slightly sinuous lacking the projections or any serrations.

**Other material examined (28♂♂ 13♀♀):**

**BURKINA FASO:** NORD: Touffé (13°53'N, 1°57'W), viii.2005, local collector (1♂ PMOC); SAHEL: Gorom-Gorom, Essakane, 264m (14°23'N, 0°06'E), 26-27.viii.2012, P. Moretto (1♂ 1♀ PMOC); **CHAD:** LAC: Ngouri (13°38'N, 15°22'E), x-xi.1958, P. Renaud (1♂ NMPC); N'DJAMENA: Fort Lamy [=N'Djamena] (12°07'N, 15°03'E), M. André (1♂ MNHL; 1♂ PMOC); **MALI:** KOULIKORO: Nara (15°10'N, 7°17'W), 1918, R. Chuudeau (1♂ MNHN); **MAURITANIA:** GUIDIMAKA: Region du Guidimaka (15°14'N, 12°15'W), 1908, G. Audan (1♂ MNHN); NOUAKCHOTT: Nouakchott (18°05'N, 15°58'W), x-xi.1966 (1♂ NMB); **NIGER:** AGADEZ: Tatei (15°11'N, 9°31'E), 1912, R. Chuudeau (1♂ MNHN); MARADI: entre Maradi et Gona Aja (13°48'N, 7°46'E), 2.vii.1980, P. Leblanc (1♂ MHNL); ZINDER: entre Guezzan et le Chad (15°00'N, 11°00'E), Mission Transaharienne (1♀ MNHN); TILLABÉRI: Tillabéri (14°12'N, 1°27'E), 18.xi.1972 (1♀ NMB); **NIGERIA:** BORNO: Maiduguri (11°50'N, 13°07'E), 1948-1949, Mrs Newman (1♀ BMNH); **SENEGAL:** [no precise locality] (1♂ 1♀ ZMHB); [no precise locality] (1♀ MTD); [no precise locality] (1♂ BMNH); [no precise locality] (2♂♂ 1♀ IRSNB); DIOURBEL: Region de Djourbel [=Diourbel] (14°39'N, 16°14'W), 1930, Trochain (1♀ MNHN); M'Bambey [=Bambey] (14°42'N, 16°27'W), 8.viii.1939, J. Risbec (2♂♂ MRAC); FATICK: Diouroup (14°21'N, 16°32'W), 14-18.viii.2007 (1♂ PMOC); KAOLAK: Nioro du Rip (13°45'N, 15°46'W), 10-11.viii.2009 (1♂ PMOC); KOLDA: Forêt de Bakor (12°55'N, 14°48'W), 31.vii-2.viii.2008, P. Moretto (1♂ PMOC); SAINT-LOUIS: 25-35km S of Richard Toll (16°10'N, 15°41'W), 20.ix.1989, H. van der Valk (2♂♂ RMNH); Richard Toll (16°28'N, 15°41'W), 20.ix.1989, H. van der Valk (1♂ RMNH); Richard Toll (16°28'N, 15°41'W), 15.viii.1991, J. Morati (1♂ 1♀ MHNL); Richard Toll (16°28'N, 15°41'W), 7-9.viii.1995, P. Moretto (6♂♂ 3♀♀ PMOC); Saint-Louis (16°02'N, 16°29'W), 1906, G. Mélou (1♀ MNHN); THIÈS: Region de Mbour (14°25'N, 16°58'W), vii.1995, P. Moretto (1♂ 2♀♀ MHNL); Mbour (14°25'N, 16°58'W), 3-15.viii.1996, P. Moretto (1♂ 1♀ PMOC); **SUDAN:** EAST DARFUR: El Lait (11°57'N, 27°03'E), 28.vii.1988 (1♂ RMNH); NORTH DARFUR: El Fasher [=Al Fashir] (13°37'N, 25°21'E), 28.ix.1987 (1♀ RMNH); SOUTH DARFUR: Kshalongo (11°56'N, 24°56'E), 8.x.1988 (1♂ RMNH).

**Diagnosis:** see under *C. heros*. A large-bodied species which is easily identified, although generally slightly smaller in size compared to *C. heros* and *C. karlwernerii*.

**Biology:** this species is found along the Sahelian savanna belt and has been collected in pitfall traps and at light. Although likely to have a preference for elephant dung, smaller individuals have been found under cattle dung in Senegal (pers. comm. P. Moretto, 2016). Specimens have been caught between July and November.

**Distribution** (Pl. 28: fig. 8): Senegal, Mauritania, Mali, Burkina Faso, Niger, Nigeria, Chad, Sudan.

## 29. *Catharsius karlweneri* Moretto, 2008

(Pl. 29: figs. 1-8; Pl. 30: fig. 29)

*Catharsius karlweneri* Moretto, 2008: 41.

**Type locality:** “Sagala Hills, Kenya”

**Name-bearing type:** Holotype ♂ in PMOC:

“// KENYA XII.93 / Sagala Hills / Werner leg. // HOLOTYPE / *Catharsius* / *karlweneri* n.sp. / P.Moretto det. 2008 [red card; partially handwritten] //”

**Redescription:** Colour: Black, pubescence brown. **Male** (Pl. 29: figs. 1, 2, 5): **Head:** anterior clypeal edge broadly arcuate, with a very slight concavity centrally; clypeal margin continuous; clypeal surface transversely rugulate centrally, turning more granulose towards the clypeogenal suture; posterior portion behind cephalic horn granulose; genal edge rounded and obtusely angled, surface covered evenly with poorly-formed longitudinal, granules; lateral edge of clypeogenal suture raised into an apical projection at the junction with the margin; suture well defined to base of cephalic horn; cephalic horn stout and straight, wide on basal third with edges converging evenly; horn perpendicular to clypeus in lateral view. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin rounded, lateral margin almost straight. Pronotal disc with transverse carina anteriorly and depressed strongly on each side of the midline; carina forms just above the fovea in lateral view; carina angled obliquely forward to a sharp, forward and upward-pointing projection on each side of the midline, the lateral portion of carina gently sinuous; central portion between the two projections gently sinuous, emarginate medially, with a gentle bow of the carina on either side of the midline. Surface of pronotal disc covered evenly in circular granules; lateral declivity with fovea and surface completely granulose; anterior declivity granulose centrally, the lateral portions with a broad excavation, its surface smooth, extending from the edges of the carina towards the anterior margin but stopped by an area of granulation surrounding the excavation. **Elytra:** quite straight, giving a triangular aspect to the body in rear view; carinate basally; basal portion of elytra with fine alutaceous microsculpture; basolateral portion distinctly bulbous; elytral striae well developed with weak punctures. First elytral interstriae punctured, the other interstriae with fine diagonal wrinkles; epipleural carina well-developed, extending almost the whole length of the elytra,

with a slight notch near the base. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence. **Legs:** protibia tridentate; mesa- and metatibia with a smooth apical margin. Tarsomeres with reddish-brown pubescence. **Aedeagus** (Pl. 29: fig. 7): parameres almost as long as phallobase, curved laterally and pointed at apex. Endophallus with large *lamella copulatrix* in medial region (Pl. 30: fig. 29).

**Female** (Pl. 29. figs. 3, 4, 6): **Head:** anterior clypeal edge evenly arcuate with continuous clypeal margin; clypeal surface transversely rugulate centrally, turning more granulose towards the clypeogenal suture; posterior portion behind cephalic carina granulose; genal edge rounded and almost at right angles, surface covered evenly with poorly-formed longitudinal granules; clypeogenal suture to base of cephalic carina; clypeal carina raised, with four well defined tubercles, the two central tubercles being placed posteriorly to the lateral tubercles; a suture joins the four tubercles together. From the carina extends anteriorly a raised shield-shaped region with well-defined lateral margins. **Pronotum:** anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateroanterior margin rounded, lateral margin gently arcuate. Pronotal disc with transverse carina anteriorly; carina gently arcuate and emarginate centrally, its total length as wide as the distance between the eyes. Surface of pronotal disc covered evenly in circular granules; lateral declivity with fovea and surface completely granulose. Anterior declivity completely granulose. **Elytra:** quite straight, giving a triangular aspect to the body in rear view; carinate basally; basal portion of elytra with fine alutaceous microsculpture; basolateral portion distinctly bulbous; elytral striae well developed with weak punctures. First elytral interstriae punctured, the other interstriae with fine diagonal wrinkles; epipleural carina well-developed, extending almost the whole length of the elytra, with a slight notch near the base. **Pygidium:** transverse, fully margined, with fine ovaline punctures throughout. **Ventrites:** covered in thick brown pubescence; metasternum with long well-developed sulcus; the first and sixth sternites with long pubescence. **Legs:** protibia tridentate; mesa- and metatibia with a smooth apical margin. First metatarsomere very broad apically, gently arcuate laterally.

**Length:** male 29-40mm; female 29-38mm.

**Variation:** in smaller males the anterior declivity is completely granulose, the cephalic horn is reduced to a short point or in some cases slightly bifid and the pronotal carina is reduced becoming slightly sinuous lacking the projections or any serrations.

**Other material examined** (44♂♂ 40♀♀):

**KENYA:** **KAJIADO:** Amboseli Lodge (2°40'S, 37°17'E), xii.1992, D. Keith (1♀ MHNL); **KILIFI:** Kilifi (3°30'S, 39°55'E), v.1987 (1♀ ZSM); **KITUI:** Mutha (1°48'S, 38°26'E), iv.1969, B. Watulege (5♂♂ 4♀♀ NMK); **KWALE:** Mbungu (4°05'S, 39°23'E), Hauser (1♂ 1♀ ZMHB); **MAKUENI:** Mitoanday [=Mtito Andei] (2°41'S, 38°10'E), 23.xi.1982, Fickler (1♀ ZSM); Mito Andei (2°41'S, 38°10'E), 6.xii.1986, M. & A. Ritchie (1♀ NMK); **TAITA-TAVETA:** Bungule (3°51'S, 38°40'E), 1.xii.2005, E. Vingerhoedt (2♂♂ 1♀ PMOC); Bura (3°27'S, 38°19'E), xii.1991, K. Werner (1♂

JLMC); Bura (3°27'S, 38°19'E), i.1991, Werner (1♀ *paratype*, PMOC; 1♀ JLMC); de Bura à Taveta (3°25'S, 38°00'E), i-iv.1904, C. Alluaud (1♂ MNHN); Kilaguni, Tsavo West National Park (2°54'S, 38°04'E), F. Vieuxgué (4♂♂2♀♀ MHNH); Kilaguni Lodge, Tsavo West National Park, (2°54'S, 38°04'E), xi.1974, Hüdepohl (1♀ ZSM); Ngulia Lodge (3°01'S, 38°13'E), i.1977, D.J. Peason (1♂ 1♀ NMK); Sagala Hills (3°28'S, 38°35'E), xii.1991, Werner (1♂ *paratype*, PMOC); Sagala Hills (3°28'S, 38°35'E), 15-30.i.1993, G. Beinhundner (1♂ *paratype*, PMOC); Sagala Hills (3°28'S, 38°35'E), xii.1993, Werner (*allotype*♀, 1♀ *paratype*, PMOC); Teita [=Taita] (3°22'S, 38°22'E), 1892, F.J. Jackson (1♂ BMNH); Tsavo (3°00'S, 38°28'E), iv.1994, Champanhet (1♀ *paratype*, PMOC); Tsavo National Park (2°45'S, 38°49'E), 28.xi.1988 (2♂ *paratypes*, PMOC); Tsavo National Park (2°45'S, 38°49'E), 24.xii.1970, M. Gorgas (1♀ MHNH); Tsavo National Park, Manyani, 550m (3°06'S, 38°30'E), 30.xii.1972, J. Krikken (1♂ RMNH); Tsavo National Park, Mzinga, 600m (3°21'S, 38°39'E), 27.xii.1972, J. Krikken (1♀ RMNH); Tsavo East National Park (2°45'S, 38°49'E), 8.vi.1972, C. Smeenk (1♂ RMNH); Tsavo East National Park, Aruba Road, 500m (3°21'S, 38°39'E), 28.ix.1974, J. Krikken (1♀ RMNH); Tsavo East National Park, Voi Safari Lodge, 600m (3°21'S, 38°35'E), 1-6.i.1973, J. Krikken (14♂♂ 12♀♀ RMNH); Tsavo East National Park, Voi Safari Lodge, 600m (3°21'S, 38°35'E), 26.xi.1974, J. Krikken & A. van Berge Henegouwen (1♂ 1♀ RMNH); Tsavo West National Park, Kilaguni, 800m (2°54'S, 38°04'E), 8.xii.1975, C.F. Dewhurst (2♂♂ 3♀♀ SANC); Voi (3°24'S, 38°33'E), 30.xi.1972, C. Smeenk (1♂ 3♀♀ RMNH); Voi (3°24'S, 38°33'E), 5.xii.1972, C. Smeenk (1♂ RMNH); Voi (3°24'S, 38°33'E), 13.iv.1988, P. Dauguet (1♂ *paratype*, PMOC); Voi (3°24'S, 38°33'E), xii.1991, K. Werner (1♂ 1♀ MHNH; 2♂♂ JLMC); Voi (3°24'S, 38°33'E), 3-4.xii.1996, K. Werner & R. Lizler (1♂ *paratype*, PMOC); Voi (3°24'S, 38°33'E), i.1993, Werner (1♀ *paratype*, PMOC); Voi (3°24'S, 38°33'E), i.1993 (1♂ 1♀ *paratypes*, IRSNB); Voi (3°24'S, 38°33'E), 23.xi.1997, M. Snižek (1♂ 1♀ NMPC); near Voi (3°24'S, 38°33'E), xi.1992, K. Werner (1♂ *paratype*, PMOC); TANA RIVER: Galana Game Ranch, Lali Hills area, 250m (3°01'S, 39°16'E), 2-3.vi.1975, Davis & Dewhurst (1♂ SANC); TANZANIA: KILIMANJARO: 10km N Moshi (3°15'S, 37°20'E), xi.1992, Werner (2♂♂ MHNH).

**Diagnosis:** see under *C. heros*. An unmistakable large-bodied species.

**Biology:** the distribution of this species is centred around the Acacia-Commiphora bushlands of the south-east Kenya and north-eastern Tanzania. It has been collected on or under elephant dung as well as at light. Specimens have been caught between November and June.

**Distribution** (Pl. 29: fig. 8): Kenya, Tanzania.

### Identification key to the Afrotropical species of the *C. molossus* species group

A key to the African species of the *C. molossus* group is provided based on major males with well-developed characters. Minor males can be confidently identified by dissecting the *lamella copulatrix* and females can be determined by association with male specimens or from the descriptions given in the revision. Numbers alongside the species refer to the revision text and plates.

1. Pronotal disc with two large forward-protruding horns anteriorly; anterior declivity with orange-brown pubescence.....22. *C. mirabilis* Felsche
- Pronotal disc carinate anteriorly; anterior declivity without pubescence.....2
2. Pronotal disc with four tubercles along carina anteriorly.....15. *C. ulysses* Boheman
- Pronotal disc without four tubercles along carina anteriorly.....3
3. Pronotal disc with a transverse carina anteriorly.....4
- Pronotal disc with an interrupted carina, curving back on each side following the slope of the anterior declivity.....26. *C. severini* Gillet

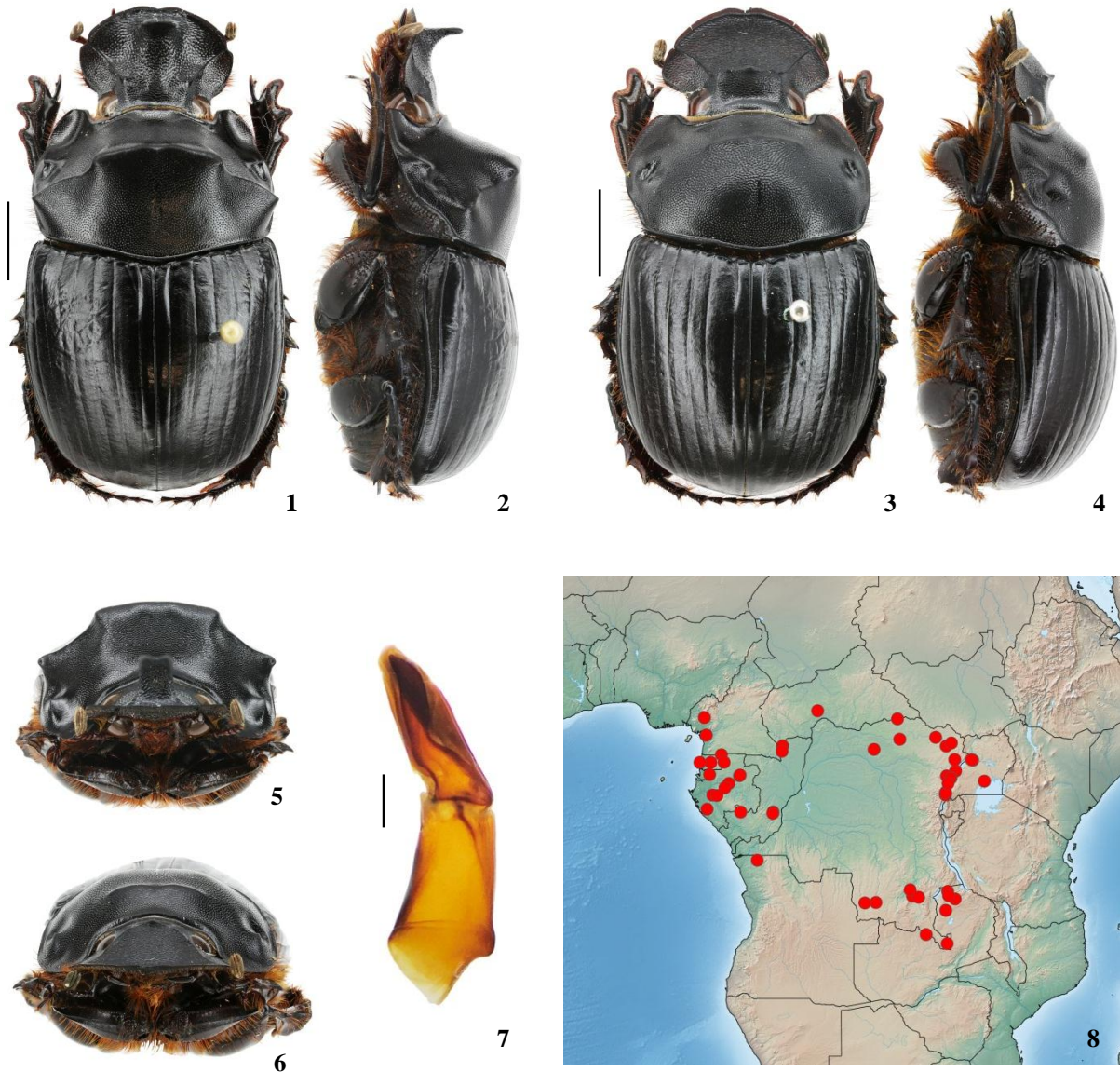
4. Elytra with irregularly-shaped vesicular granules.....7. *C. rhinoceros* (Klug)
  - Elytra without vesicular granules.....5
  
5. lateral edge of clypeogenal suture raised into an apical projection at the junction with the margin .....6
  - lateral edge of clypeogenal suture rounded or emarginate at the junction with the margin .....8
  
6. lateral edges of pronotal carina with short projections.....28. *C. lepinayi* Boucomont
  - pronotal carina with short projections centrally.....7
  
7. pronotal carina emarginate centrally with a gentle bow of the carina on either side of emargination. Distributed in E. Africa.....29. *C. karlwernerii* Moretto
  - pronotal carina weakly emarginate centrally, carina straight either side of the emargination. Distributed in S. Africa.....27. *C. heros* Boheman
  
8. pronotal transverse carina with a distinct obtuse angle between midline and termination point.....9
  - pronotal transverse carina arcuate or triangular without any distinct angles.....15
  
9. pronotal disc completely granulose.....10
  - pronotal disc with large ovaline smooth regions.....12
  
10. cephalic horn short and bidentate; central portion of disc as wide as the distance between the eyes is extended forward.....1. *C. platynotus* Felsche
  - cephalic horn apically sharp or rounded; pronotal disc not extended forward centrally.....11
  
11. lateral edges of pronotal carina with short projections; elytral interstriae with uneven punctures and some alutaceous microsculpture.....19. *C. achates* (Olivier)
  - lateral edges of pronotal carina without projections; elytral interstriae with deep punctures throughout and alutaceous microsculpture.....14. *C. adamastor* Gillet
  
12. lateroanterior angle of pronotum obtuse.....13
  - lateroanterior angle of pronotum rounded.....14
  
13. width of pronotal carina considerably wider than the widest point of the lateral pronotal margin; the first mesa- and metatarsomeres very broad apically.....18. *C. bradshawi* Lansberge

- width of pronotal carina no wider than the widest point of the lateral pronotal margin; no broadening of the mesa- and metatarsomeres.....20. *C. polynices* Kolbe
  
- 14. anterior declivity completely granulose.....17. *C. thersander* sp. nov.
- anterior declivity granulose except for a “M” shaped smooth region basally as wide as the distance between the eyes and extending halfway up the anterior declivity.....  
.....16. *C. telemachus* sp. nov.
  
- 15. anterior declivity with distinct depression under carina one third of the distance from the midline to the edge of the carina.....16
- anterior declivity without depression under the carina.....18
  
- 16. lateral margin of pronotum concave.....4. *C. gorilloides* Felsche
- lateral margin of pronotum convex.....17
  
- 17. lateroposterior edge of pronotal disc at 45° to the posterior margin; distributed in C. Africa (east of the Dahomey Gap).....5. *C. gorilla* (Thomson)
- lateroposterior edge of pronotal disc less than 45° to the posterior margin; distributed in W. Africa (west of the Dahomey Gap).....6. *C. leo* sp. nov.
  
- 18. pronotal carina broadly arcuate.....19
- pronotal carina triangular.....22
  
- 19. lateroanterior angle of pronotum angled.....20
- lateroanterior angle of pronotum rounded.....21
  
- 20. elytral interstriae smooth with the occasional fine puncture; protibia tridentate .....  
.....23. *C. princeps* Kolbe
- elytral interstriae rugose with some alutaceous microsculpture; protibia quadridentate.....  
.....21. *C. juheli* Josso
  
- 21. elytra with a triangular aspect in rear view; distributed in W. Africa.....25. *C. genieri* Moretto
- elytra with a rounded aspect in rear view; distributed in S. & E. Africa.....  
.....24. *C. obtusicornis* Boheman

22. genae parallel sided in dorsal view; pronotal margin interrupted medially; anterior declivity almost perpendicular to the pronotal disc in lateral view.....23  
 – genae rounded in dorsal view; pronotal margin complete; anterior declivity sloped forward in lateral view.....24
23. anterior declivity with a large “V” shaped depression.....2. *C. gibbicollis* Gerstaecker  
 – anterior declivity without depression.....3. *C. chinai* Ferreira
24. protibia tridentate.....13. *C. hertli* Ferreira  
 – protibia quadridentate.....25
25. lateral margin of pronotum with a small fold raised apically, half way along the length of the margin.....26  
 – lateral margin of pronotum without an interruption; pronotal carina with angular projection one third of the way along from the midline.....28
26. large triangular cephalic horn.....27  
 – cephalic horn miniscule and tubercular.....10. *C. duciformis* Ferreira
27. cephalic horn laterally flattened and basally broad; distributed south of the Congo basin and west of the Lualaba.....9. *C. dux* Harold  
 – cephalic horn, narrow, parallel-sided and apically pointed; distributed north of the Congo basin.....8. *C. dominus* sp. nov.
28. margin of clypeus rounded; cephalic horn laterally flattened and bifid.....12. *C. satyrus* Kolbe  
 – margin of clypeus angled; cephalic horn short, conical and pointed.....11. *C. spectabilis* Gillet

PLATE 1

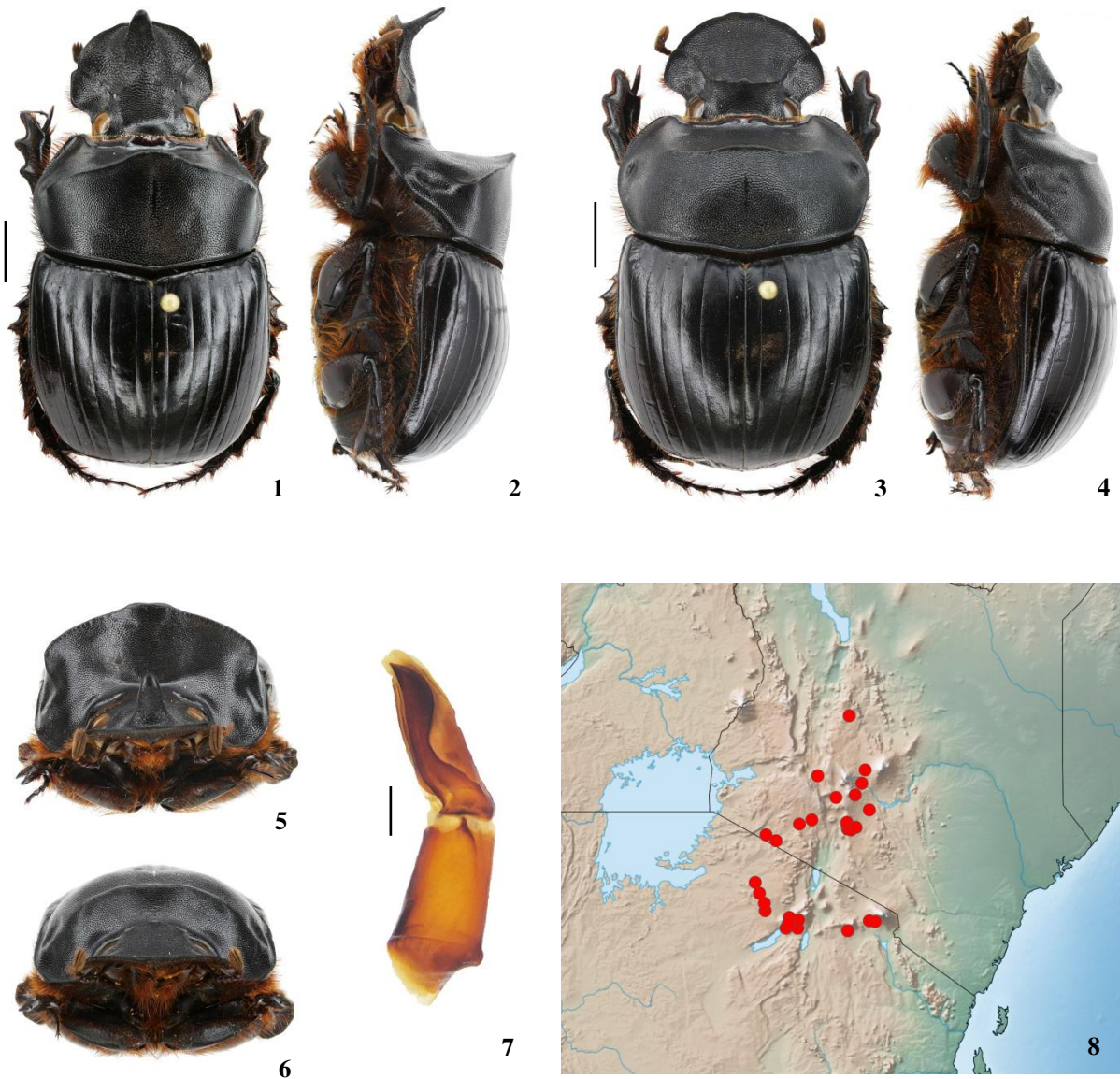
*Catharsius platynotus* Felsche, 1907



**Male** - Uganda, Toro, xi.1905, Lady Jackson (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 2

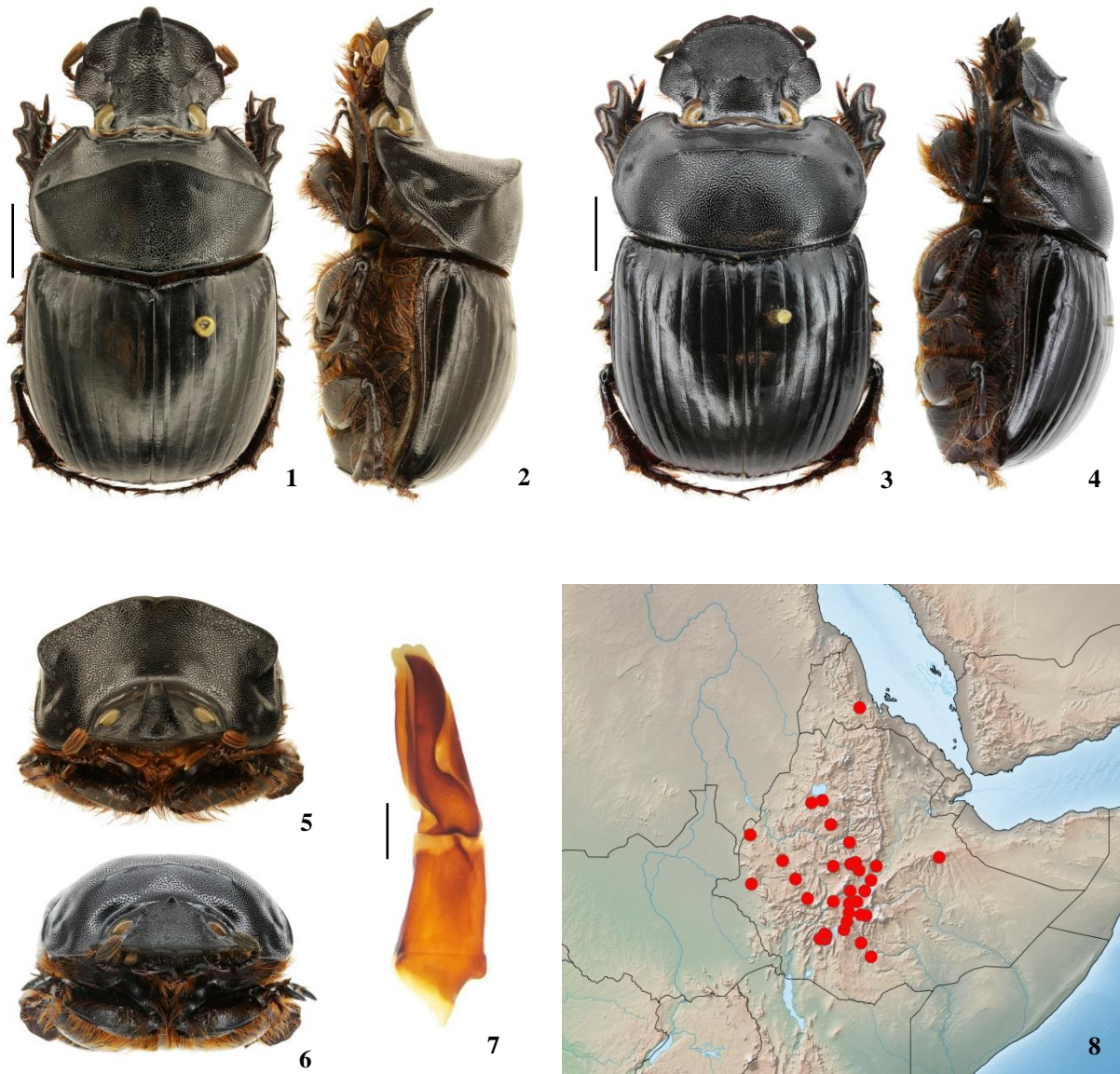
*Catharsius gibbicollis* Gerstaecker, 1884



**Male** - Tanzania, Simba Camp, Ngorongoro Crater, 2319m, 12-14.iv.2012, R. Smith & H. Takano (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 3

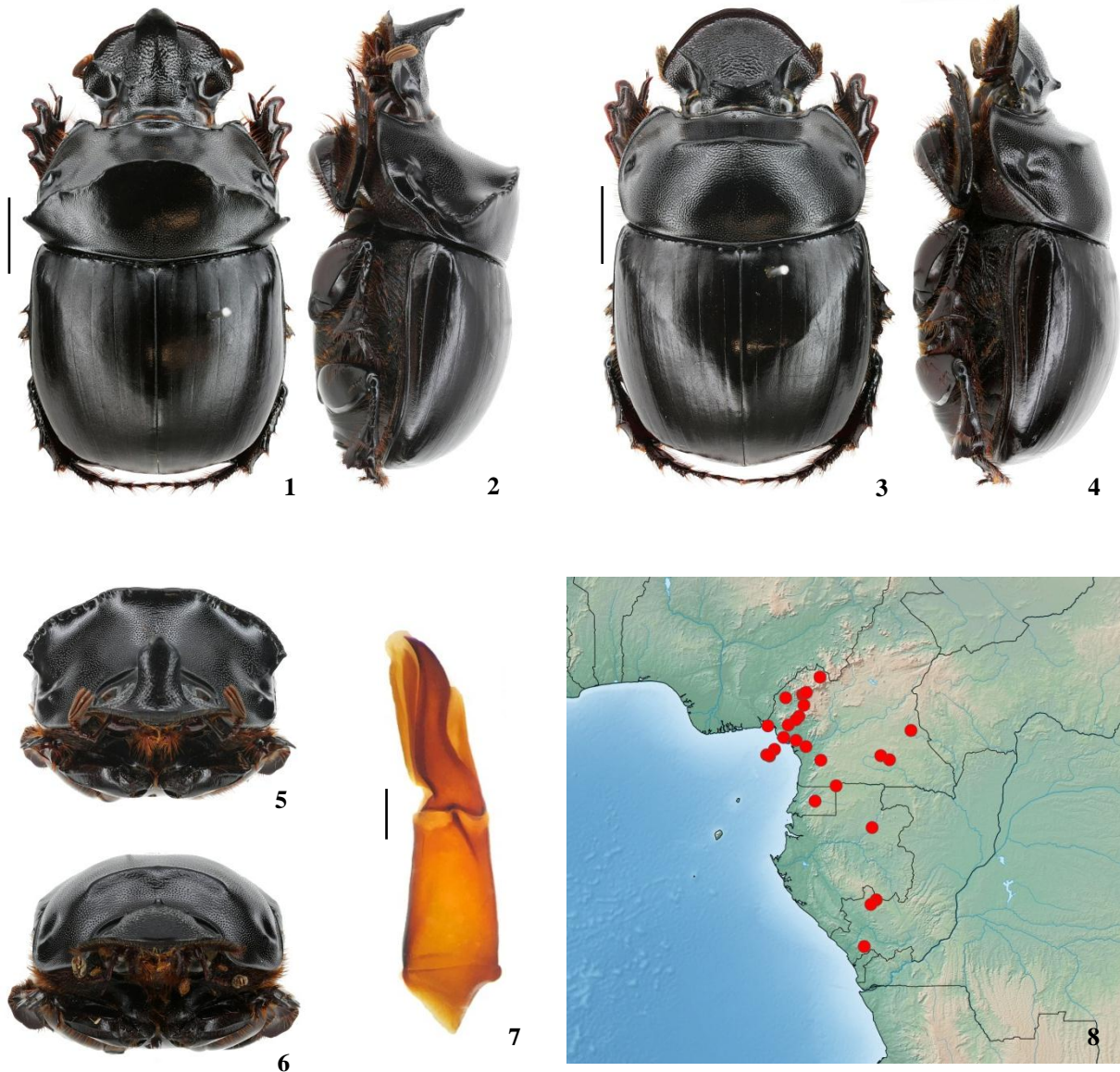
*Catharsius chinai* Ferreira, 1960



**Male** - Ethiopia, Hosaena, 2300m, 28.v.1974, G. de Rougemont (MRAC): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - Ethiopia, [no precise locality], A. Raffray (BMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 4

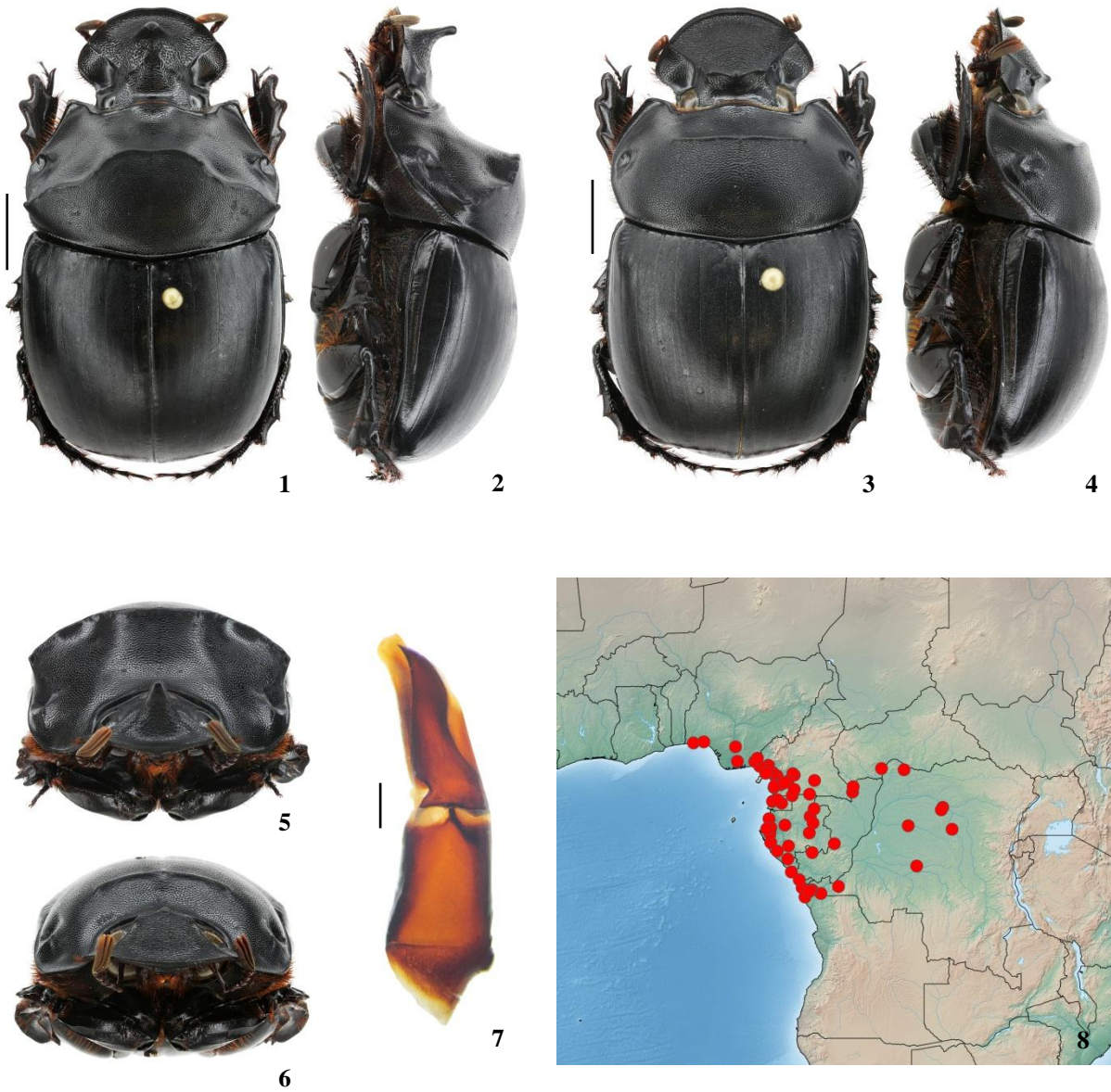
*Catharsius gorilloides* Felsche, 1907



**Male** - Cameroon, Baliland, Lübeck (ZMHB): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus;  
**Female** - Cameroon, Edea (ZMHB): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 5

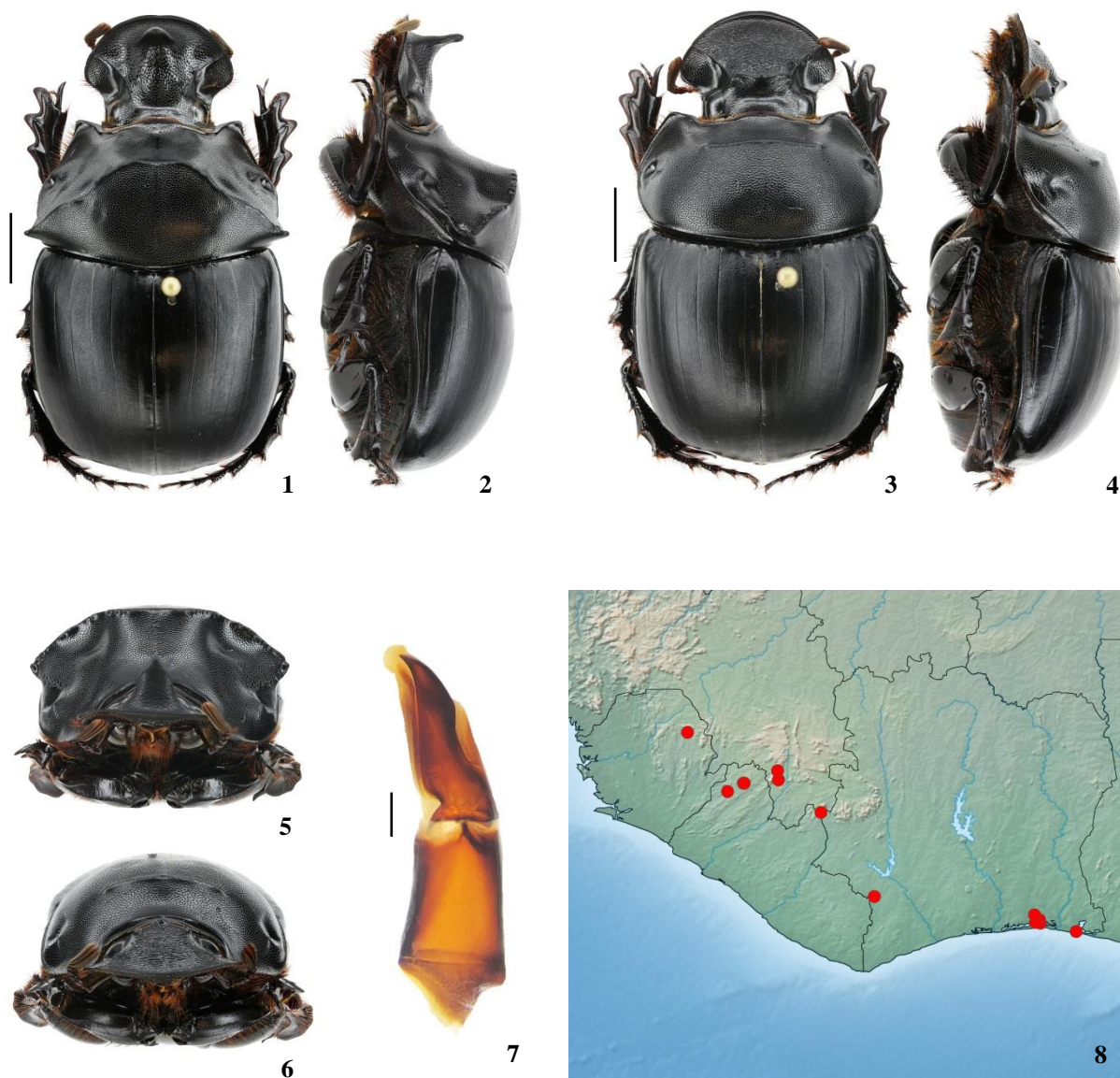
*Catharsius gorilla* (Thomson, 1858)



**Male** - Central African Republic, Parc National Ndoki, Camp 1, 13.ii-6.iii.2002, P. Moretto & A. Monziagou (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 6

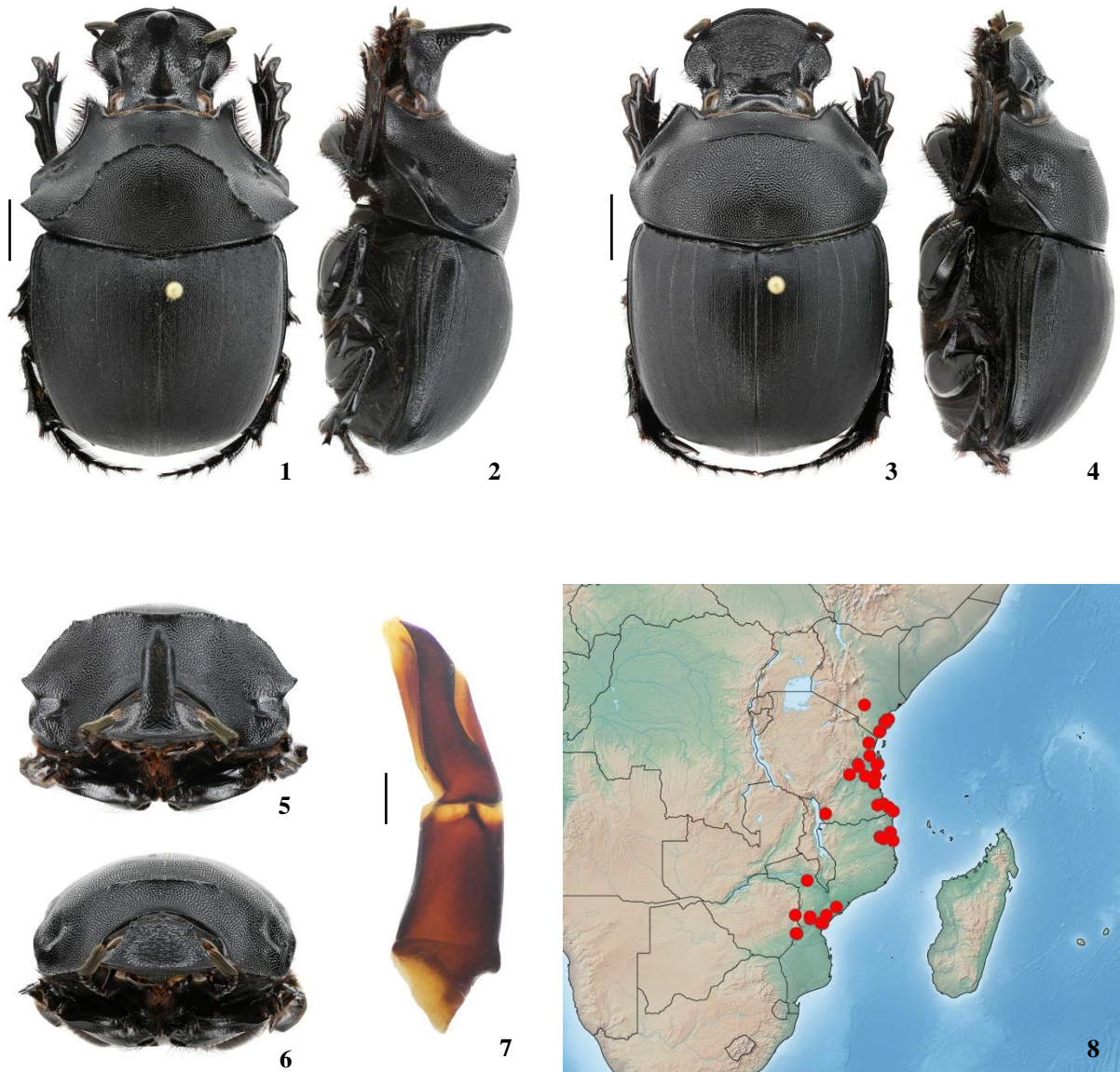
*Catharsius leo* sp. nov.



**Male holotype** - Sierra Leone, Loma Mountains, farmland/forest mosaic, 11-15.vi.2016, Takano, Miles & Goff (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female paratype**: Ivory Coast, Parc National du Banco, Banco Forest, 39-48m, 23-30.iv.2017, A. Aristophanous, M. Aristophanous, M. Geiser & P. Moretto (BMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 7

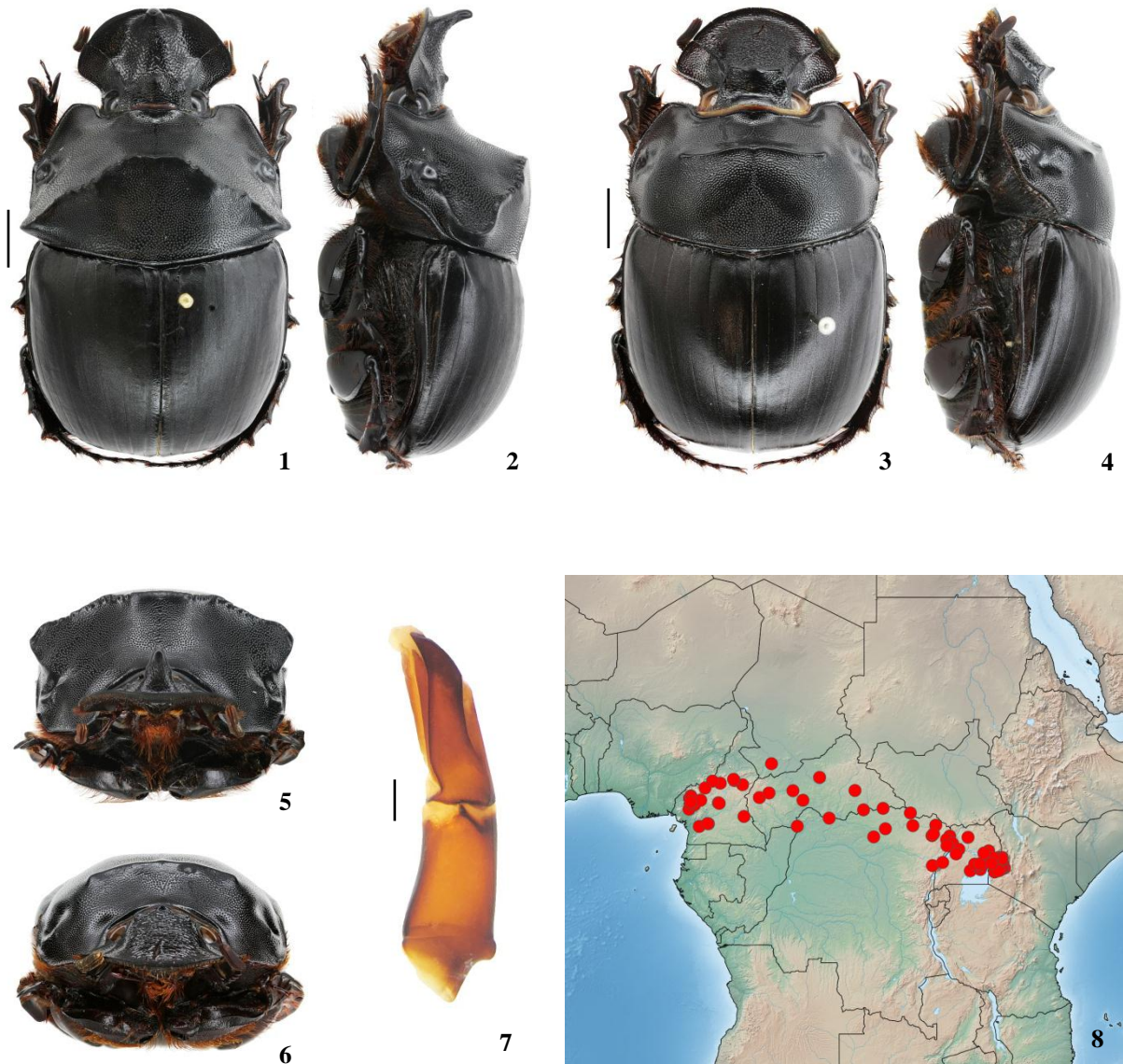
*Catharsius rhinoceros* (Klug, 1855)



**Male** - Tanzania, Rufiji, 150m, ii.2015, local collectors (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 8

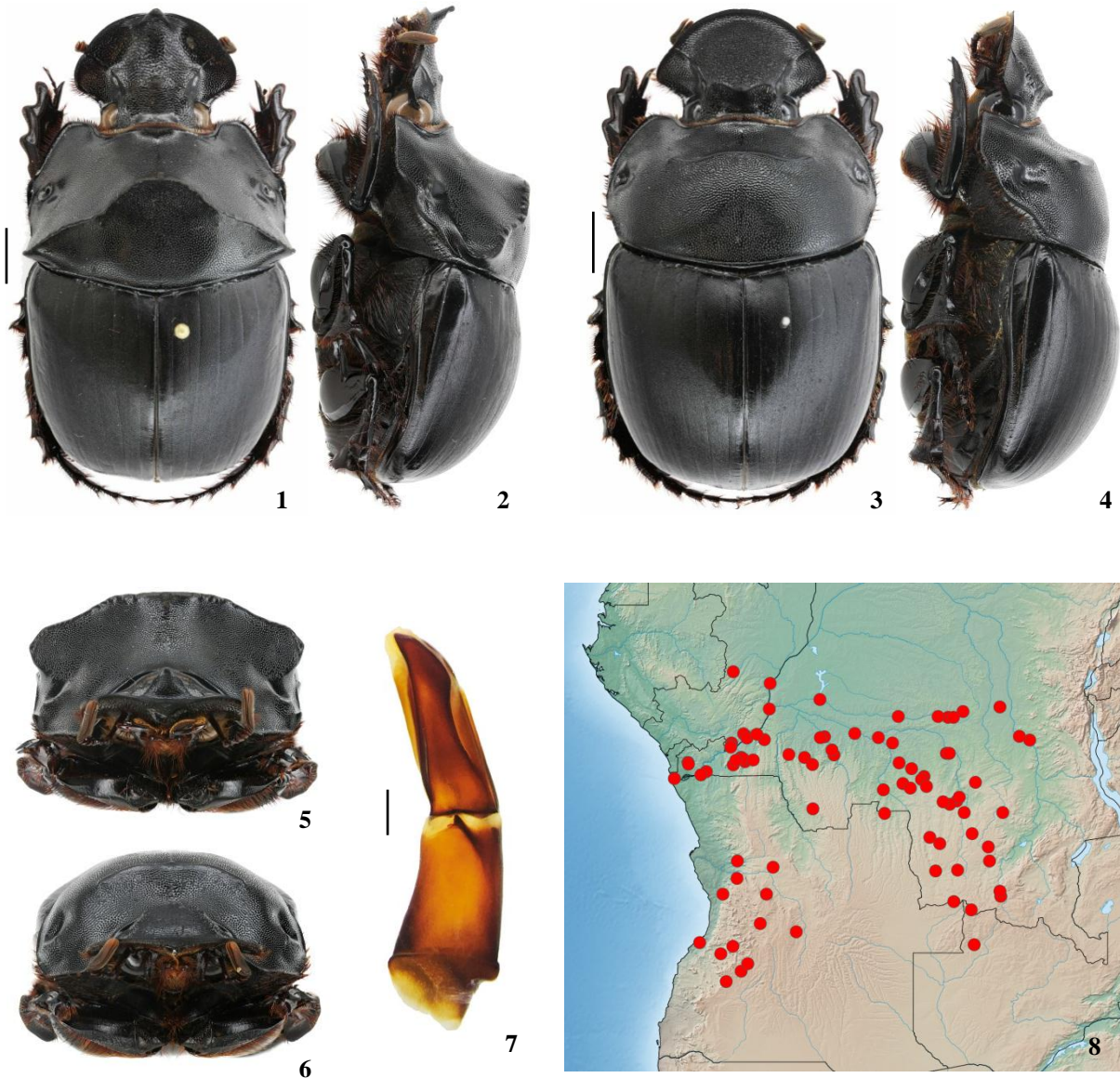
*Catharsius dominus* sp. nov.



**Male holotype** - Uganda, Mbale-Kumi Road, 3700ft., 15-17.viii.1911, S.A. Neave (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female paratype** - Cameroon, Babua, 4.v.1914 (BMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 9

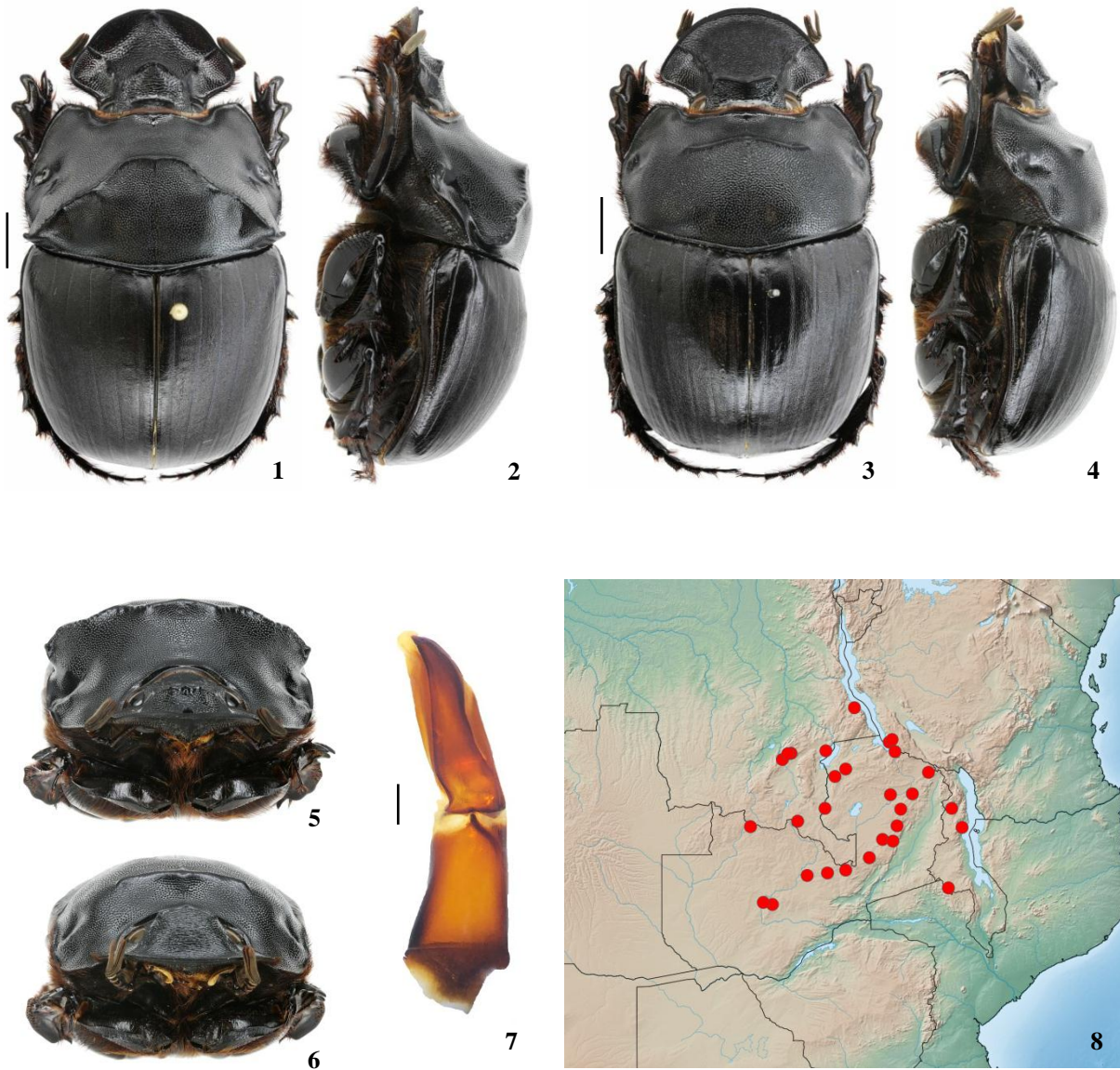
*Catharsius dux* Harold, 1878



**Male** - Angola, Catabola, 15-25.xi.2012, T. Lackner (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 10

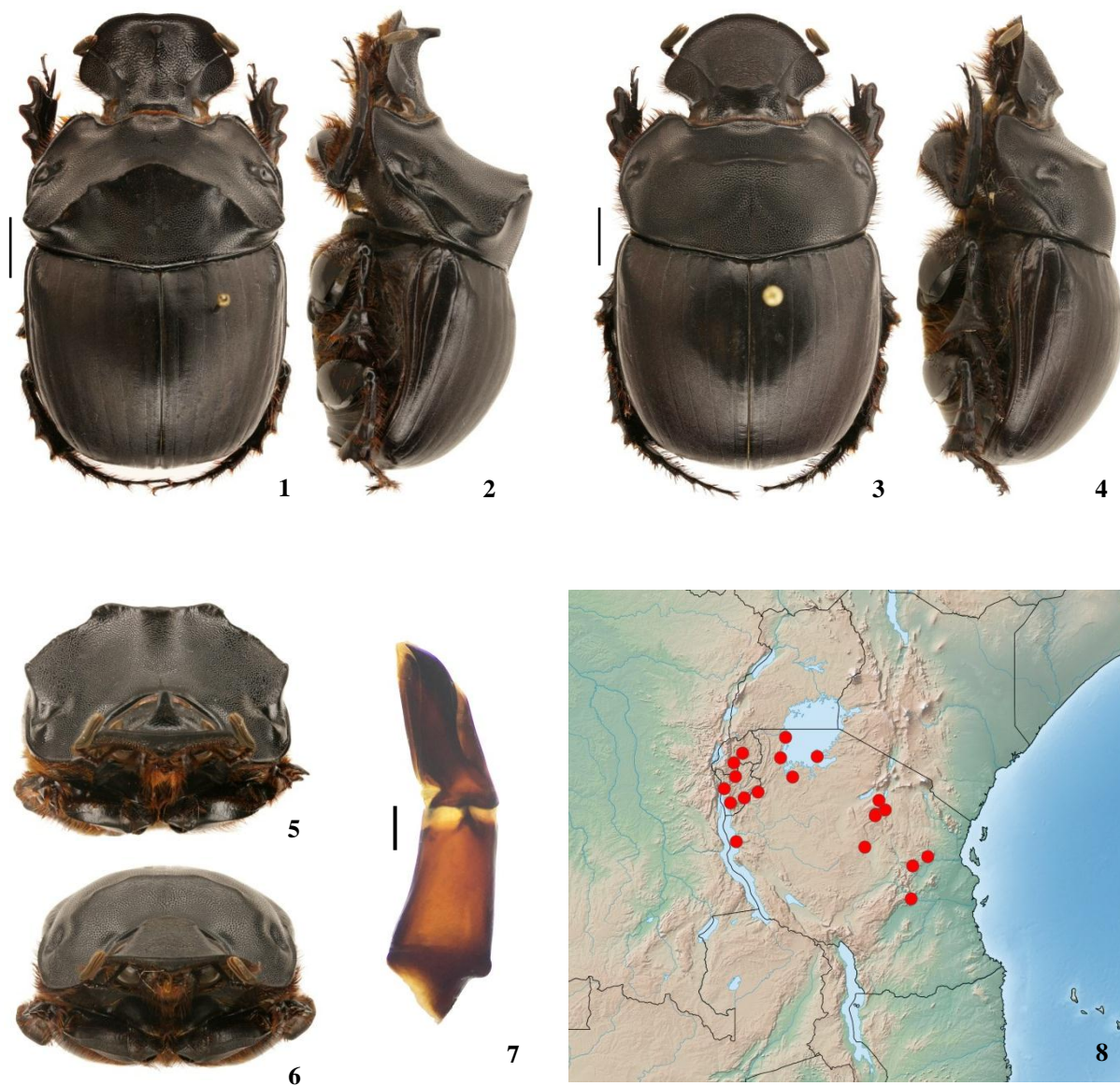
*Catharsius duciformis* Ferreira, 1959



**Male** - Zambia, Kacheleko, Kafue National Park, 1260m, 21-26.xi.2013, R. Smith, H. Takano & D. Oram (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 11

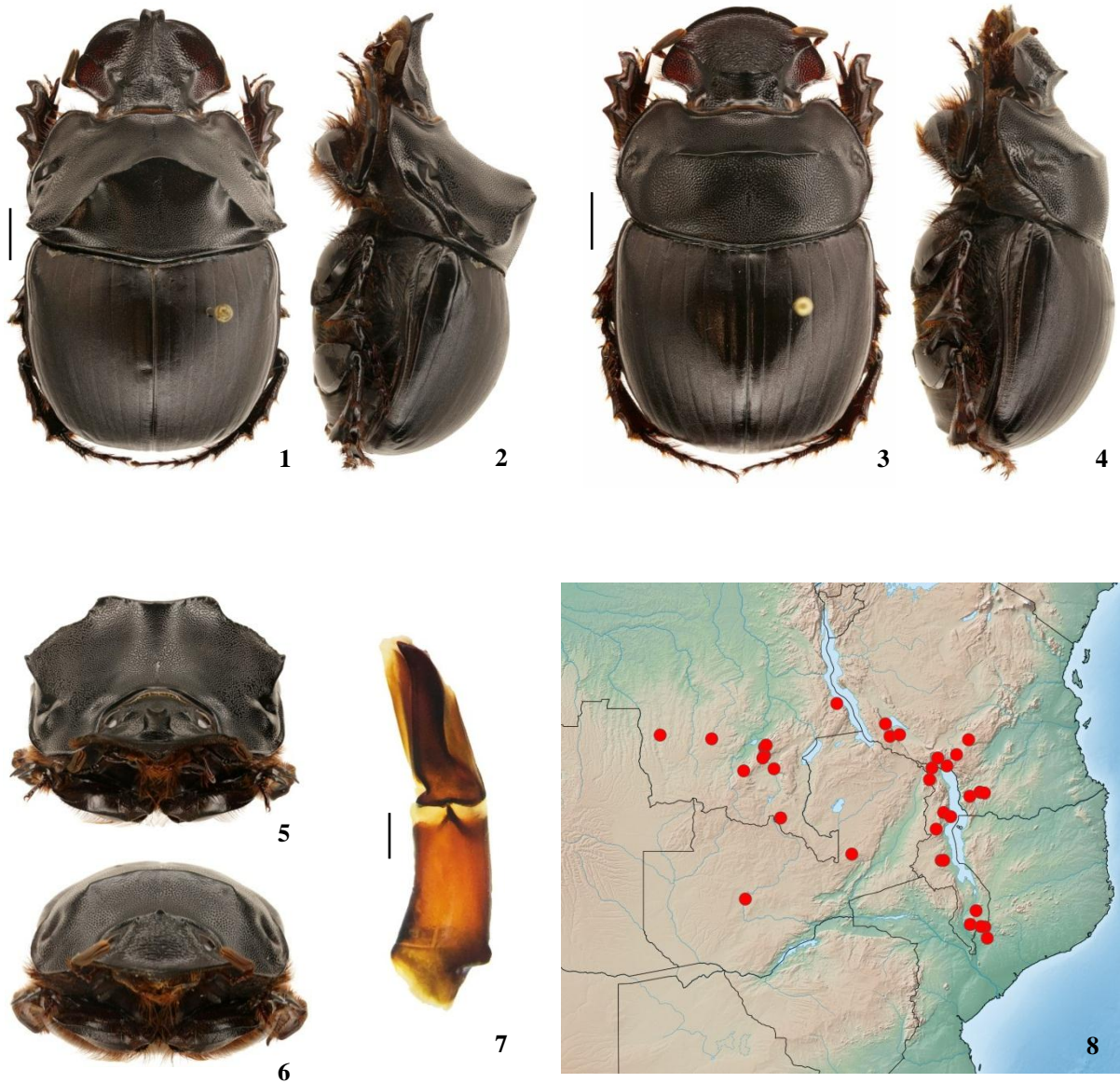
*Catharsius spectabilis* Gillet, 1918



**Male** - Tanzania, Bukoba, i.1913 (ZMHB): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus;  
**Female** - Tanzania, Giting, Mount Hanang, 1964m, 21-24.v.2012, R. Smith & H. Takano (BMNH): 3.  
dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 12

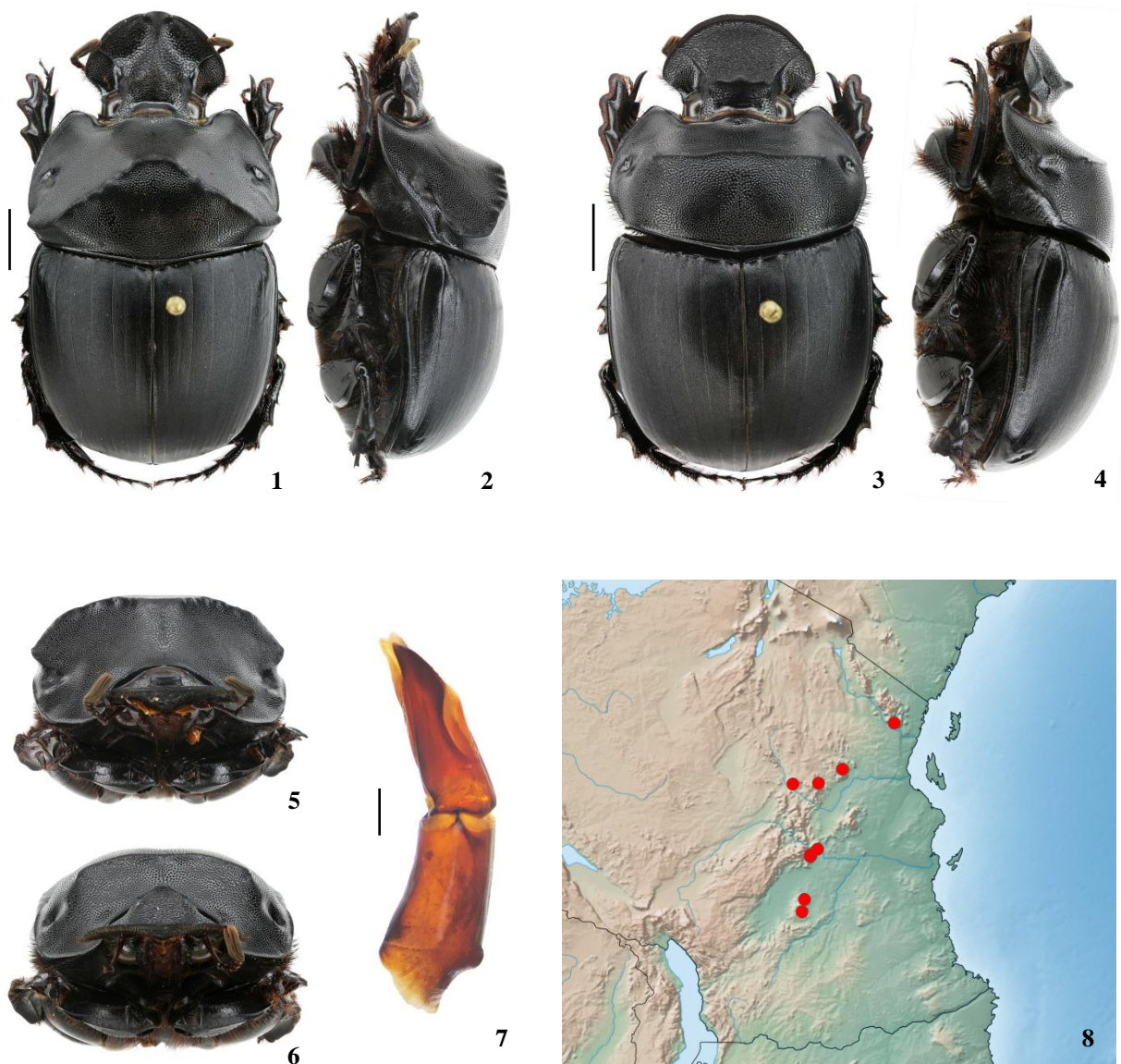
*Catharsius satyrus* Kolbe, 1893



**Male** - Malawi, Mlanje, 17.ii.1913, S.A. Neave (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 13

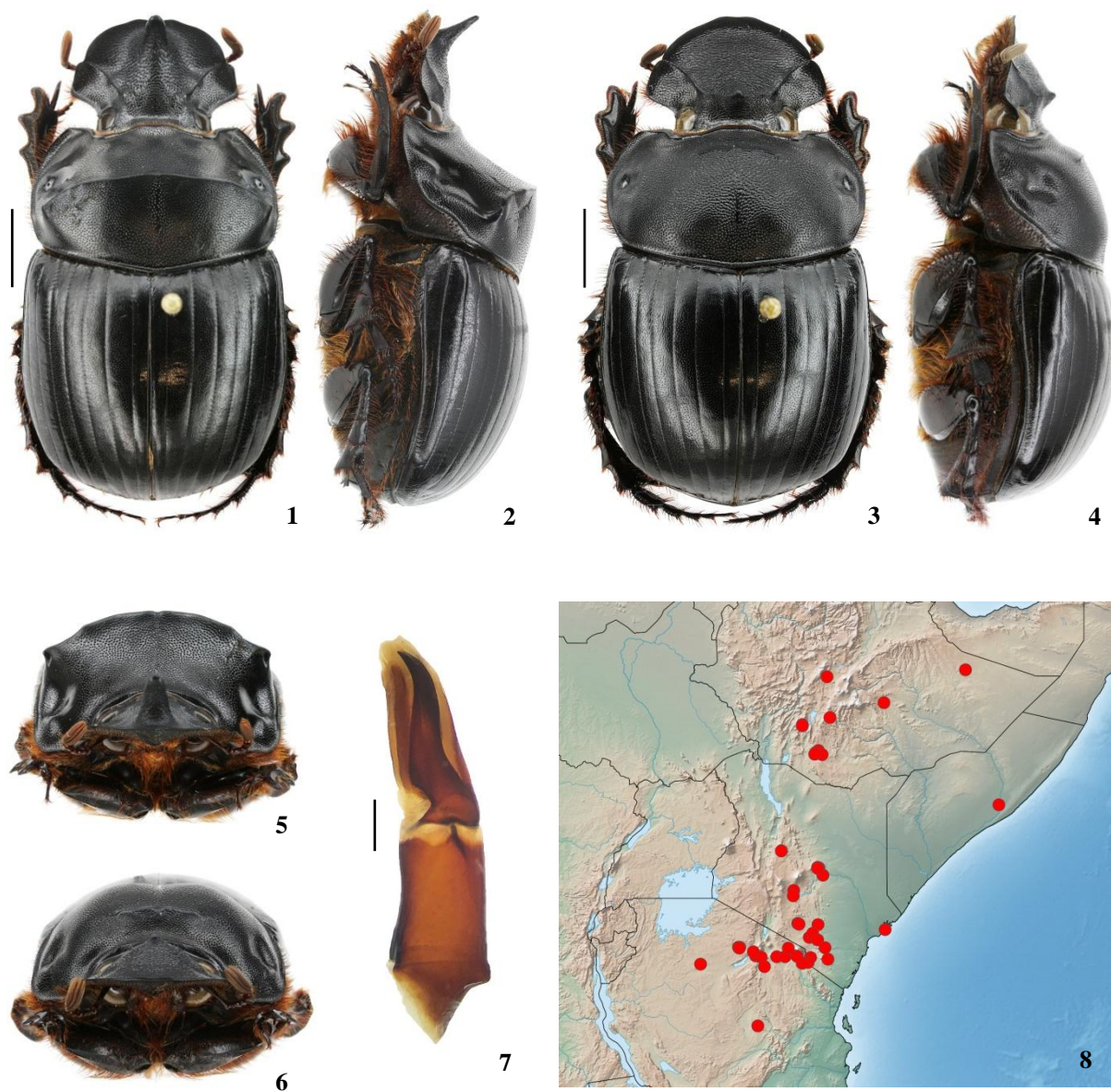
*Catharsius hertli* Ferreira, 1964



**Male** - Tanzania, Njia Panda, Udzungwa Mountains National Park, 970m, 12-14.iv.2011, R. Smith & H. Takano (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - Tanzania, Mwanihana, Udzungwa Mountains National Park, 1350m, 15.iv.2011, R. Smith & H. Takano (BMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 14

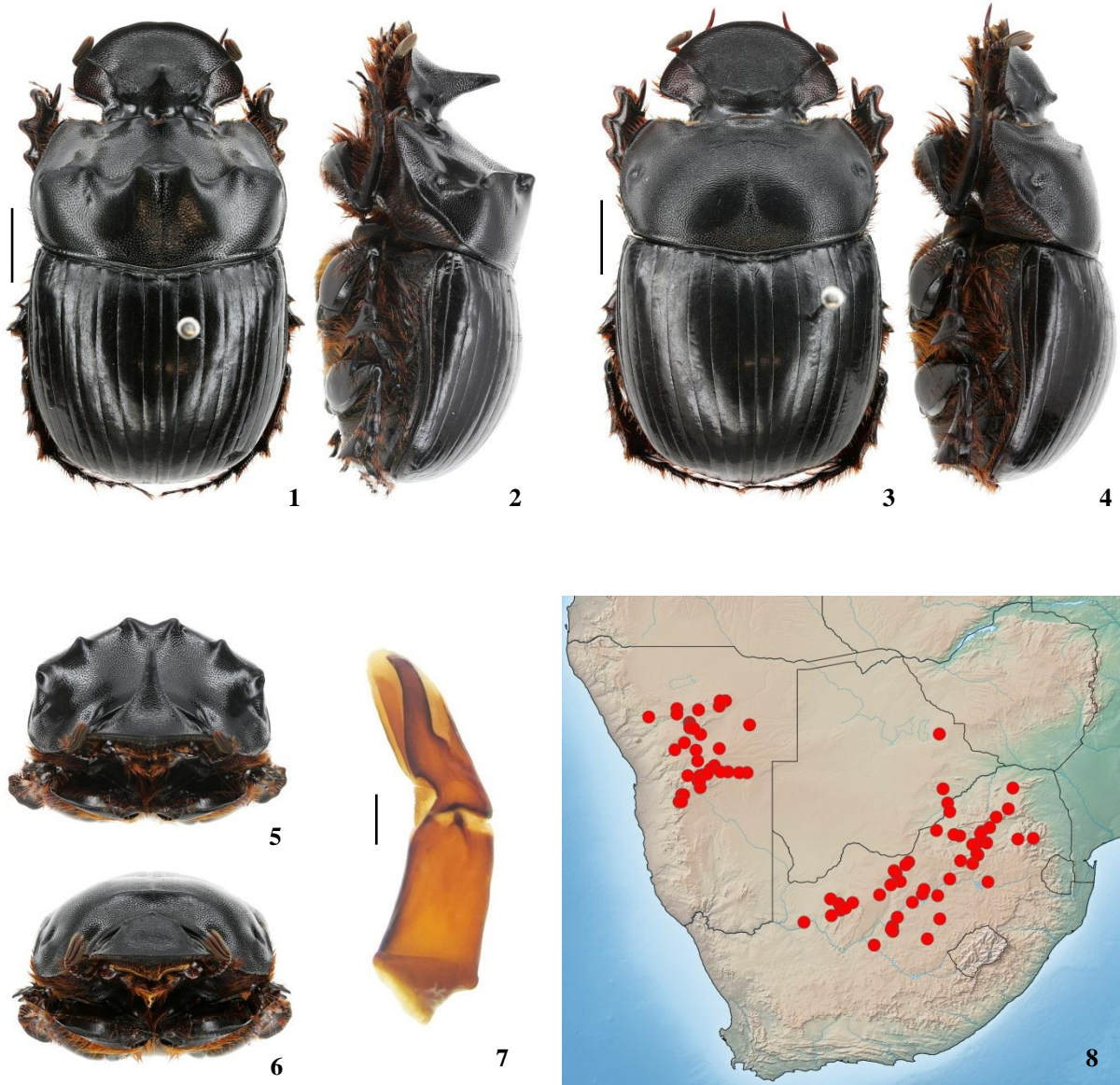
*Catharsius adamastor* Gillet, 1932



**Male** - Tanzania, Ndarakwai, 1310m, 5-7.iv.2012, R. Smith & H. Takano (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - Tanzania, Mto wa Mbu, 963m, 21.x.2011, R. Smith & H. Takano (BMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 15

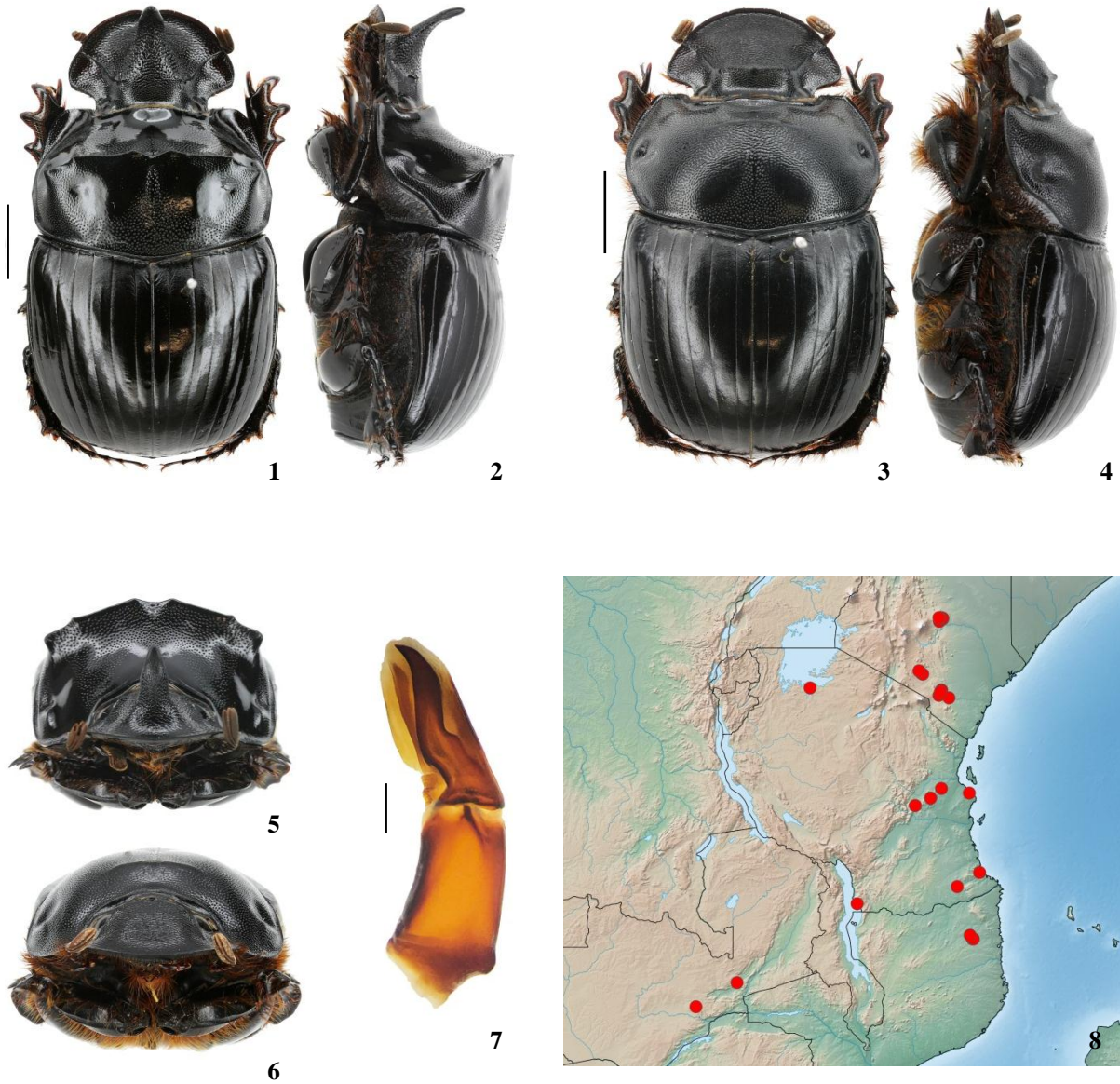
*Catharsius ulysses* Boheman, 1857



**Male** - South Africa, 60km NW Buffelsdoorn, 13.i.1974, L. Pitsi (SANC): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - Namibia, 46km SW Otavi, 12.ii.1974, Davis & Kirsten (SANC): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 16

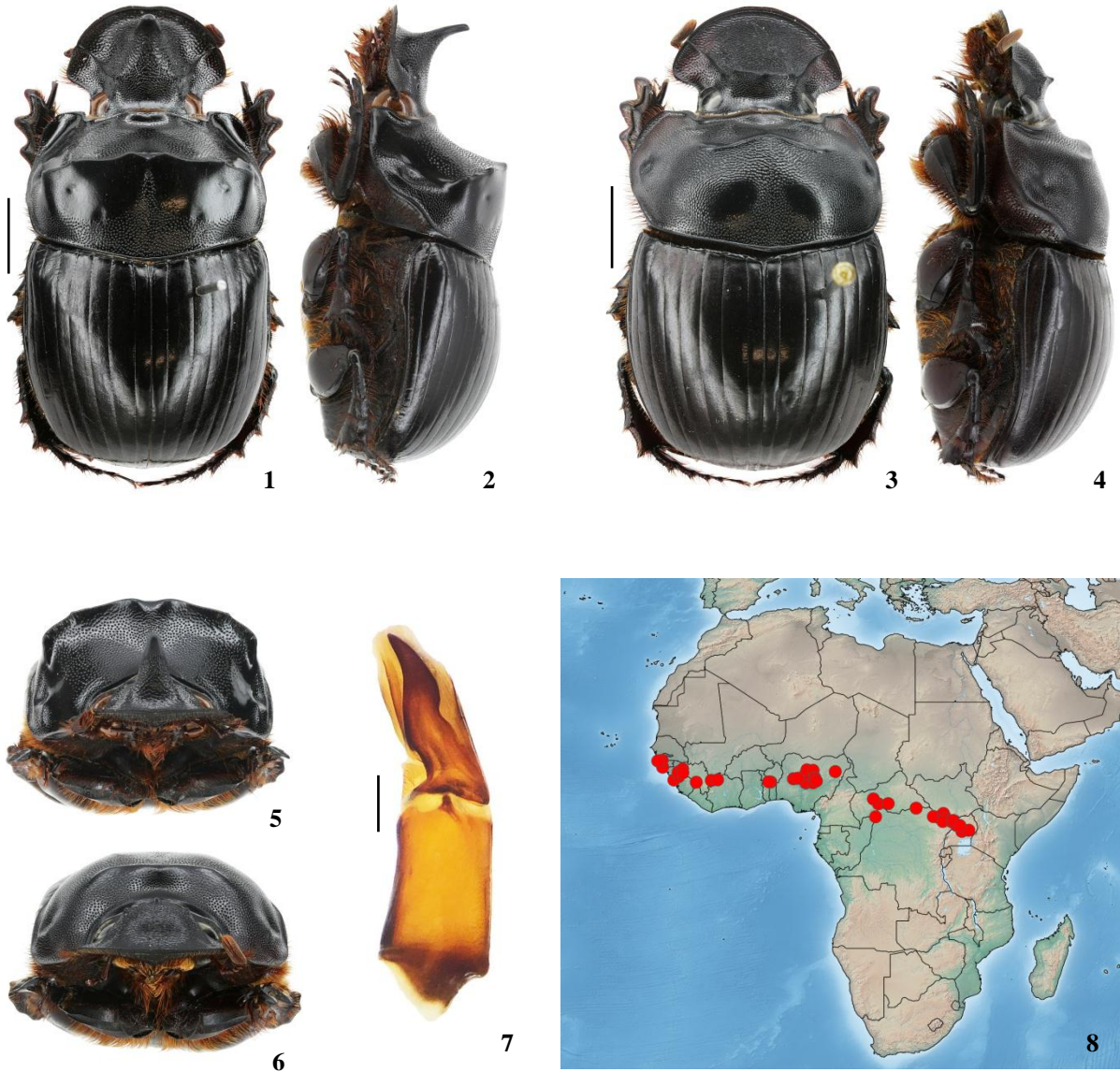
*Catharsius telemachus* sp. nov.



**Male holotype:** Tanzania, Dar es Salaam (ZMHB): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female paratype:** Kenya, Meru National Park, Mulika Lodge, 700m, 9.iv.1981, J. Krikken (RMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map:** 8.

PLATE 17

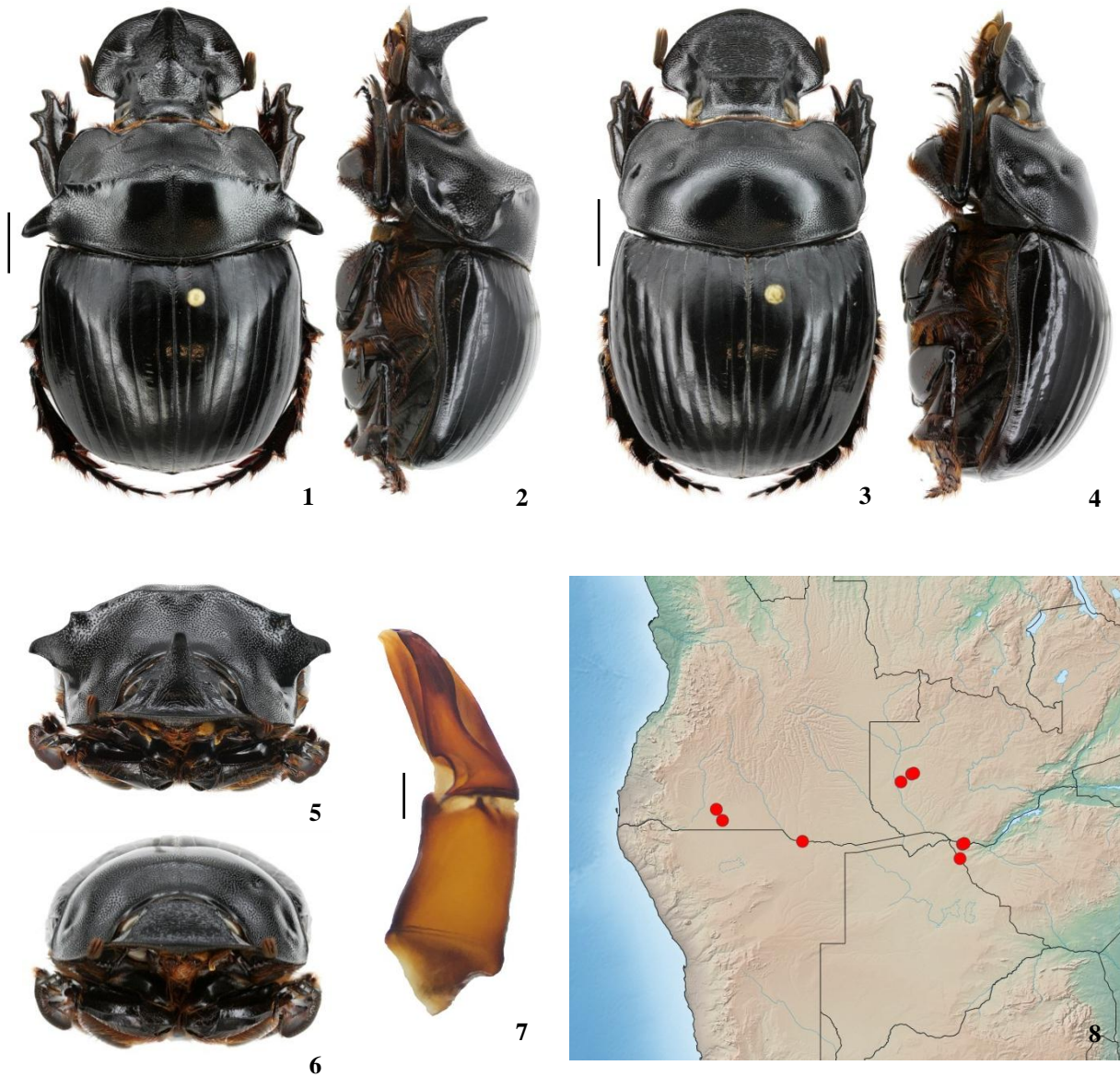
*Catharsius thersander* sp. nov.



**Male holotype** - Uganda, Entebbe, F.J. Jackson (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female paratype** - Nigeria, Samaru, 7.ix.1969, P.H. Ward (BMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 18

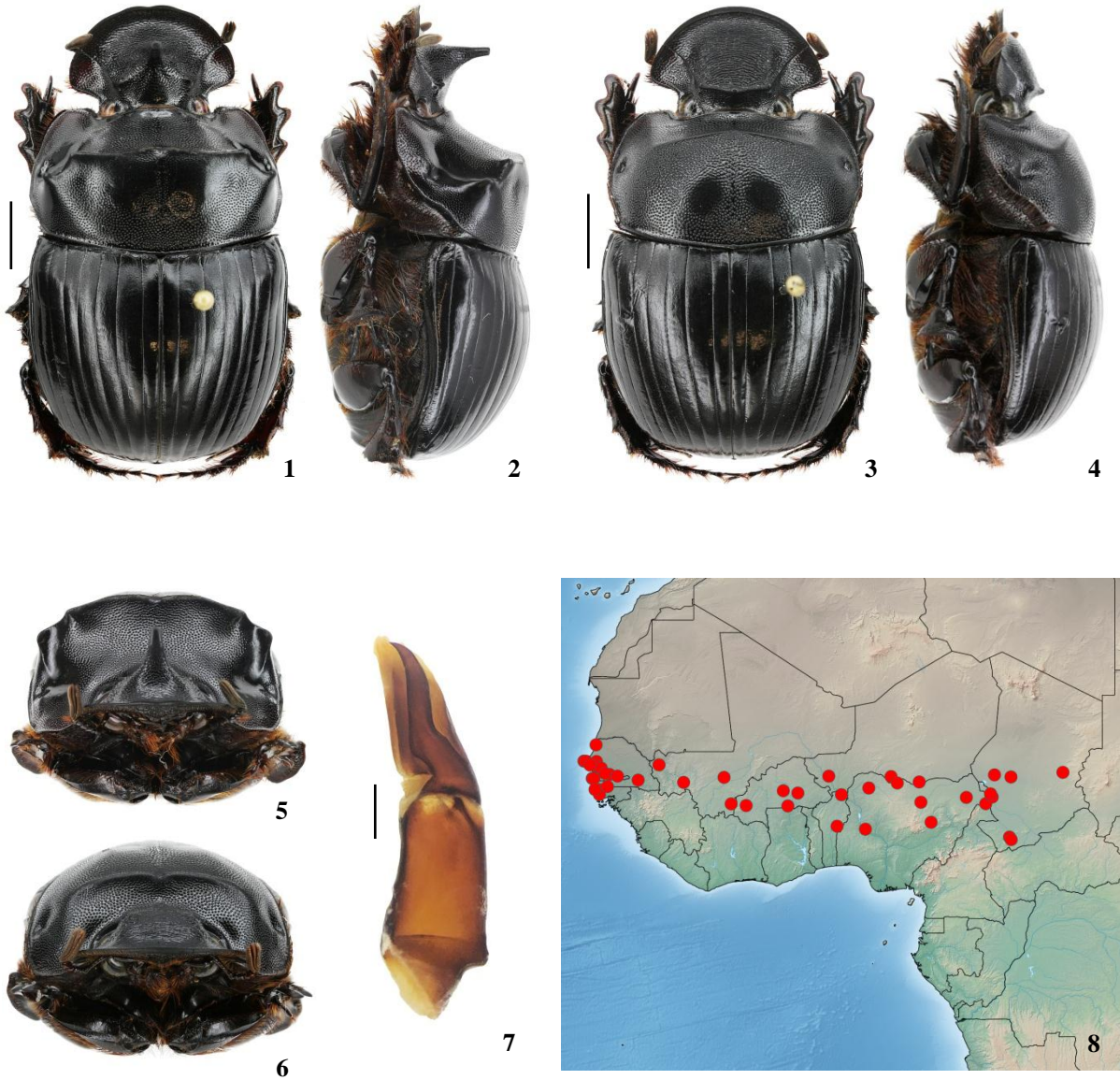
*Catharsius bradshawi* Lansberge, 1887



**Male** - Zambia, Ndanda, 1090m, 10-11.xi.2013, R. Smith, H. Takano & D. Oram (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 19

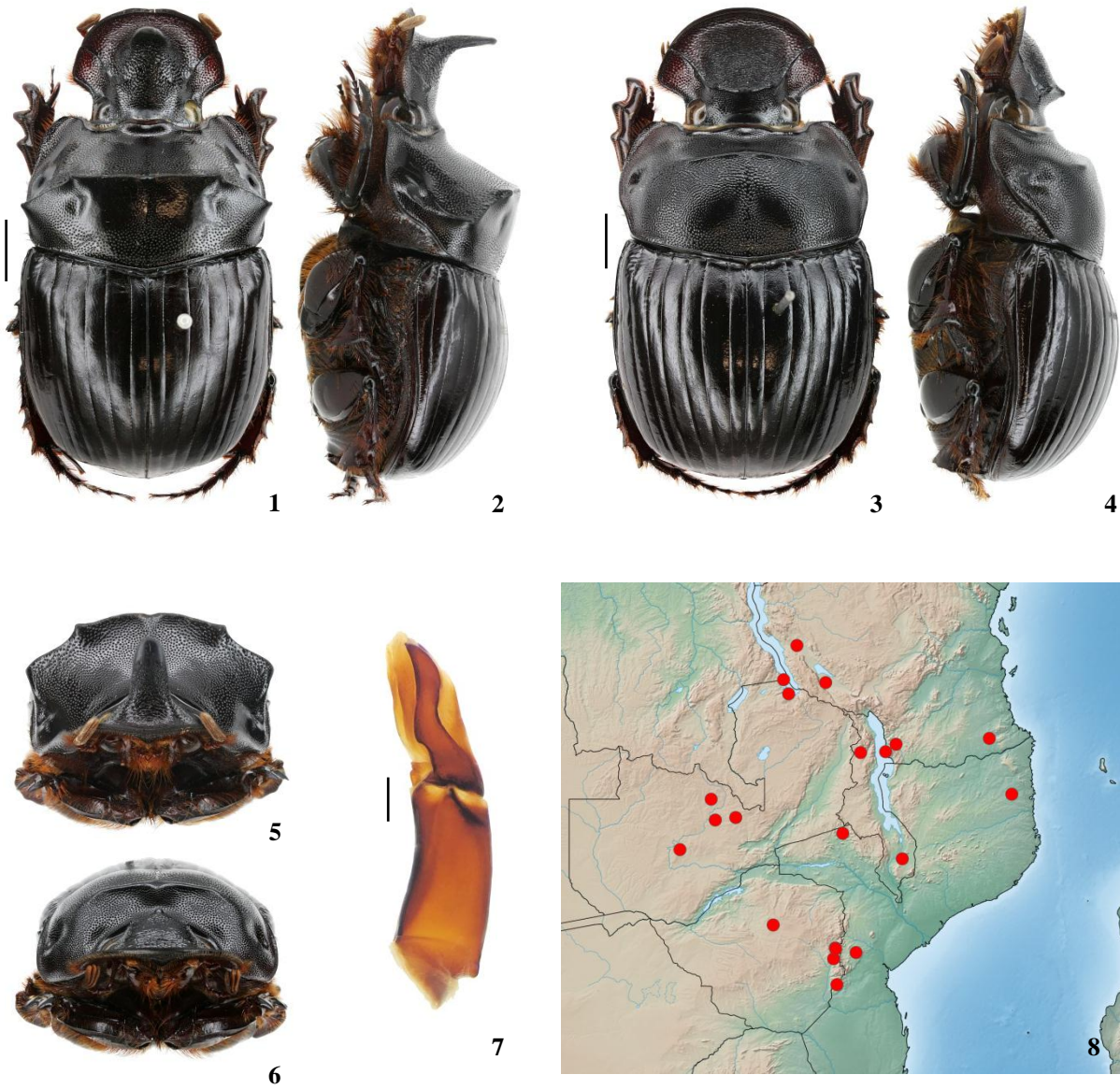
*Catharsius achates* (Olivier, 1789)



**Male** - Chad, Fort Lamy, M. André (MHNL): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus;  
**Female** - Burkina Faso, Ouagadougou, 1976, M. Delpont (MHNL): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 20

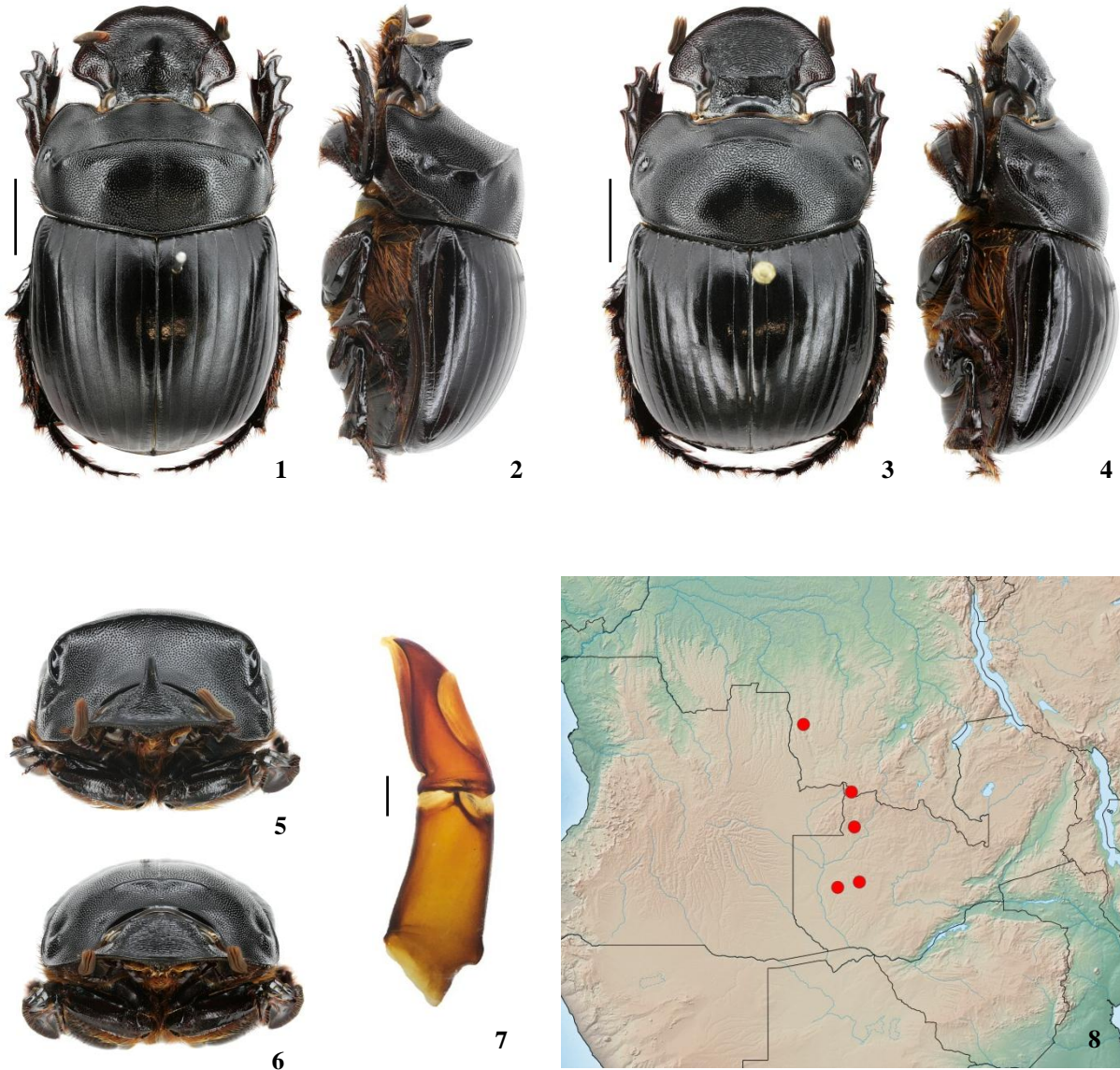
*Catharsius polynices* Kolbe, 1893



**Male** - Zimbabwe, Chirinda, x.1905, G.A.K. Marshall (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - Zimbabwe, Umtali, xi.1895, G.A.K. Marshall (BMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 21

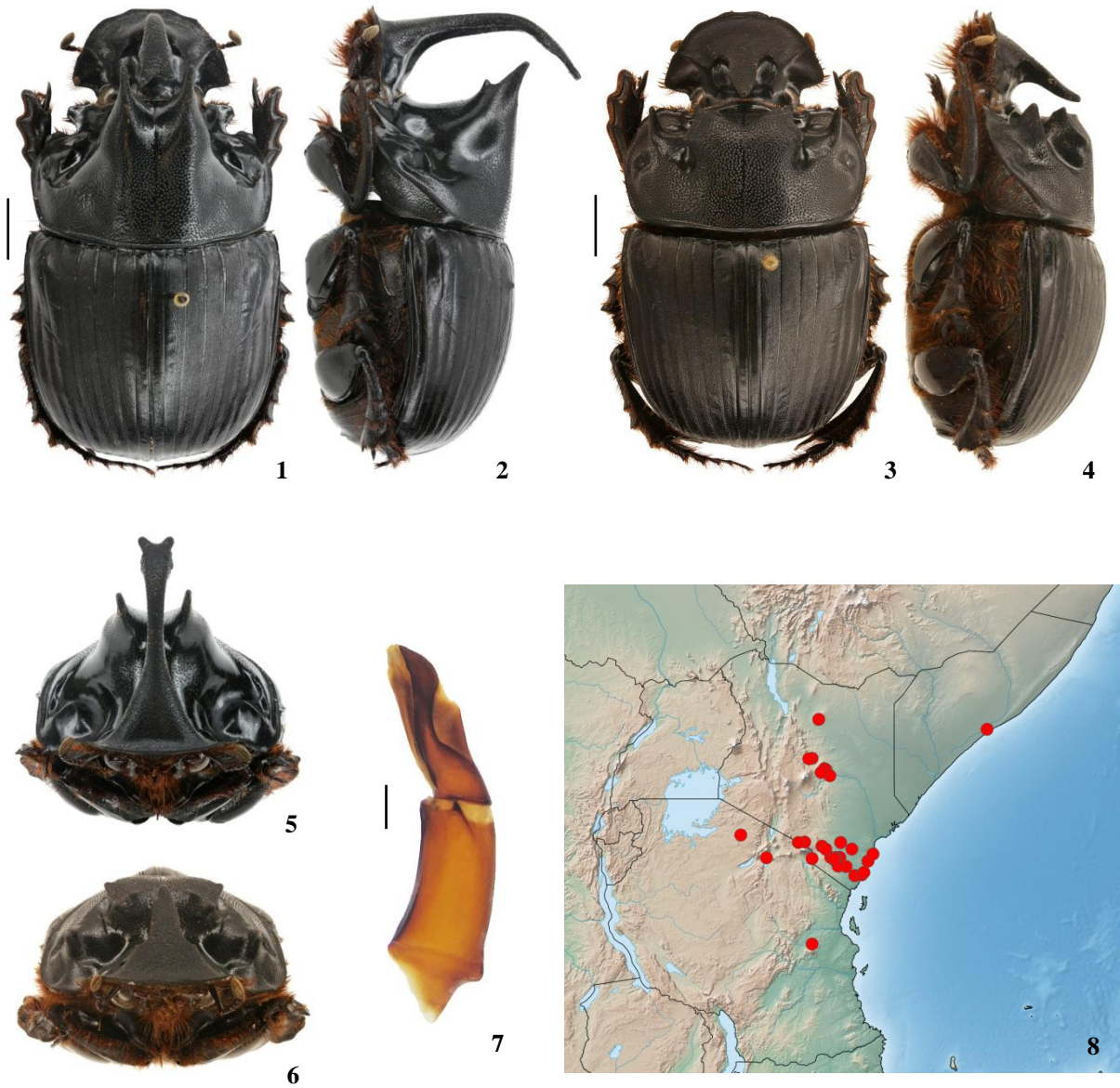
*Catharsius juheli* Josso, 2011



**Male** - Zambia, Lukwakwa, West Lunga National Park, 1147m, 4-8.xi.2013, R. Smith, H. Takano & D. Oram (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - Zambia, Ndanda, 1090m, 10-11.xi.2013, R. Smith, H. Takano & D. Oram (BMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 22

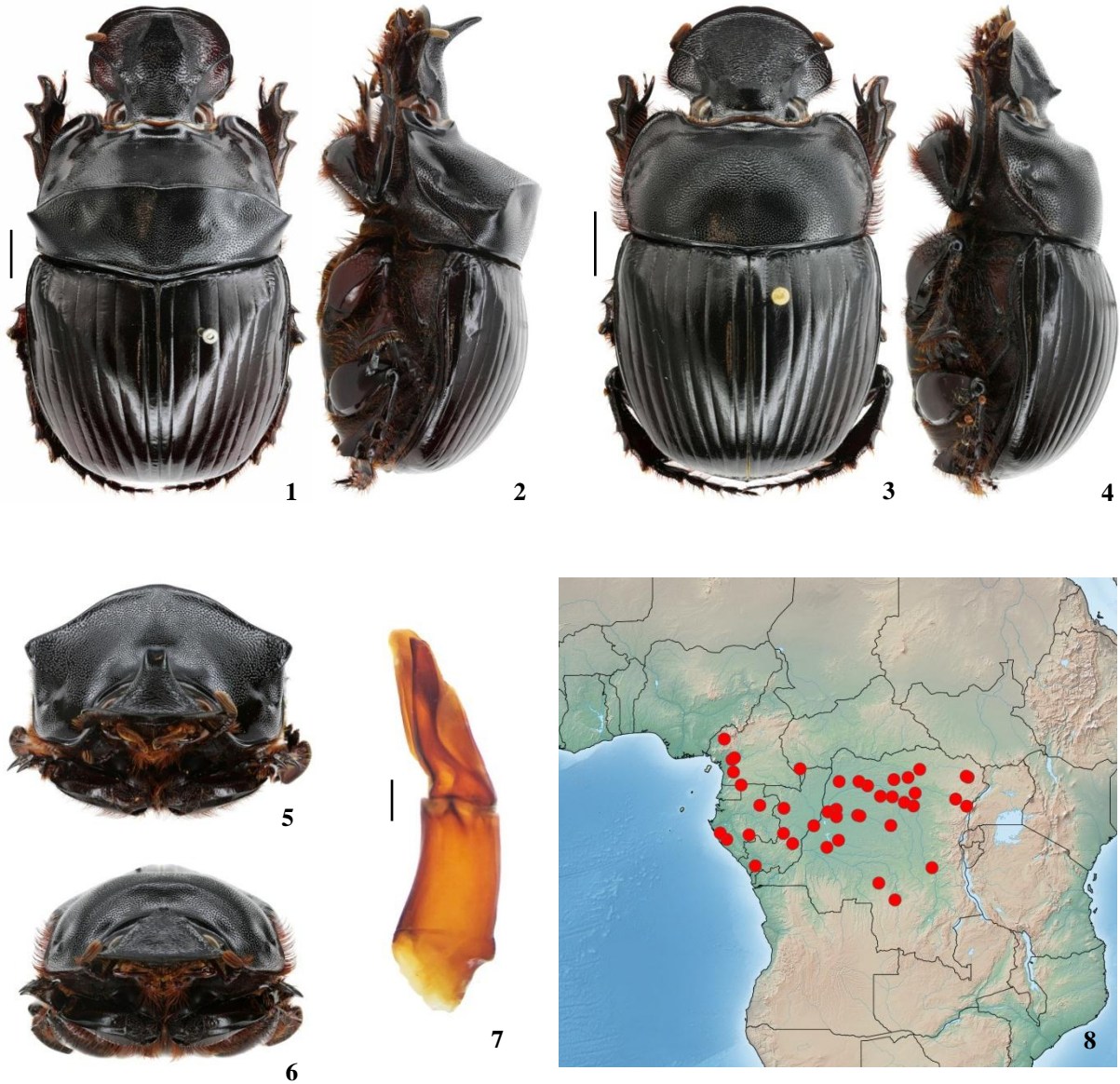
*Catharsius mirabilis* Felsche, 1901



**Male** - Kenya, Mackinnon Road, vii.1973 (RMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - Kenya, Meru National Park, Mulika Lodge, 650m, 13.iv.1981, J. Krikken (RMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 23

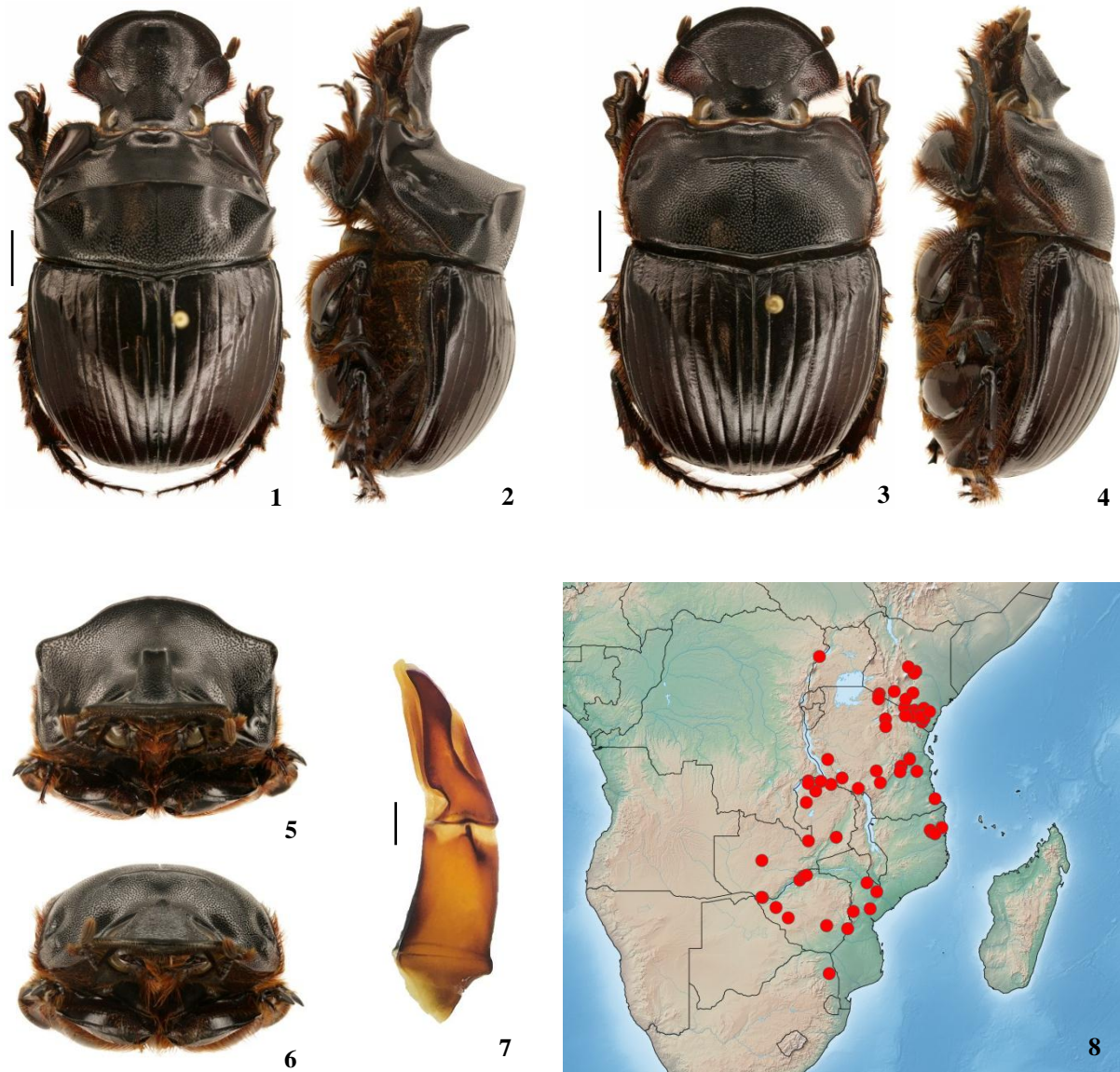
*Catharsius princeps* Kolbe, 1893



**Male** - D.R. Congo, Bopoto, F. Oram (MTD): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus;  
**Female**: Gabon, near Ndougou, 1-12.xii.1982, H.W. Hielkma (RMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 24

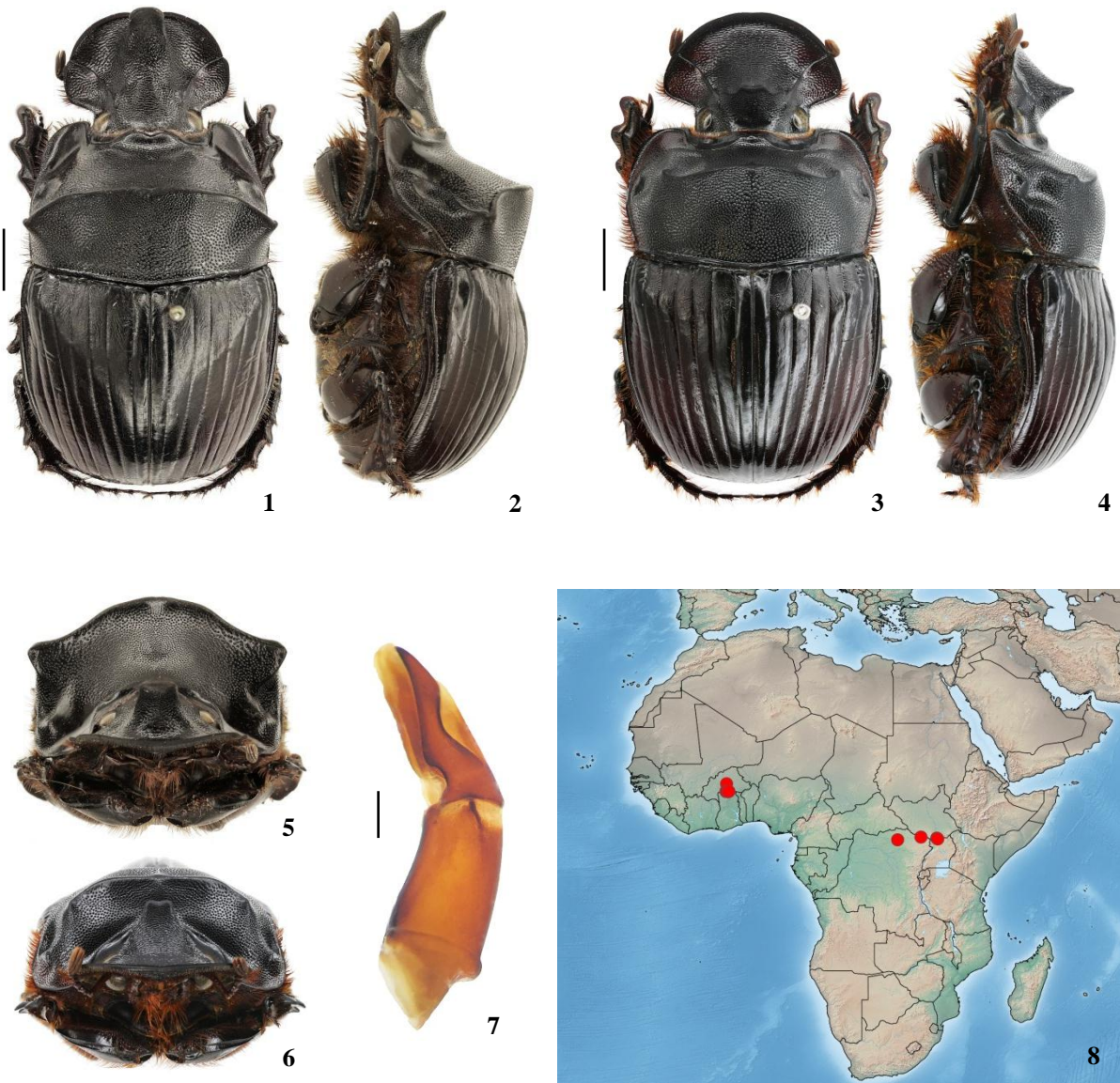
*Catharsius obtusicornis* Boheman, 1857



**Male** - Zambia, Nkwali, South Luangwa Game Management Area, 529m, 10-18.xi.2012, R. Smith & H. Takano (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - Zambia, Nkamba Bay, Sumbu National Park, 873m, 23-25.xi.2012, R. Smith & H. Takano (BMNH): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 25

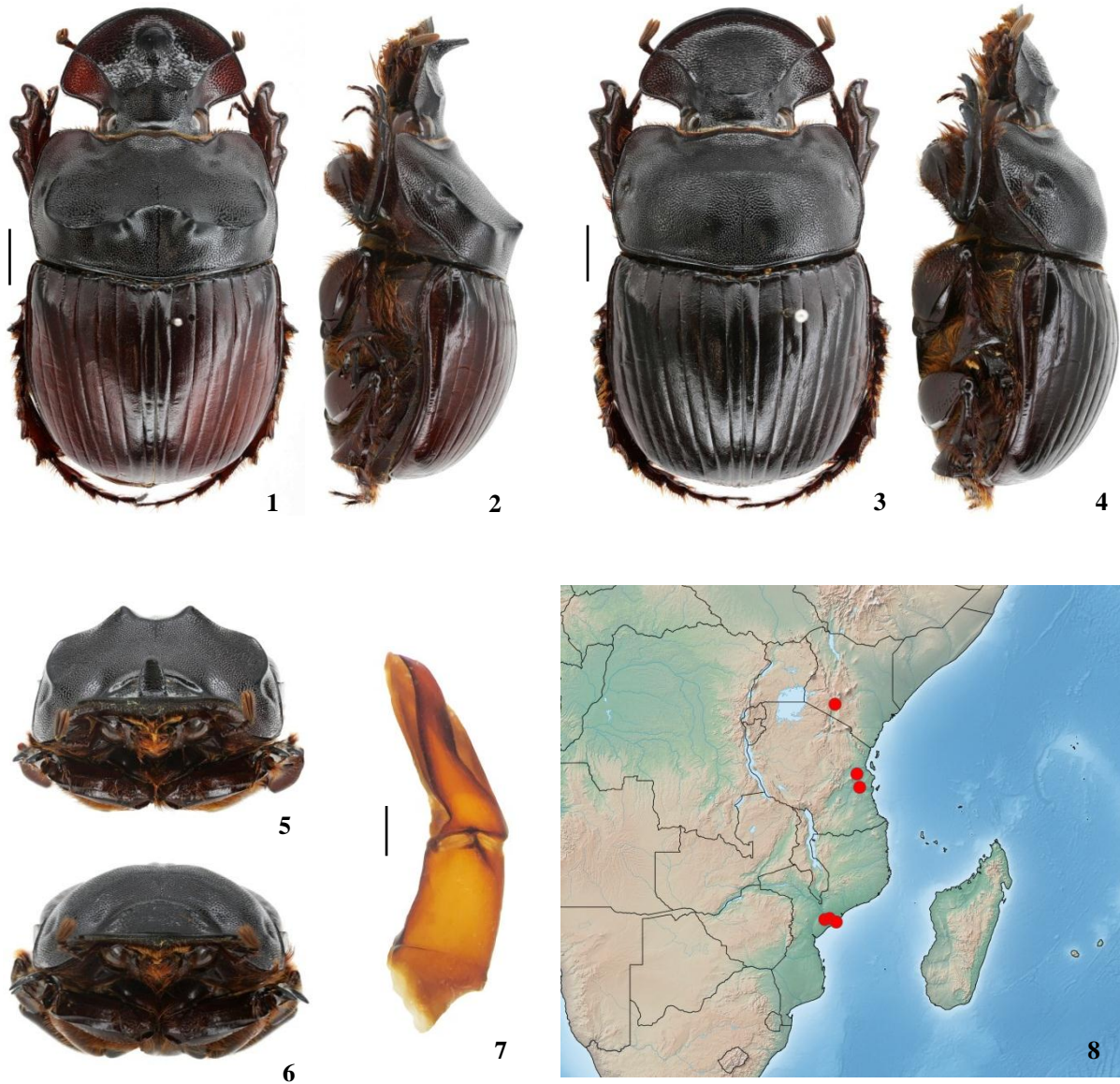
*Catharsius genieri* Moretto, 2014



**Male** - D.R. Congo, Parc National de la Garamba, Cellule II, 29.v.1952, H. de Saeger (MRAC): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 26

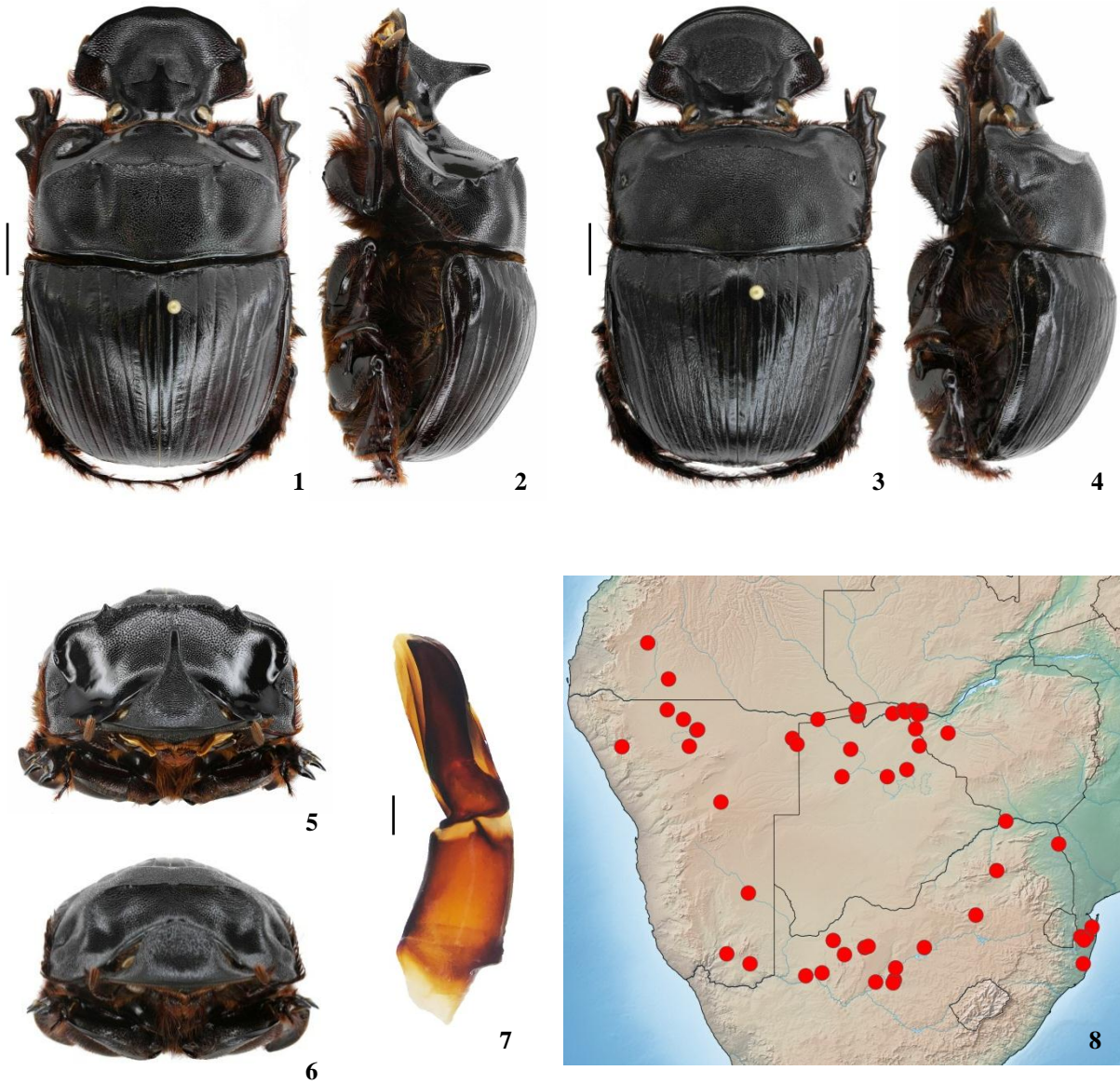
*Catharsius severini* Gillet, 1907



**Male** - Mozambique, [no precise locality] (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 27

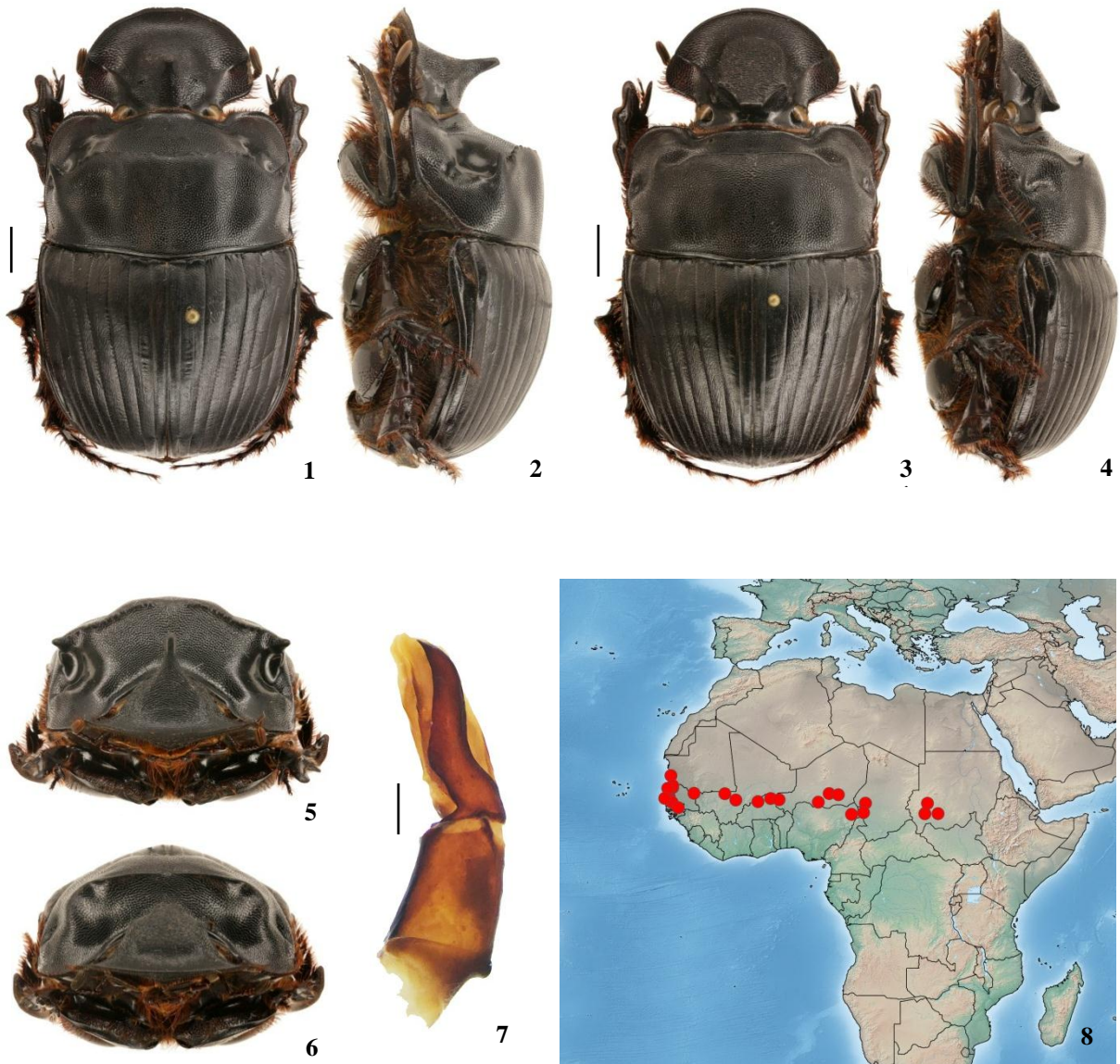
*Catharsius heros* Boheman, 1860



**Male** - Mozambique, Maputo Special Reserve, West Gate, 22m, 21-30.xi.2016, M. Aristophanous, J. Cristóvão, G. László & W. Miles (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 28

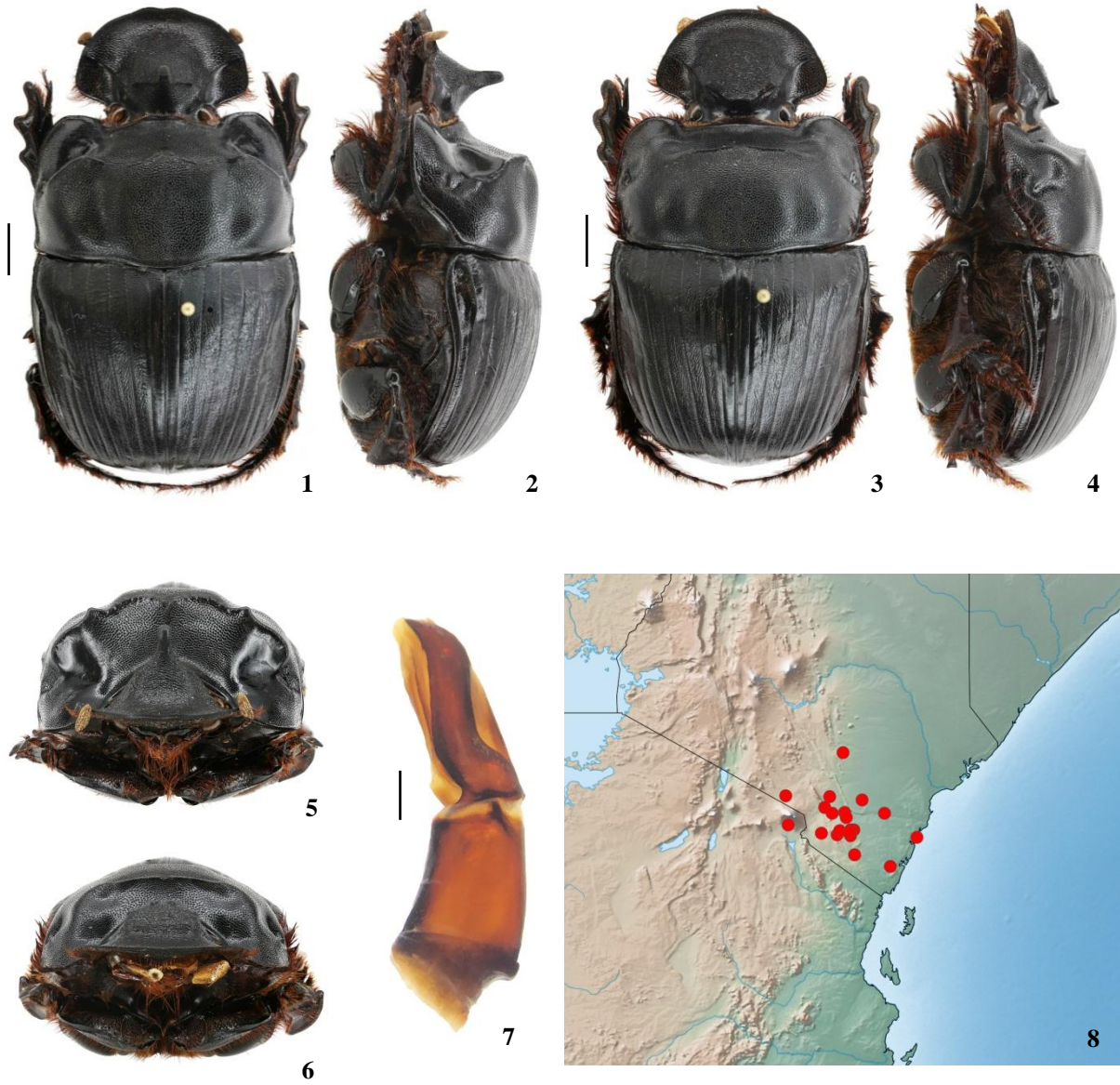
*Catharsius lepineyi* Boucomont, 1934



**Male** - Burkina Faso, Gorom-Gorom, Essakane, 264m, 26-27.vii.2012, P. Moretto (PMOC): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female** - *idem.*: 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 29

*Catharsius karlwernereri* Moretto, 2008



**Male** - Kenya, Taveta, F.J. Jackson (BMNH): 1. dorsal view; 2. lateral view; 5. frontal view; 7. aedeagus; **Female allotype** - KENYA, Sagala Hills, xii.1993, Werner (PMOC): 3. dorsal view; 4. lateral view; 6. frontal view; **Distribution map**: 8.

PLATE 30



*Lamella Copulatrix* of the *C. molossus* group. 1. *C. platynotus*; 2. *C. gibbicollis*; 3. *C. chinai*; 4. *C. gorilloides*; 5. *C. gorilla*; 6. *C. leo* sp. nov.; 7. *C. rhinoceros*; 8. *C. dominus* sp. nov.; 9. *C. dux*; 10. *C. duciformis*; 11. *C. spectabilis*; 12. *C. satyrus*; 13. *C. hertli*; 14. *C. adamastor*; 15. *C. ulysses*; 16. *C. telemachus* sp. nov.; 17. *C. thersander* sp. nov.; 18. *C. bradshawi*; 19. *C. achates*; 20. *C. polynices*; 21. *C. juheli*; 22. *C. mirabilis*; 23. *C. princeps*; 24. *C. obtusicornis*; 25. *C. genieri*; 26. *C. severini*; 27. *C. heros*; 28. *C. lepinyi*; 29. *C. karlwernerii*.



## Chapter 6: Conclusions and future directions

### Overview

An integrative systematic approach has resulted in the revision of the Afrotropical members of the mega-diverse dung beetle genus *Catharsius*. Two genera, *Copridaspidus* and *Catharsiocopris*, were synonymised with *Catharsius* and 128 Afrotropical species are recognised of which 39 species are new to science. **Only the revision of the 29 Afrotropical species of the *C. molossus* group is presented in this thesis.**

### Phylogenetic analyses

The morphological phylogenetic analyses of all *Catharsius* taxa resulted in a largely well-resolved tree enabling the genus to be split into five species groups supported by synapomorphic characters of the internal sclerites of the genitalia. Although the support at the nodes was affected by the character-to-taxon ratio which was poor due to the limited codable characters, it is suggested that there is future scope for further investigation of characters using electron microscopy and morphometric analyses techniques which have been shown to greatly improve the resolution and support of trees (Souza et al., 2014). One study has shown that the sculpture of the elytral closure of a ground beetle investigated by electron microscopy yielded a number phylogenetically informative characters (Roig-Juñent et al., 2011). It would be of great interest to study the fossil specimen of *Metacatharsius rusingae* Paulian and include it as part of a phylogenetic analysis of a larger dataset comprising taxa of the two genera in the tribe *Catharsiini* and estimate the divergence times and the evolutionary history of the tribe.

The results of the DNA sequencing were very disappointing and sequence data for only a very limited number of taxa (15) could be included in the molecular phylogenetic analyses. Although the resulting trees from both the morphological and molecular phylogenies were largely congruent, more sequence data for a greater number of taxa would be required to critically test this hypothesis. Despite isolating specimens in the field specifically for the purposes of DNA extraction, these specimens stored in ethanol and kept at -20°C could not be sequenced and a protocol has been outlined in Chapter 3 for the improved storage of dung beetle specimens for sequencing. DNA usually degrades very quickly over the first few years (Overballe-Peterson et al., 2012) and dependent upon climatic conditions, continues to degrade at a slower rate over time (Zimmerman et al., 2008). Storing specimens in ethanol and at cold temperatures slows this degradation process (Pearson et al., 2015). It would be interesting to attempt DNA extraction and sequencing from pinned *Catharsius* specimens to see

whether the results are better than for specimens stored in ethanol. Geiser et al. (2016) successfully sequenced a large number of Prionoceridae taxa from both dried and wet samples.

#### Capitalising on specimen locality data

There is great deal of potential for the large amount of geographical data that has been extracted from each studied specimens. From the distribution data in its most basic form, areas that are undersampled can be inferred by plotting all of the localities from where *Catharsius* have been collected on a map. Fieldwork can then be targeted at specific regions to fill the gaps in species distribution. In reality however, many of these areas are still inaccessible (the central Congo Basin) or too politically unstable to visit (Niger, Chad, Central African Republic, Sudan). It is surprising that there are very few records from countries such as Ghana, Guinea and Mozambique, countries where for example the butterfly fauna is well known (Larsen, 2005; Congdon et al., 2010). The greatest scope for the distribution data is perhaps to use Species Distribution Models (Elith & Leathwick, 2009) to statistically analyse and predict distribution based on different parameters such as climate and vegetation or perhaps to a lesser extent, species-specific traits such as dung type. Understanding the form that species range limits take, their causes and their consequence are key issues in ecology and evolutionary biology (Gaston, 2009).

The distributional data of *Catharsius* may also be useful in delimiting the boundaries of the many terrestrial ecosystems in Africa. It was observed (but untested) that two sister species, *C. africanus* and *C. phidias*, were broadly distributed in two ecoregions when plotted onto the terrestrial ecosystems map of Olsen et al. (2002), the former in the West Sudanian savannas and the latter in the Sahelian Acacia savannas. The distribution however appears to be “better” correlated when plotted on an earlier, more detailed vegetation map of Africa (White, 1983), where both aforementioned ecoregions are split further into two, with *C. africanus* and *C. phidias* being distributed in a more narrowly defined Sudanian and Sahelian savannas (region 29a and 43 of White, 1983). Ecosystem boundaries are nuanced (Nilsson & Grelsson, 1995) and perhaps the distribution of these dung beetles may provide stronger definition to these boundaries and more accurately delimit ecoregions.

Dung beetles are excellent indicators of habitat quality and whilst a recent study (Beck et al., 2018) into another model group for habitat quality, Lepidoptera, showed that protected areas were unrelated to the spatial distribution of species richness in hawkmoths, this is likely to be the opposite for dung beetles and in particular *Catharsius*, where species richness is likely to be correlated with the presence of mammals in particular the monogastric herbivores (E. Raine, DPhil thesis in prep.).

## Diet and dung preference

*Catharsius* species are mainly coprophagous but a few species are known to be necrophagous. Although many of the specimens studied as part of the revision had collection data associated with each specimen, many species have only ever been collected at light and their dung preference is unknown. A recent study has shown that molecular based gut content analyses successfully identified the mammal host (Gomez & Kolokotronis, 2016). Understanding the diet of dung beetles could not only be of wider practical use in mammal biodiversity assessment models, but in a genus such as *Catharsius* where both coprophagous and necrophagous species exist, these traits could be mapped onto phylogenies to investigate the evolutionary aspect of their diet.

## Future directions

Only one of the five species groups, the *C. molossus* group, was fully revised and a major goal is for the rest of the species groups to be treated in a similar manner culminating in the publication of a monograph of all of the Afrotropical members of the genus. It is hoped this work will be a blueprint for future taxonomic revisions of dung beetles and that the data presented in this revision will, from a purely revisional perspective, help others in the location of type specimens, interpret handwritten labels and understand ambiguous historical localities.

As a final thought, it is worth mentioning that the time and perhaps more importantly, the financial cost of undertaking a large monographic work cannot be understated. It was only through the continuous study of a group of beetles during the four year period of the doctoral studies as well as funding from independent sources to visit collections that the revision was successfully accomplished. In order to fully grasp the intricacies of a group of organisms, a large volume of specimens need to be studied, whether molecular data is available or not. The important *entente cordiale* that generally exists between natural history institutions across the world enables the sharing of knowledge through the access to and loan of specimens. Even with the excellent digitisation projects making museum collections more widely available on the internet, in the current state, the data that can be extracted for the purposes of a revision remain limited. Having an overview of a collection through digital photographs is useful for targeting the collections that are of greatest importance for the group being studied, but ultimately, specimens still need to be physically examined. It has been reported that museums are in financial crisis (Heath, 2018) and some museums struggle to pay for the couriership of specimens (personal observation), perhaps the safest and only option for transporting specimens between two institutions, aside from hand-carrying. Despite the availability of grants such as SYNTHESYS ([www.synthesys.info](http://www.synthesys.info)) for the purposes of studying museum specimens within the European Union (EU), for many researchers studying tropical flora and fauna, a visit to a collection

outside of the EU is a prerequisite. It is patently clear that for a European researcher studying the taxonomy of a group of Brazilian frogs, visits to museum collections in Brazil would be incredibly important for the comprehensiveness of the work. Taxonomy can be taught and learnt but has been virtually removed from school and undergraduate curricula (Leather, 2009; Leather & Quicke, 2009) and despite a list of recommendations put forward for developing a strategy for taxonomy and systematics in the UK following the 2008 House of Lords Report, very little progress appears to have been made (personal observation).

My recent experiences of producing a monographic revision has persuaded me that because of the time and educational structure afforded to a doctoral student, it provides an ideal opportunity to undertake rigorous taxonomic work on a grand scale. Taxonomy and in particular descriptive taxonomy should once more be on the graduate curriculum and it is hoped that in future, many more taxonomic revisions and monographs will be published as the result of graduate studies.

I would conclude by echoing the sentiments of Rev. Frederick Hope in his introduction to his 1837 *Coleopterist's Manual*, where the here-revised genus *Catharsius* was first described, by aiming, through this revision, to “render the tyro’s first attempts at systematic entomology more engaging than at present” (Hope, 1837: vi).



## REFERENCES

- ADUSE-POKU, K., VINGERHOEDT, E. & WAHLBERG, N. 2009. Out-of-Africa again: A phylogenetic hypothesis of the genus *Charaxes* (Lepidoptera: Nymphalidae) based on five gene regions. *Molecular Phylogenetics and Evolution* 53: 463–478.
- ANDERSSON, C.J. 1872. *Notes on the birds of Damara Land and the adjacent countries of South-West Africa*. John Van Voorst, London, 392 pp.
- ANONYMOUS. 1897. Recent Changes in the Map of East Africa. *Proceedings of the Royal Geographical Society and Monthly Record of Geography, London* 9(8): 490–496.
- ANONYMOUS. 1929. [Obituary.] Frederick John Jackson. *Ibis* 71(2): 344–348.
- ARROW, G.J. 1931. *The Fauna of British India including Ceylon and Burma. Coleoptera Lamellicornia. Part III (Coprinae)*. Taylor & Francis, London 1–428.
- BAI, M., McCULLOUGH, E., SONG, K-Q., LIU, W-G. & YANG, X-K. 2011. Evolutionary constraints in hind wing shape in Chinese dung beetles (Coleoptera: Scarabaeinae). *PLOS ONE*. 6(6): e21600. [doi.org/10.1371/journal.pone.0021600](https://doi.org/10.1371/journal.pone.0021600)
- BAKER, R.H. & GATESY, J. 2002. Is morphology still relevant? *Experientia Supplementum* 92: 163–174.
- BALTHASAR, V. 1967. The scientific results of the Hungarian soil zoological expedition to the Brazzaville-Congo. 22. Scarabaeidae und Coprinae. *Opuscula Zoologica. Instituti zoosystematici Universitatis Budapestinensis* 7(2): 47–73.
- BARBERO, E., PALESTRINI, C. & ROGGERO, A. 2003. *Revision of the genus Phalops Erichson, 1848 (Coleoptera: Scarabaeidae: Onthiphagini)*. Monografie di Museo Regionale di Scienze Naturali, Torino 38, 378 pp.
- BECK, J., TAKANO, H., BALLESTEROS-MEIJA, L. KITCHING, I.J. & MCCAIN, C.M. 2018. Field sampling biases against small-ranged species of high conservation value: a case study on the sphingid moths of East Africa. *Biodiversity & Conservation* 13 doi:10.1007/s10531-018-1613-z
- BIONDI, M., URBANI, F. & D'ALESSANDRO, P. 2015. Relationships between the geographic distribution of phytophagous insects and different types of vegetation: A case study of the flea beetle genus *Chaetocnema* (Coleoptera: Chrysomelidae) in the Afrotropical Region. *European Journal of Entomology* 112(2): 311–327.
- BOHEMAN, C.H. 1857. *Insecta Caffraria annis 1838-1845 a J.A. Wahlberg collecta amici auxilios sultus descripsit. Pars. II: Coleoptera*. Officina Norstedtiana. Holmiae 2: 1–395.
- BOHEMAN, C.H. 1860. *Coleoptera Caffraria annis 1838-1845 a J.A. Wahlberg collecta*. Öfversigt Kongliga Svenska Vetenskapsakademiens Förhandlingar 17(3): 107–120.
- BOOTH, A.H. 1958. The Niger, the Volta and the Dahomey Gap as Geographic Barriers. *Evolution* 12(1): 48–62.
- BOUCHARD, P., GREBENNIKOV, V.V., SMITH, A.B.T. & DOUGLAS, H. 2009. Biodiversity of Coleoptera. In: Footitt, R.G., & ADLER, P.H. Eds. *Insect biodiversity: science and society*. Blackwell Publishing, Oxford, 656 pp.

- BOUCHARD, P., BOUSQUET, Y., DAVIS, A.E., ALONSO-ZARAZAGA, M.A., LAWRENCE, J.F., LYAL, C.H.C., NEWTON, A.F., REID, C.A.M., SCHMITT, M., SLIPINSKI, S.A. & SMITH, A.B.T. 2011. Family group names in Coleoptera (Insecta). *Zookeys* 88: 1–972.
- BOUCOMONT, A. 1920. Coprophaga Africana. Genre nouveau et especes nouvelles. *Revue de Zoologie africaine. Tervuren, Brussels* 8(2): 261–269.
- BOUCOMONT, A. 1934. Mission J. de Lepiney au Soudan français, 1933-1934. *Bulletin de la Société de Sciences Naturelles et Physiques de Maroc* 14(1–3): 25–27.
- BRAZEAU, M.D. 2011. Problematic character coding methods in morphology and their effects. *Biological Journal of the Linnean Society* 104(3): 489–498.
- BROADLEY, D.G. & COTTERILL, F.P.D. 2004. The reptiles of southeast Katanga, an overlooked “hot spot”. *African Journal of Herpetology* 53(1): 35–61.
- BRUSCA, R.C. & BRUSCA, G.J. 2003. *Invertebrates*. Sinauer Associates, Sunderland, Massachusetts, 936 pp.
- BURMEISTER, H. 1846. *Genera quaedam insectorum. Iconibus illustravit et descripsit. Vol. I. Berolini sumtibus A. Burmeister* 1838–1846.
- CAMBEFORT, Y. & LUMARET, J.-P. 1984. Nidification et larves des Oniticellini afrotropicaux (Coleoptera: Scarabaeidae). *Bulletin de la Société Entomologiques de France* 88: 542–569.
- CAMBEFORT, Y. & NGUYEN-PHUNG, T. 1996. On the genus *Copris* Müller, 1764: Definition and phylogenetic survey of the Afrotropical species-groups (Coleoptera: Scarabaeidae). *Journal of African Zoology* 110(4): 271–289.
- CAMBEFORT, Y. & WALTER, P. 1991. Dung Beetles in Tropical Forests in Africa. In: Hanski, I & Cambefort, Y. Eds. *Dung Beetle Ecology*, Princeton University Press, Princeton 198–210.
- CARPENTER, J.M. 2003. Critique of Pure Folly. *The Botanical Review* 69(1): 79–92.
- CASTELNAU, F. 1840. *Histoire Naturelle des Insectes Coléoptères. Avec une introduction renfermant L'Anatomie et la Physiologie des Animaux Articulés, par M.Brullé, P.Duménil*. Paris 2: 1–564.
- CAVALLI-SFORZA, L.L. & EDWARDS, A.W.F. 1967. Phylogenetic analysis: Models and estimation procedures. *Evolution* 21: 550–570.
- CHASE, M.J., SCHLOSSBERG, S., GRIFFIN, C.R., BOUCHE, P.J.C., DJENE, S.W., ELKAN, P.W., FERREIRA, S., GROSSMAN, F., KOHI, E.M., LANDEN, K., OMONDI, K., PELTIER, A., SELIER, S.A.J. & SUTCLIFFE, R. 2016. Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ* 4: e2354, doi:10.7717/peerj.2354
- COHEN, A.S. & SCHWARTZ, H.L. 1983. Speciation in molluscs from Turkana Basin. *Nature* 304: 659–660.
- COSTELLO, M.J., HOULDING, B. & JOPPA, L.N. 2014. Further evidence of more taxonomists discovering new species, and that most species have been named: response to Bebbler et al. (2014). *New Phytologist* 202: 739–740.

- COX, C.L., RABOSKY, A.R.D., HOLMES, I.A., REYES-VELASCO, J., ROELKE, C.E., SMITH, E.N., FLORES-VILLELA, O., McGUIRE, J.A. & CAMPBELL, J.A. 2018. Synopsis and taxonomic revision of three genera in the snake tribe Sonorini. *Journal of Natural History* 52(13-16): 945–988.
- CRAWFORD ANGUS, H. 1898. A Year in Azimba and Chitipaland: The Customs and Superstitions of the People. *The Journal of the Anthropological Institute of Great Britain and Ireland* 27: 316–325.
- CRITICAL ECOSYSTEMS PARTNERSHIP FUND. 2018. Biodiversity Hotspots. <https://www.cepf.net/our-work/biodiversity-hotspots/> (accessed 30.viii.2018)
- CRUICKSHANK, R.H. 2002. Molecular markers for the phylogenetics of mites and ticks. *Systematic & Applied Acarology* 7: 3–14.
- DAVIS, A.L.V. & DEWHURST, C.F. 1992 Climatic and biogeographical associations of Kenyan and northern Tanzanian dung beetles (Coleoptera: Scarabaeidae). *African Journal of Ecology* 31: 290–305.
- DAVIS, A.L.V. & PHILLIPS, T.K. 2005. Effect of Deforestation on a Southwest Ghana Dung Beetle Assemblage (Coleoptera: Scarabaeidae) at the Periphery of Ankasa Conservation Area. *Environmental Entomology* 34(5): 1081–1088.
- DAVIS, A.L.V. & PHILLIPS, T.K. 2009. Regional Fragmentation of Rain Forest in West Africa and Its Effect on Local Dung Beetle Assemblage Structure. *Biotropica* 41(2): 215–220.
- DAVIS, A.L.V., FROLOV, A.V. & SCHOLTZ, C.H. 2008. *The African Dung Beetle Genera*. Protea Book House, Pretoria, 272 pp.
- DAVIS, A.L.V., SCHOLTZ, C.H. & CHOWN, S.L. 1999. Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *Journal of Biogeography* 26: 1039–1055.
- DAVIS, A.L.V., SCHOLTZ, C.H. & DESCHODT 2005. A dung beetle survey of selected Gauteng nature reserves: implications for conservation of the provincial scarabaeine fauna. *African Entomology* 13(1): 1–16.
- DAVIS, A.L.V., van AARDEL, R.J., SCHOLTZ, C.H. & DELPORT, J.H. 2002. Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. *Global Ecology & Biogeography* 11: 191–209.
- DAVIS, A.L.V., van AARDEL, R.J., SCHOLTZ, C.H. & DELPORT, J.H. 2003. Convergence between dung beetle assemblages of a post-mining vegetational chronosequence and unmined dune forest. *Restoration Ecology* 11(1): 29–42.
- DE GEER, C. 1778. *Mémoires pour servir à l'Histoire des Insectes (tom.1-7. 1752-1778)*. Hesselberg, Stockholm 7: 1–950.
- DE QUEIROZ, K. 2005. Different species problems and their resolution. *BioEssays* 27(12): 1263–1269.
- DE QUEIROZ, K. 2007. Species Concepts and Species Delimitation. *Systematic Biology* 56(6): 879–886.
- DEJEAN, P.F.M.A. 1833. *Catalogue des coléoptères de la collection de M. le comte Dejean*. Mequignon-Marvie pere et fils, Paris, 443 pp.

- DESCHAMPS, H. 1963. Quinze ans de Gabon (Les débuts de l'établissement français, 1839-1853). *Revue française d'histoire d'outre-mer* 50: 283–345.
- DOUBE, B.M. & MOOLA, F. 1988. The effect of the activity of the African dung beetle *Catharsius tricornutus* De Geer (Coleoptera: Scarabaeidae) on the survival and size of the African buffalo fly, *Haematobia thirouxi potans* (Bezzi) (Diptera: Muscidae), in bovine dung in laboratory. *Bulletin of Entomological Research* 78: 63–73.
- DOWN, R. 1989. "Old" preservative methods. In: Horie, C.V. Ed. *Conservation of Natural History Specimens: Spirit Collections*. The Manchester Museum and Department of Environmental Biology, The University of Manchester, 115 pp.
- EDMONDS, W.D. 1972. Comparative Skeletal Morphology, Systematics and Evolution of the Phanaeine Dung Beetles (Coleoptera: Scarabaeidae). *The University of Kansas Science Bulletin*, 49: 731–874.
- EDMONDS, W.D. & HALFFTER, G. 1978. Taxonomic review of immature dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Systematic Entomology* 3(4): 307–331.
- EDMONDS, W.D. & ZIDEK, J. 2009. A taxonomic revision of the neotropical genus *Coprophanaeus* Olsoufieff, 1924 (Coleoptera: Scarabaeidae, Scarabaeinae). *Insecta Mundi* 129: 1–111.
- EDWARDS, A.W.F. 1972. *Likelihood*. Cambridge University Press, Cambridge, 296 pp.
- ELITH, J. & LEATHWICK, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution & Systematics* 40: 677–697.
- EMLÉN, D.J., LAVINE, L.C. & EWEN-CAMPEN, B. 2007. On the origin and evolutionary diversification of beetle horns. *Proceedings of the National Academy of Sciences of the United States of America* 104(1): 8661–8668.
- ESCHMEYER, W.N., FRICKE, R., FONG, J.D. & POLACK, D. 2010. Marine fish biodiversity: a history of knowledge and discovery (Pisces). *Zootaxa* 2525: 19–50.
- FABRICIUS, J.C. 1775. *Systema entomologiae*. In Officina Libraria Kortii, Flensbvirgi et Lipsiae, 832 pp.
- FABRICIUS, J.C. 1781. *Species insectorum, exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin, adiectis observationibus, descriptionibus*. Tom.I. Carol. Ernest. Bohnii, Hamburgi et Kilonii, VIII: 1–552.
- FELSCHE, C. 1901. Beschreibungen coprophage Scarabaeiden. *Deutsche Entomologische Zeitschrift* 2: 135–155.
- FELSCHE, C. 1907. Coprophage Scarabaeiden. *Deutsche Entomologische Zeitschrift* (3): 273–296.
- FARRIS, J.S. 1982. Outgroups and parsimony. *Systematic Zoology* 31: 328–334.
- FERREIRA, M.C. 1959. Exploration du Parc National de l'Upemba. Scarabaeini, Gymnopleurini, Canthonini and Coprini. *Institut des Parcs Nationaux du Congo et du Rwanda. Mission H.De Saeger (1946-1949)*. Fascicule 58: 1–33.
- FERREIRA, M.C. 1960a. Descricao de especies novas de *Catharsius* s.str.. *Novos Taxa Entomológicos* 23: 3–8.

- FERREIRA, M.C. 1960b. Revisao das especies Africanas de *Catharsius* s.str. do Grupo Adamastor e descricao de especies novas. *Revista Entomologia Moçambique* 3(1): 1–73.
- FERREIRA, M.C. 1960c. Revisao das especies Etiopicas do subgenera *Catharsius* s.str.. *Revista Entomologia Moçambique* 3(2): 155–270.
- FERREIRA, M.C. 1962. Exploration du Parc National de la Garamba: Coprinae. *Institut des Parcs Nationaux du Congo et du Rwanda. Mission H.de Saeger (1949-1952)*. Fascicule 30: 1–123.
- FERREIRA, M.C. 1963. Contribuicao para o conhecimento dos Escarabidos africanos. *Novos Taxa Entomológicos* 30: 3–39.
- FERREIRA, M.C. 1964. Contribuicao para o estudo dos Escarabidos africanos. *Novos Taxa Entomológicos* 35: 3–9.
- FERREIRA, M.C. 1971. Contribuicao para o estudo dos Escarabideos Africanos. Descricao de uma especie nova de *Catharsius* s.str.. *Novos Taxa Entomológicos* 96: 5–6.
- FERREIRA, M.C. 1972. Os Escarabideos de Africa (sul do Saara). I. *Revista de Entomologia de Mocambique* 11: 5–1088.
- FITCH, W.M. 1971. Toward defining the course of evolution: minimum change for a specific tree topology. *Systematic Zoology* 20: 406–416.
- FOREY, P. & KITCHING, I.J. 2000. Experiments in coding multistate characters. In: Scotland, R.W. & Pennington, R.T. eds. *Homology and systematics: coding characters for phylogenetic analysis*. Taylor & Francis, London, 54–80.
- FREY, G.F. 1974. Neue Lamellicornia aus der Zoologischenn Staatssammlung in Munchen. *Entomologische Arbeiten aus dem Museum G.Frey* 25: 276–280.
- GAIGER, F. & VANIN, S.A. 2008. On the utility of female genitalia in the systematics of Curculionidae: examples from Entimin and Hylobiina (Coleoptera: Curculionidae). *Annales de la Société Entomologique de France*, 44(1): 47–57.
- GASTON, K.J. 1991. The magnitude of global insect species richness. *Conservation Biology* 5(3): 283–296.
- GASTON, K.J. 2009. Geographical range limits of species. *Proceedings of the Royal Society B* 276: 1391–1393.
- GEBIEN, H. 1907. Verzeichnis der im Naturhistorischen Museum zu Hamburg vorhandenen Typen von Coleopteren. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg* 24: 195–228.
- GEISER, M.F., HAGMANN, R., NAGEL, P. & LOADER, S.P. 2016. A first broad-scale molecular phylogeny of Prionoceridae (Coleoptera: Cleroidea) provides insight into taxonomy, biogeography, and life history evolution. *Arthropod Systematics & Phylogeny* 74(1): 3–21.
- GEMMINGER, M. & HAROLD, E. von. 1869. *Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus. Tom. IV. Scarabaeidae*. Monachii, Sumptu E.H. Gummi. 4: 979–1346.
- GEOFFROY, E.L. 1762. *Histoire des insectes*. Chez Durand, Paris, 523 pp.
- GÉNIER, F. 1996. A revision of the Neotropical genus *Onterius* Erichson (Coleoptera: Scarabaeidae, Scarabaeinae). *The Memoirs of the Entomological Society of Canada* 128 (Supplement 170): 3–170.

- GÉNIER, F. 2009. Le genre *Eurysternus* Dalman, 1824 (Scarabaeidae: Scarabaeinae: Oniticellini), revision taxonomique et clés de détermination illustrées. *Pensoft Publishers*, Sofia, 430 pp.
- GENIER, F. 2017. Taxonomic notes on two Southern African *Catharsius* Hope, 1837 (Coleoptera, Scarabaeidae, Scarabaeinae). *Catharsius La Revue*, 16: 1–10.
- GENIER, F. & JOSSO, J-F. 2016. Notes on Afrotropical *Catharsius* species described by Edgar von Harold (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 4072(3): 333–342.
- GENIER, F. & MORETTO, P. 2017. *Digitonthophagus* Balthsar, 1959: taxonomy, systematics, and morphological phylogeny of the genus revealing an African species complex (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa*, 4248(1): 1–110.
- GERSTAECKER, A. 1884. Bestimmungen der von Herrn Dr.G.A.Fischer während seiner Reise nach dem Massai-Land gesammelten Coleopteren. *Jahresbuch der hamburgischen Wissenschaftlichen Anstalten. Hamburg* 1: 43–63.
- GILL, B.D. 1991. Dung Beetles in Tropical American Forests. In: Hanski, I & Cambefort, Y. Eds. *Dung Beetle Ecology*, Princeton University Press, Princeton 211–229.
- GILLET, J.J.E. 1907. Contribution à l'étude des coprophages de la faune Africaine. *Annales de la Société entomologique de Belgique* 51(3): 177–184.
- GILLET, J.J.E. 1907. Remarques sur quelques coprides du Museo Civico de Gênes. *Annali del Museo Civico di Storia Naturale "Giacomo Doria"*. *Genova* 3(3): 587–603.
- GILLET, J.J.E. 1911a. Coprophaga Africana. Descriptions d'espèces nouvelles et remarques diverses. *Annales de la Société entomologique de Belgique* 55(11): 308–312.
- GILLET, J.J.E. 1911b. Pars 38. Scarabaeidae: Coprinae. I. in S. Schenkling (ed.), *Coleopterorum Catalogus*. W.Junk, Berlin 3–100.
- GILLET, J.J.E. 1918. Coprides nouveaux de la région éthiopienne et remarques diverses. *Zoologische Mededelingen. Leiden* 4: 146–158.
- GILLET, J.J.E. 1932. Lamellicornes Coprophages. *Bulletin et Annales de la Société entomologique de Belgique* 72(11-12): 323–332.
- GODFRAY, H.C.G. 2002. Challenges for taxonomy. *Nature* 417: 17–19.
- GODFRAY, H.C.G. 2007. Linnaeus in the information age. *Nature* 446: 259–260.
- GODFRAY, H.C.G. & KNAPP, S. 2004. Introduction. Taxonomy for the twenty-first century. *Philosophical Transactions of the Royal Society B* 359: 559–569.
- GODFRAY, H.C.G., MAYO, S.J. & SCOBLE, M.J. 2008. Pragmatism and Rigour can Coexist in Taxonomy. *Evolutionary Biology* 35: 309–311.
- GOLOBOFF, P.A. 1993. Estimating character weights during tree search. *Cladistics* 9: 83–91.
- GOLOBOFF, P.A. 1999. Analyzing large data sets in reasonable times: Solutions for composite optima. *Cladistics* 15(4): 415–428.

- GOLOBOFF, P.A., FARRIS, J.S. & NIXON, K.C. 2003. *TNT: tree analysis using new technology*. Version 1.0.
- GOLOBOFF, P.A., CARPENTER, J.M., ARIAS, J.S. & ESQUIVEL, D.F.M. 2008. Weighting against homoplasy improves phylogenetic analysis of morphological datasets. *Cladistics* 24: 758–773.
- GOMEZ, A. & KOLOKOTRONIS, S.O. 2017. Genetic information of mammalian meal source in dung beetle gut contents. *Mitochondrial DNA Part A, DNA Mapping, Sequencing & Analysis* 28(4): 612–615.
- GRECHKO, V.V. 2013. The Problems of Molecular Phylogenetics with the Example of Squamate Reptiles: Mitochondrial DNA markers. *Molecular Biology* 47(1): 55–74.
- GUÉRIN-MÉNEVILLE, F.E. 1847. *Voyage en Abyssinie par T.Lefébvre. Insectes*. Paris 6(4): 243–398.
- HALFFTER, G.V. & MATTHEWS, E.G. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomologica Mexicana*, 12-14: 1–312.
- HANSKI, I. & CAMBEFORT, Y. 1991. *Dung Beetle Ecology*. Princeton University Press, US, 481 pp.
- HAROLD, E. von. 1877. Coleopterorum species novae. *Mitteilungen der munchner entomologischen Verein. Munchen* 1: 97–111.
- HAROLD, E. von. 1878. Diagnosen neuer Coleopteren aus dem innern Africa. *Mitteilungen der munchner entomologischen Verein. Munchen* 2: 99–111.
- HAROLD, E. von. 1879. Bericht über die von der Herren A.v. Homeyer und P. Pogge in Angola und im Lunda-Reiche gesammelten Coleopteren. *Coleopterologische Hefte* 16: 1–224.
- HAROLD, E. von. 1880. Beschreibung neuer, auf einer Reise in Ostafrika, vözüglich in den Distrikten von Taita und Ukamba auf einer Tour von Mombassa nach den Kenia, von Hrn.J.M.Hildebrandt gesammelten Coleopteren. *Monatsbericht der königlichen preussischen Akademie des Wissenschaften zu Berlin* : 260–270.
- HAUSER, D.L. & PRESCH, W. 1991. The effect of ordered characters on phylogenetic reconstruction. *Cladistics* 7(3): 243–265.
- HAVIRD, J.C. & MIYAMOTO, M.M. 2010. The importance of taxon sampling in genomic studies: an example from the cyclooxygenases of teleost fishes. *Molecular Phylogenetics and Evolution* 56(1): 451–455.
- HAWKINS, J.A., HUGHES, C.E. & SCOTLAND, R.W. 1997. Primary homology assessment, characters and character states. *Cladistics* 13: 275–283.
- HEATH, F. 2018. *Endangered: Is there hope for the Natural History Museum?* New Culture Forum, London, 35 pp.
- HEATH, A., NEWPORT, M.A. & HANCOCK, D. 2002. *The Butterflies of Zambia*. The Lepidopterist's Society, South Africa, 137 pp.
- HEATH, T.A., HEDTKE, S.M. & HILLIS, D.M. 2008. Taxon sampling and the accuracy of phylogenetic analyses. *Journal of Systematics and Evolution* 46(3): 239–257.

- HENNIG, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana, 263 pp.
- HIGGS, N.D. 2016. Taxonomy in trouble? An ocean science perspective. *Ocean Challenge* 21(2): 10–11.
- HILLIS, D.M., MORITZ, C. & MABLE, B.K. 1996. *Molecular Systematics*, Sinauer Associates, Sunderland, Massachusetts, 655 pp.
- HILLIS, D.M., CHAMBERLAIN, D.A., WILCOX, T.P. & CHIPPINDALE, P.T. 2000. A new species of subterranean blind salamander (Plethodontidae: Hemidactyliini: Eurycea: Typhlomolge) from Austin, Texas, and a systematic revision of central Texas paedomorphic salamanders. *Herpetologica* 57(3): 266–280.
- HOPE, F.W. 1837. *The Coleopterist's Manual, containing the Lamellicorn insects of Linneus and Fabricius*. Pt.1. Henry Bohn, London, 121 pp.
- HOPKINS, G.W. & FRECKLETON, R.P. 2002. Decline in the numbers of amateur and professional taxonomists: implications for conservation. *Animal Conservation* 5: 245–249.
- HUANG, J-P. 2017. The Hercules beetles (subgenus *Dynastes*, genus *Dynastes*): a revisionary study based on the integration of molecular, morphological, ecological, and geographic analyses. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, No.206, 32 pp.
- HUELSENBECK, J.P., RONQUIST, F.R., NIELSEN R. & BOLBACK, J.P. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294: 2310–2314.
- JAMIESON, G.A. 1959. Dr. Bradshaw of Pandamatenka. *The Central African Journal of Medicine* 5(7): 371–373.
- JANSSENS, A. 1949. Contribution a l'étude des coléoptères Lamellicornes. XIV. Notes sure quelques Scarabaeinae nouveaux ou peu connus. *Bulletin Institut royal des Sciences naturelles des Belgique* 25(43): 1–6.
- JEFFROY, O., BRINKMANN, H, DELSUC, F. & PHILIPPE, H. 2006. Phylogenomics: the beginning of incongruence? *Trends in Genetics* 22(4): 225–231.
- JOSSO, J-F. 2011. Description de quatre nouvelles especes de Scarabaeidae de Zambie, appartenant aux genres *Catharsius* Hope, 1837, *Copris* Müller, 1764, *Pleuronitis* Lansberge, 1875 et *Onthophagus* Latreille, 1802. *Catharsius La Revue* 3: 1–8.
- JOSSO, J.-F. & PRÉVOST, P. 2002. *Revision du genre Diastellopalpus*. *Collection Systematique 3. Magellanes, Paris*, 136 pp.
- JOSSO, J-F. & PREVOST, P. 2009. Description de trois nouvelles especes de *Catharsius* de Zambie et de Tanzanie. *Les Cahiers Magellanes Hors-serie* 31: 1–7.
- JOSSO, J-F. & PREVOST, P. 2018. Description de nouvelles especes de *Catharsius* de Zambie et de DRC. *Catharsius La Revue*, in press.
- KIMURA, M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120.
- KLEMPERER, H.G. 1981. Nest construction and larval behaviour of *Bubas Bison* (L.) and *Bubas bubalus* (Ol.) (Coleoptera: Scarabaeidae). *Ecological Entomology* 6: 23–33.

- KLEMPERER, H.G. 1982. Normal and atypical nesting behaviour of *Copris lunaris* (L.): comparison with related species (Coleoptera: Scarabaeidae). *Ecological Entomology* 7: 69–83.
- KLUG, J.C.F. 1855. Diagnosen der neuer Coleopteren aus Mossambique. *Berichten der Koniglich-Preussischen Akademie der Wissenschaften. Berlin* 20: 643–660.
- KLUGE, A.G. 1998. Total evidence or taxonomic congruence: cladistics or consensus classification. *Cladistics* 14: 151–158.
- KOLBE, H.J. 1893. Ueber afrikanische Mistkäfer (*Catharsius*, *Diastellopalpus*). *Sitzungsbericht der Gesellschaft naturforschender Freunde zu Berlin* 131–151.
- KOLBE, H.J. 1897. *Coleopteren: die Käfer Deutsch-Ost-Afrikas*. D. Reimer, Berlin, 392 pp.
- KRELL, F.-T. 2007. Dung beetle sampling protocols. *Denver Museum of Nature and Science Technical Report* 6: 1–11.
- KUMAR, S., STECHER, G., LI, M., KNYAZ, C. & TAMURA, K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549.
- LACORDAIRE, J.T. 1856. *Histoire naturelle des insectes. Genera des coléoptères, ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome troisième*. Libraire Encyclopédique de Roret, Paris, 594 pp.
- LANSBERGE, J.W. van. 1887. Note III. Cinq espèces nouvelles de Coléoptères exotiques appartenant au Musée de Leyde. *Notes from the Leyden Museum. Leyden* 9: 107–112.
- LATREILLE, P.A. 1802. *Histoire naturelle des crustacés et des insectes. Volume III*. F. Dufart, Paris, 467 pp.
- LEATHER, S.R. 2009. Taxonomic chauvinism threatens the future of entomology. *Biologist* 56(1): 10–13.
- LEATHER, S.R. & QUICKE, D.J.L. 2009. Where would Darwin have been without taxonomy? *Journal of Biological Education* 43(2): 51–52.
- LEE, G-E., HAN, T., JEONG, J., KIM, S-H., PARK, I.G. & PARK, H. 2015. Molecular phylogeny of the genus *Dicronocephalus* (Coleoptera, Scarabaeidae, Cetoniinae) based on mtCOI and 16S rRNA genes. *Zookeys* 501: 63–87.
- LEE, M.S.Y. & PALCI, A. 2015. Morphological phylogenetics in the Genomic Age. *Current Biology* 25(19): 922–929.
- LEGG, D.A., SUTTON, M.D. & EDGECOMBE, G.D. 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications* 4:2485 doi:10.1038/ncomms2485
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus I. Laurentii Salvi, Holminae*, 824 pp.
- LOSEY, J.E. & MACE, V. 2006. The economic value of ecological services provided by insects. *Bioscience* 56(4): 311–323.

- LUMARET, J.P. & PAULIAN, R. 1977. Les larves des Scarabeidae (Coleoptera). 6. Le genre *Copris* Geoffroy. *Annales de la Société Entomologique de France*, 13(3): 469–485.
- MACLEAY, W.S. 1819. *Horae entomologicae, or, Essays on the annulose animals*. S. Bagster, London, 162 pp.
- MADDISON, W.P. & MADDISON, D.R. 2009. *Mesquite*: a modular system for evolutionary analysis. Version 3.10.
- MALDANER, M.E., VAZ-DE-MELLO, F.Z., TAKIYA, D.M. & FERREIRA, D.C. 2018. Molecular phylogeny of the *Coprophanaeus* (*Megaphanaeus*) (Coleoptera: Scarabaeidae: Scarabaeinae) and the position of *C. bellicosus*. *Insect Systematics and Evolution* 1–15.
- MASUMOTO, K. 1973. Observation of the nidification of *Synapsis davidi* Fairmaire. *Entomological Review of Japan* 25: 60–62.
- MAYDEN, R.L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. In: Claridge, M.F., Dawah, A.H. & Wilson, M.R. Eds. *Species: The Units of Biodiversity*, Chapman & Hall, London, 442 pp.
- MAYR, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York, 334 pp.
- MAYR, E. 1982. *The growth of biological thought*. Belknap Press, Cambridge, Massachusetts, 974 pp.
- MEDINA, C.A., MOLANO, F. & SCHOLTZ, C.H. 2013. Morphology and terminology of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) male genitalia. *Zootaxa*, 3626(4): 455–476.
- MEIER, R. 1994. On the inappropriateness of presence/absence recoding, for non-additive multistate characters in computerized cladistics analyses. *Zoologischer Anzeiger*, 232: 201–212.
- MENDES, L.F., BIVAR DE SOUSA, A., FIGUEIRA, R. & SERRANO, A.R.M. 2013. Gazetteer of the Angolan localities known for beetles (Coleoptera) and butterflies (Lepidoptera: Papilionoidea). *Boletim da Sociedade Portuguesa de Entomologia*, 228(VII-14): 258–292.
- MLAMBO, S., SOLE, C.L. & SCHOLTZ, C.H. 2011. Phylogeny of the African ball-rolling dung beetle genus *Epirinus* Reiche (Coleoptera: Scarabaeidae: Scarabaeinae). *Invertebrate Systematics* 25(3): 197–207.
- MLAMBO, S., SOLE, C.L. & SCHOLTZ, C.H. 2014. Affinities of the African Canthonini dung beetles of the Eastern Arc Mountains. *Organisms Diversity & Evolution* 14(1): 115–120.
- MLAMBO, S., SOLE, C.L. & SCHOLTZ, C.H. 2015. A molecular phylogeny of the African Scarabaeinae (Coleoptera: Scarabaeidae). *Arthropod Systematics and Phylogeny* 73(2): 303–321.
- MONAGHAN, M.T., INWARD, D.J.G., HUNT, T. & VOGLER, A.P. 2007. A molecular phylogenetic analysis of the Scarabaeinae (dung beetles). *Molecular Phylogenetics and Evolution* 45: 674–692.
- MONTREUIL, O. 1998. Analyse phylogénétique et paraphylie des Coprini et Dichotomiini (Coleoptera: Scarabaeidae). Scénario Biogéographique. *Annales de la Société Entomologique de France* 34(2): 135–148.

- MORETTO, P. 2008. *Catharsius karlwernerii*, nouvelle espece d'Afrique de l'Est. Revision des *Catharsius* Hope, 1837 du groupe *heros* (Coleoptera, Scarabaeidae). *Entomologia Africana* 13(2): 38–44.
- MORETTO, P. 2014. Description de *Catharsius genieri*, nouvelle espece d'Afrique de l'Ouest (Coleoptera, Scarabaeidae, Coprini). *Entomologia Africana* 19(2): 59–64.
- MÜLLER, O.F. 1764. *Fauna Insectorum Fridrichsdaliana*. Lipsiae: Hafniae et Gleditsch, 96 pp.
- MÜLLER, G. 1941. Nuovi Coleotteri dell'Africa orientale. *Atti del Museo Civico di Storia Naturale di Trieste* 14(23): 319–352.
- MUTANEN, M., WAHLBERG, N. & KAILA, L. 2010. Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings of the Royal Society B* 277(1695): 2839–2848.
- NABHAN, A.R. & SARKAR, I.N. 2012. The impact of taxon sampling on phylogenetic inference: a review of two decades of controversy. *Briefings in Bioinformatics* 13(1): 122–134.
- NGUYEN-PHUNG, T. & CAMBEFORT, Y. 1986a. Revision des especes Afro-tropicale du genre *Copris*. I. Le Groupe *integer*. *Nouvelle Revue d'Entomologie* 3(4): 401–416.
- NGUYEN-PHUNG, T. & CAMBEFORT, Y. 1986b. Revision des especes Afro-tropicale du genre *Copris*. III. Le Groupe *inhalatus*. *Revue Française d'Entomologie* 8(3): 100–106.
- NGUYEN-PHUNG, T. & CAMBEFORT, Y. 1987. Revision des especes Afro-tropicale du genre *Copris*. II. Le Groupe *jacchus*. *Annales de la Société entomologique de France* 23(1): 67–75.
- NICHOLS, E., SPECTOR, S., LOUZADA, J., LARSEN, T., AMEZQUITA, S. & FAVILLA, M.E. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* 141(6): 1461–1474.
- NILSSON, C. & GRELSSON, G. 1995. The fragility of ecosystems: A review. *Journal of Applied Ecology* 32: 677–692.
- NIXON, K.C. 2002. *WinClada*, Version 1.0.
- NUNN, G.B., THEISEN, B.F., CHRISTENSEN, B. & ARCTANDER, P. 1996. Simplicity-correlated size growth of the nuclear 28S ribosomal RNA D3 expansion segment in the crustacean order Isopoda. *Journal of Molecular Evolution* 42: 211–223.
- OLSEN, D.M., DINERSTERIN, E., WIKRAMNAYAKE, E.D., BURGESS, N.D., POWELL, G.V.N., UNDERWOOD, E.C., D'AMICO, J.A., ITOUA, I., STRAND, H.E., MORRISON, J.C., LOUCKS, C.J., ALLNUTT, T.F., RICKETTS, T.H., KURA, Y., LAMOREUX, J.F., WETTENGEL, W.W., HEDAO, P. & KASSEM, K.R. 2010. Terrestrial Ecoregions of the World: A New Map of Life on Earth. *Bioscience* 51(11): 933–938.
- OLIVIER, A.G. 1789. *Entomologie, ou histoire naturelle des insectes, avec leurs caractères génériques et spécifiques, leur description, leur synonymie, et leur figure enluminée. Coléoptères*. Baudouin, Paris, 190 pp.
- OVERBALLE-PETERSON, S., ORLANDO, L. & WILLERSLEV, E. 2012. Next-generation sequencing offers new insights into DNA degradation. *Trends in Biotechnology* 30(7): 364–368.

- PÄÄBO, S., POINAR, H., SERRE, D., JAENICKE-DESPRES, V., HEBLER, J., ROHLAND, N., KUCK, M., KRAUSE, J., VIGILANT, L. & HOFREITER, M. 2004. Genetic Analyses from Ancient DNA. *Annual Review of Genetics* 38: 645–679.
- PACKER, L., MONCKTON, S.K., ONUFERKO, T.M. & FERRARI, R.R. 2018. Validating taxonomic identifications in entomological research. *Insect Conservation & Biology* 11(1): 1–12.
- PAGE, R.D.M. & HOLMES, E.C. 1998. *Molecular Evolution: A Phylogenetic Approach*. Blackwell Science, Oxford, 346 pp.
- PAKENHAM, T. 1991. *The Scramble for Africa*. Weidenfield & Nicholson, London, 738 pp.
- PATWARDHAN, A., RAY, S. & ROY, A. 2014. Molecular Markers in Phylogenetic Studies - A Review. *Journal of Phylogenetics & Evolutionary Biology* 2(131). doi:10.4172/2329-9002-2-131
- PAULIAN, R. 1939. Trois nouveau coprophages de Mauretanie. *Revue française d'Entomologie* 6(1): 10–22.
- PAULIAN, R. 1976. Three fossil dung beetles (Coleoptera: Scarabaeidae) from the Kenya Miocene. *Journal of the East Africa Natural History Society and National Museum* 31(158): 1–4.
- PEARSON, S.K., TOBE, S.S., FUSCO, D.A., BULL, C.M. & GARDNER, M.G. 2015. Piles of scats for piles of DNA: deriving DNA of lizards from their faeces. *Australian Journal of Zoology* 62(6): 507–514.
- PEARSON, W.R. 2013. An introduction to Sequence Similarity (“Homology”) Searching. *Current Protocols in Bioinformatics* 42:1 doi:10.1002/0471250953.bi0301s42
- PÉRINGUEY, L. 1892. Third contribution to the South-African Coleopterous Fauna. *Transactions of the South African philosophical Society. Cape Town* 6(2): 1–94 (25–40).
- PÉRINGUEY, L. 1901. Descriptive catalogue of the Coleoptera of South Africa. *Transactions of the South African philosophical Society. Cape Town* 12: 1–563.
- PETERS, W.C.H. 1862. *Naturwissenschaftliche Reise nach Mossambique, auf Befehl Seiner Majestät des Königs Friedrich Wilhelm IV, in den Jahren 1842 bis 1848 ausgeführt, von Wilhelm C.H. Peters. Zoologie. V. Insecten und Myriopoden*. G. Reimer, Berlin 564 pp.
- PETERSEN, G. & SEBERG, O. 1998. Molecules vs Morphology. In: Karp, A., Isaac, P.G. & Ingram, D.S. Eds. *Molecular Tools for Screening Biodiversity*. Chapman & Hall, London, 498 pp.
- PLANET, P.J. 2006. Tree disagreement: measuring and testing incongruence in phylogenies. *Journal of Biomedical Informatics* 39(1): 86–102.
- PLEIJEL, F. 1995. On character coding for phylogeny reconstruction. *Cladistics*, 11: 309–315.
- POKORNÝ, S., ZÍDEK, J. & WERNER, K. 2009. *The Giant Dung Beetles of the Genus Heliocopris*. Taita Publishers, Czech Republic, 136 pp.
- POLLOCK, D.D., ZWICKL, D.J., McGUIRE, J.A. & HILLIS, D.M. 2002. Increased taxon sampling is advantageous for phylogenetic inference. *Systematic Biology* 51(4): 664–671.
- QUEDENFELDT, G. 1884. Verzeichniss der von Herrn Major a. D. von Mechow in Angola und am Quango-Strom 1878-1881 gesammelten Pectinicornen und Lamellicornen. *Berliner entomologische Zeitschrift, Berlin* 28(2): 265–340.

- RAMBAUT, A. 2009. *FigTree* [retrieved from <http://tree.bio.ed.ac.uk/software/figtree/>]
- REISS, R.A., SCHWERT, D.P. & ASHWORTH, A.C. 1995. Field preservation of Coleoptera for Molecular Genetic Analyses. *Environmental Entomology* 24(3): 716–719.
- REUTER, J.A., SPACEK, D.V. & SNYDER, M.P. 2015. High-throughput sequencing technologies. *Molecular Cell* 58(4): 586–597.
- ROGGERO, A., BARBERO, E. & PALESTRINI, C. 2015. Phylogenetic and biogeographic review of the Drepanocerina (Coleoptera: Scarabaeidae: Oniticellini). *Arthropod Systematics & Phylogeny* 73(1): 153–174.
- ROGGERO, A., DIERKENS, M., BARBERO, B. & PALESTRINI, C. 2016. Combined phylogenetic analysis of two new Afrotropical genera of Onthophagini (Coleoptera, Scarabaeidae). *Zoological Journal of the Linnean Society*, [doi:10.1111/zoj.12498](https://doi.org/10.1111/zoj.12498)
- ROGGERO, A., STANBROOK, R., JOSSO J-F., BARBERO E. & PALESTRINI, C. 2017. Phylogenetic relationships of *Epidrepanus* within the subtribe Drepanocerina (Coleoptera: Scarabaeidae: Scarabaeinae: Oniticellini), with the description of two new species. *Zootaxa* 4320(1): 1–24.
- ROIG-JUÑENT, S., SALLENAVE, S. & AGRAIN, F.A. 2011. New morphological aspects and phylogenetic considerations of *Cicindis* Bruch (Coleoptera: Carabidae: Cicindini). *Neotropical Entomology* 40(3): 331–344.
- ROKAS, A. & CARROLL, S.B. 2006. Bushes in the Tree of Life. *PLOS Biology* 4(11): e352. [doi.org/10.1371/journal.pbio.0040352](https://doi.org/10.1371/journal.pbio.0040352)
- RONQUIST, F., TESLENKO, M., van der MARK, P., AYRES, D.L., DARLING, A., HÖHNA, S., LARGET, B., LIU, L., SUCHARD, M.A. & HUELSENBECK, J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542.
- ROSEN, D.E. 1979. Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative biogeography. *Bulletin of the American Museum of Natural History* 162: 267–376.
- ROUGON, D. 1987. Coléoptères Coprophiles en zone sahelienne: Etude biocenotique comportement nidificateur, intervention dans le recyclage de la matière organique du sol. *Thèse Docteur, Université d'Orleans* [unpublished]
- SALISBURY, B.A. & KIM, J. 2001. Ancestral state estimation and taxon sampling density. *Systematic Biology* 50(4): 557–564.
- SAN MAURO, D. & AGORRETA, A. 2010. Molecular systematics: A synthesis of the common methods and the state of knowledge. *Cellular and Molecular Biology Letters* 15(2): 311–341.
- SCHÖNHERR, C.J. 1806. *Synonymia Insectorum, oder: Versuch einer Synonymie aller bisher bekannten Insecten; nach Fabricii Systema Eleutheratorum geordnet. Ersten Band.* Stockholm, 293 pp.
- SCOTLAND, R.W., OLMSTEAD, R.G. & BENNETT, J.R. 2003. Phylogenetic reconstruction: the role of morphology. *Systematic Biology* 52(4): 539–548.

- SEBASTIAN, C.R., KATHERINE, C.V., CESAR, L.G. & VICTOR HUGO, G.M. 2014. Phylogenetic analyses of four dung beetle species of Neotropical genus *Oxysternon* (Coleoptera: Scarabaeidae: Scarabaeinae) based on 28S and COI partial regions. *Advances in Computational Biology* 232: 213–219.
- SHORTHOUSE, D.P. 2010. *SimpleMappr*, an online tool to produce publication-quality maps. [retrieved from <http://www.simplemappr.net>]
- SIMON, C., FRATI, F., BECKENBACH, A., CRESPI, B., LIU, H. & FLOOK, P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America* 87: 651–701.
- SIMPSON, G.G. 1951. The species concept. *Evolution* 5: 285–298.
- SLADE, E.M., MANN, D.J., VILLANEUVA, J.F. & LEWIS, O.T. 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology* 76(6): 1094–1104.
- SOLE, C.L. & SCHOLTZ, C.H. 2010. Did dung beetles arise in Africa? A phylogenetic hypothesis based on five gene regions. *Molecular Phylogenetics and Evolution* 56(2): 631–641.
- SOUZA, T.A.J., NOLL, F.B., BICUDO H.E.M. & MADI-RAVAZZI, L. 2014. Scanning electron microscopy of male *Terminalia* and its application to species recognition and phylogenetic reconstruction in the *Drosophila saltans* group. *PLoS One* 9(6): e97156.
- TARASOV, S. & SOLODOVNIKOV, A. 2011. Phylogenetic analyses reveal reliable morphological markers to classify meg-diversity in Onthophagini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Cladistics*, 27: 1–39.
- TARASOV, S. & GENIER, F. 2015. Innovative Bayesian and Parsimony Phylogeny of Dung Beetles (Coleoptera, Scarabaeidae, Scarabaeinae) Enhanced by Ontology-Based Partitioning of Morphological Characters. *PLoS One* 10(3): e0116671.
- TARASOV, S. & DIMITROV, D. 2016. Multigene phylogenetic analysis redefines dung beetles relationships and classification (Coleoptera: Scarabaeidae: Scarabaeinae). *BMC Evolutionary Biology*, 16(257): 1–19.
- TARASOV, S., VAZ DE MELLO, F.Z., KRELL, F-T., & DIMITROV, D. 2016. A review and phylogeny of Scarabaeine dung beetle fossils (Coleoptera: Scarabaeidae: Scarabaeinae), with the description of two *Canthochilum* species from Dominican amber. De Baets K, ed. *PeerJ*. 2016;4:e1988. doi:10.7717/peerj.1988.
- THOMSEN, P.F., ELIAS, S., GILBERT, M.T.P., HAILE, J., MUNCH, K., KUZMINA, S., FROESE, D.G., SHER, A., HOLDAWAY, R.N. & WILLERSLEV, E. 2009. Non-destructive sampling of ancient insect DNA. *PLoS One* 4(4): e5048.
- THOMSON, J. 1858. Voyage au Gabon. Histoire naturelle des insectes et des arachnids recueillis pendant un voyage fait au Gabon en 1856 et 1857 par M. Henry C. Deyrolle sous les auspices de Mm. le comte de Mnischek et James Thomson précédée de l'histoire du voyage. *Archives entomologiques* 2: 7–469.
- THUY, B. & STÖHR, S. 2016. A new morphological phylogeny of the Ophiuroidea (Echinodermata) accords with molecular evidence and renders microfossils accessible for cladistics. *PLoS One* 11(5): e0156140.

- TORRES-PÉREZ, F., BORIC-BARGETTO, D., RODRIGUEZ-VALENZULA, E., ESCOBAR, C. & PALMA, R.E. 2017. Molecular phylogenetic analyses reveal the importance of taxon sampling in cryptic diversity: *Liolaemus nigriviridis* and *L. monticola* (Liolaeminae) as focal species. *Revista Chilena de Historia Natural* 90(5): <https://doi.org/10.1186/s40693-017-0068-z>
- TRIMEN, R. 1891. On Butterflies collected in Tropical South-western Africa by Mr. A.W. Eriksson. *Proceedings of the Zoological Society of London*. London 59–107.
- TSHIKAE, B.P., DAVIS, A.L.V. & SCHOLTZ, C.H. 2008. Trophic associations of a dung beetle assemblage (Scarabaeidae: Scarabaeinae) in a woodland savanna of Botswana. *Environmental Entomology* 37(2): 431–441.
- VAN DAELE, P.A.A.G., DAMMANN, P., MEIER, J.L., KAWALIKA, M., VAN DE WOESTIJNE, C. & BURDA, H. 2004. Chromosomal diversity in mole-rats of the genus *Cryptomys* (Rodentia: Bathyergidae) from the Zambezi region: with descriptions of new karyotypes. *Journal of the Zoological Society of London* 264: 317–326.
- VAN VALEN, L. 1976. Ecological Species, Multispecies and Oaks. *Taxon* 25(2-3): 233–239.
- VAN VELZEN, R., COLLINS, S.C., BRATTSTRÖM, O. & CONGDON, T.C.E. 2016. Description of a new *Cymothoe* Hübner, 1819 from northern Mozambique (Lepidoptera: Nymphalidae: Limenitidinae). *Metamorphosis* 27: 34–41.
- VAZ DE MELLO, F.Z. 2007. Revision taxonomica e analisis filogenetico de la tribu Ateuchini. *Xalapa, Veracruz, Mexico: Instituto de Ecologica*. A.C. 238 pp.
- VERDUGO, A. & DRUMONT, A. 2015. Revision du genre *Calicnemis* Laporte, 1832: approche morphologique et genetique (Coleoptera, Scarabaeidae, Dynastinae). *Revue de l'association Roussillonaise d'Entomologie* 24: 1–61.
- VOGT, L. 2002. Testing and weighting characters. *Organisms Diversity & Evolution* 2(4): 319–333.
- WALTER, P. 1978. Recherches écologiques et biologiques sur les scarabéids coprophages d'une savane du Zaïre. *Thèse Docteur d'Etat, Université des Sciences et Techniques du Languedoc, Montpellier*, 366pp. [unpublished]
- WATERHOUSE, C.O. 1888. On some Coleoptera from Eastern Equatorial Africa received from Emin Pasha. *Proceedings of the Zoological Society of London* 86–87.
- WATERHOUSE, C.O. 1891. New Scarabaeidae in the British Museum: a Fifth Contribution. *The Annals and Magazine of natural History, including Zoology, Botany and Geology*. London 6(7): 507–522.
- WEIDNER, H. 1976. Die Entomologischen Sammlungen des Zoologischen Instituts und Zoologischen Museums der Universität Hamburg, IX. Teil, Insecta VI. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 73: 87–264.
- WHEELER, Q.D. & PLATNICK, N.I. 2000. The phylogenetic species concept (sensu Wheeler & Platnick). In: Wheeler, Q.D. & Meier, R. Eds. *Species Concepts and Phylogenetic Theory: A Debate*. Columbia University Press, New York, 256 pp.
- WHEELER, Q.D. 2014. Are reports of the death of taxonomy an exaggeration? *New Phytologist* 201: 370–371.
- WHITE, F. 1983. *The Vegetation of Africa*. Unesco, Paris.

WIENS, J.J. 2001. Character analysis in morphological phylogenetics: problems and solutions. *Systematic Biology* 50(5): 689–699.

WILKINSON, M. 1995. A comparison of two methods of character construction. *Cladistics* 11: 297–308.

WORTHINGTON, S. 2017. Selection of character coding method is not phylogenetically neutral: a test case using hominoids. *Folia Primatologica* 88(5): 385–400.

YAMAMOTO, S. & MARUYAMA, M. 2017. Phylogeny of the rove beetle tribe Gymnusini sensu n. (Coleoptera: Staphylinidae: Aleocharinae): implications for the early branching events of the subfamily. *Systematic Entomology*, 43(1): 183–199.

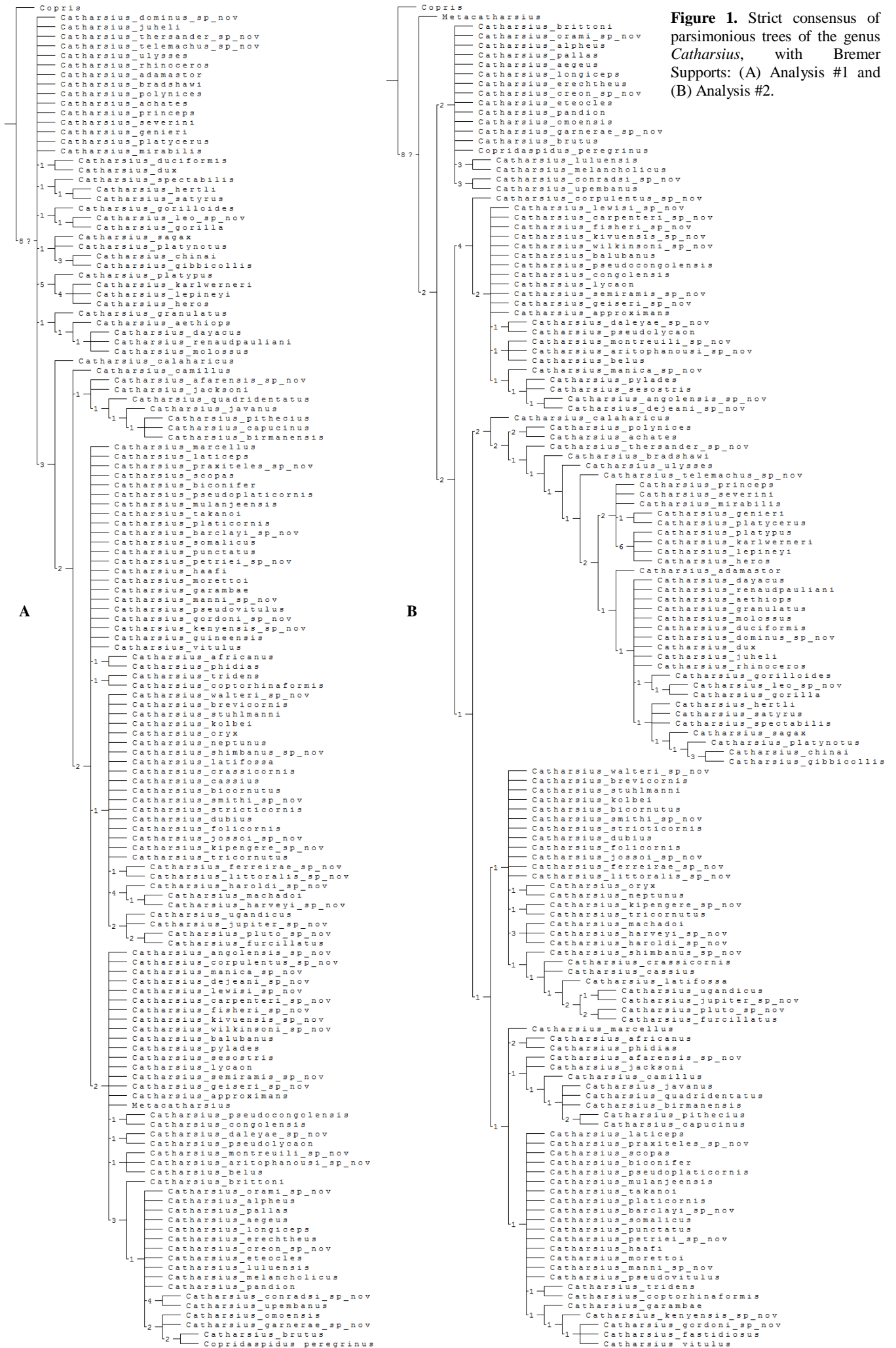
YU, Y., HARRIS, A.J. & HE, X.J. 2012. *RASP* (Reconstruct Ancestral State in Phylogenetics ) Version 2.1b.

ZIMMERMAN, J., HAJIBABAEI, M., BLACKBURN, D.C., HANKEN, J., CANTIN, E., POSFAI, J. & EVANS, T.C. 2008. DNA damage in preserved specimens and tissue samples: a molecular assessment. *Frontiers in Zoology* 5:18 doi:10.1186/1742-9994-5-18

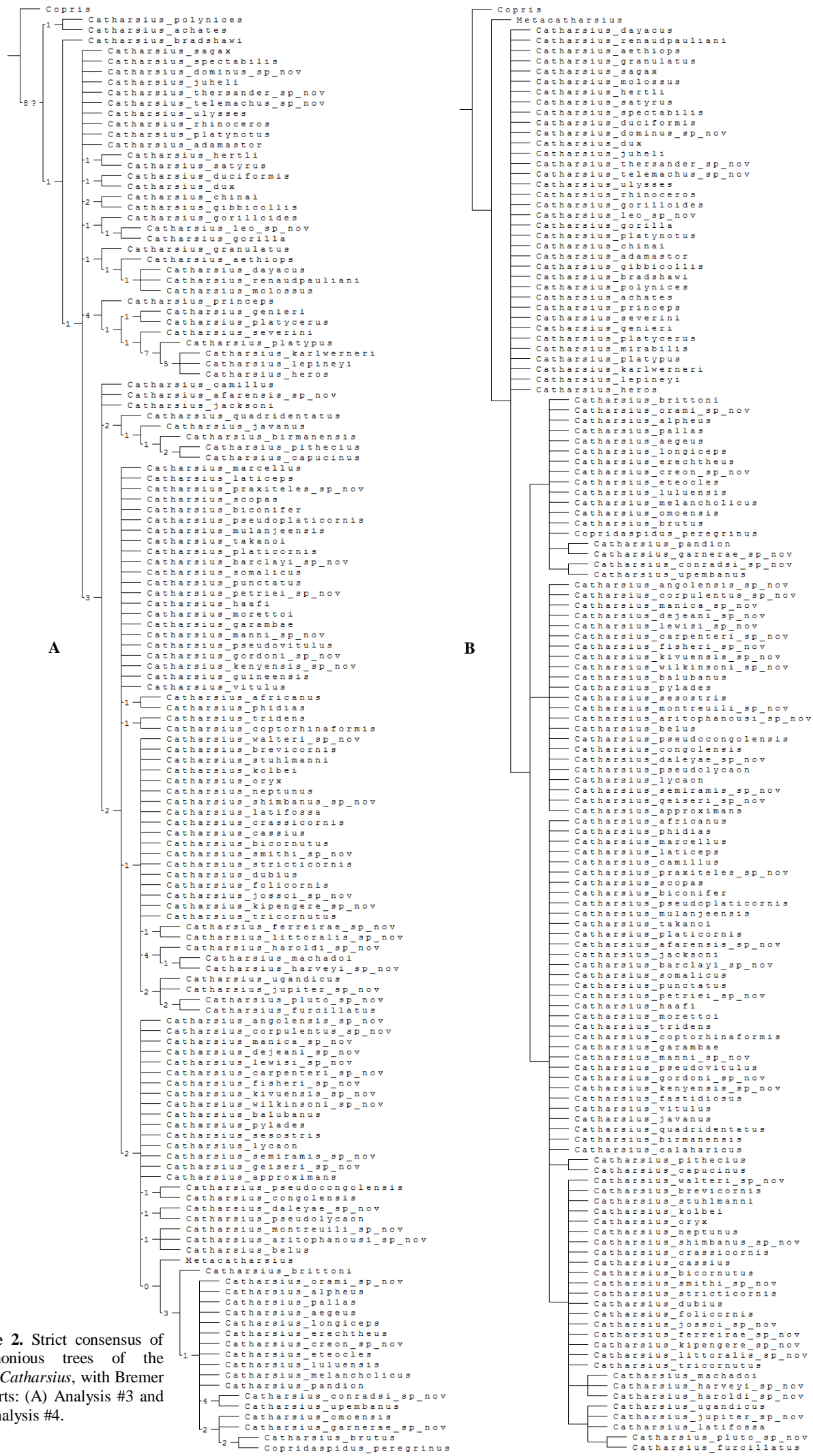


## **APPENDICES**

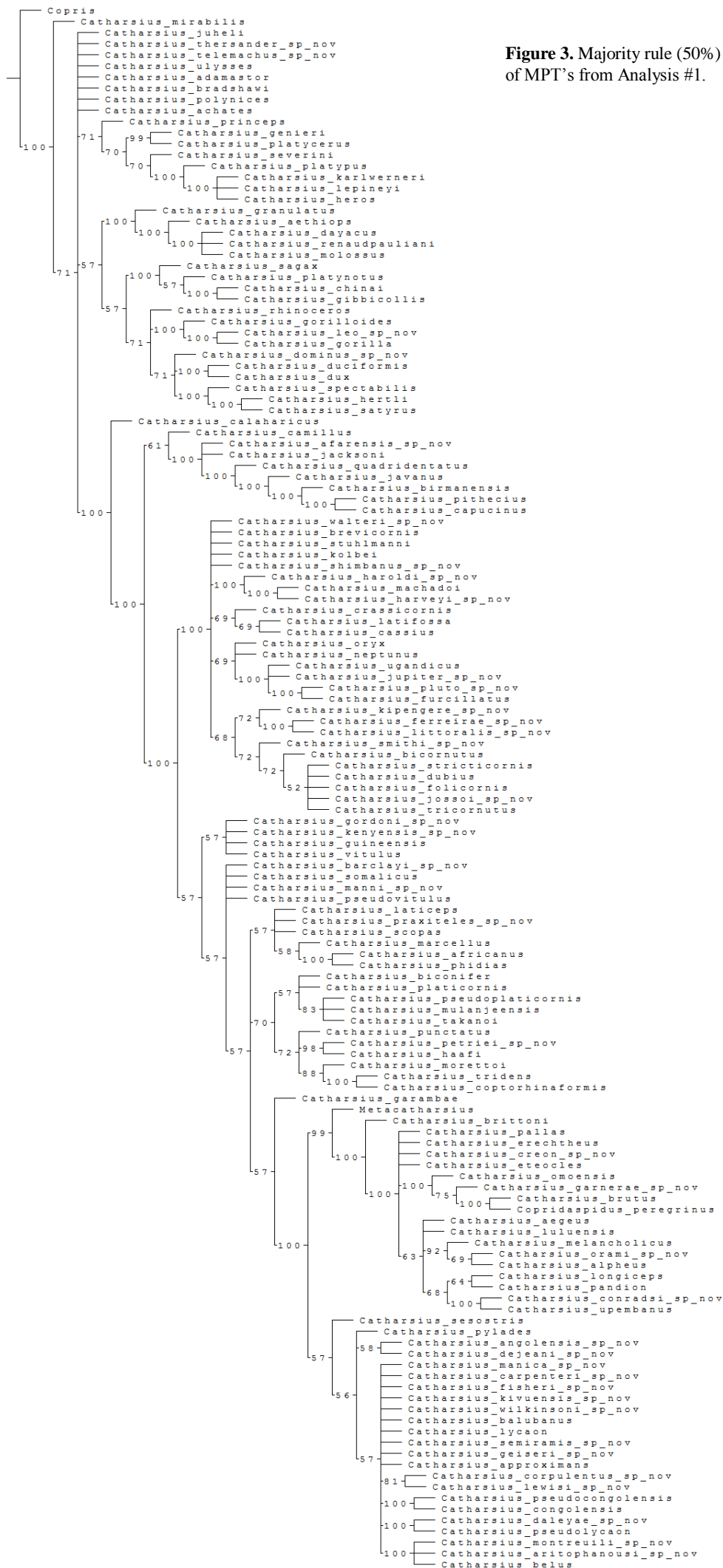
# APPENDIX I - Supplementary trees



**Figure 1.** Strict consensus of parsimonious trees of the genus *Catharsius*, with Bremer Supports: (A) Analysis #1 and (B) Analysis #2.



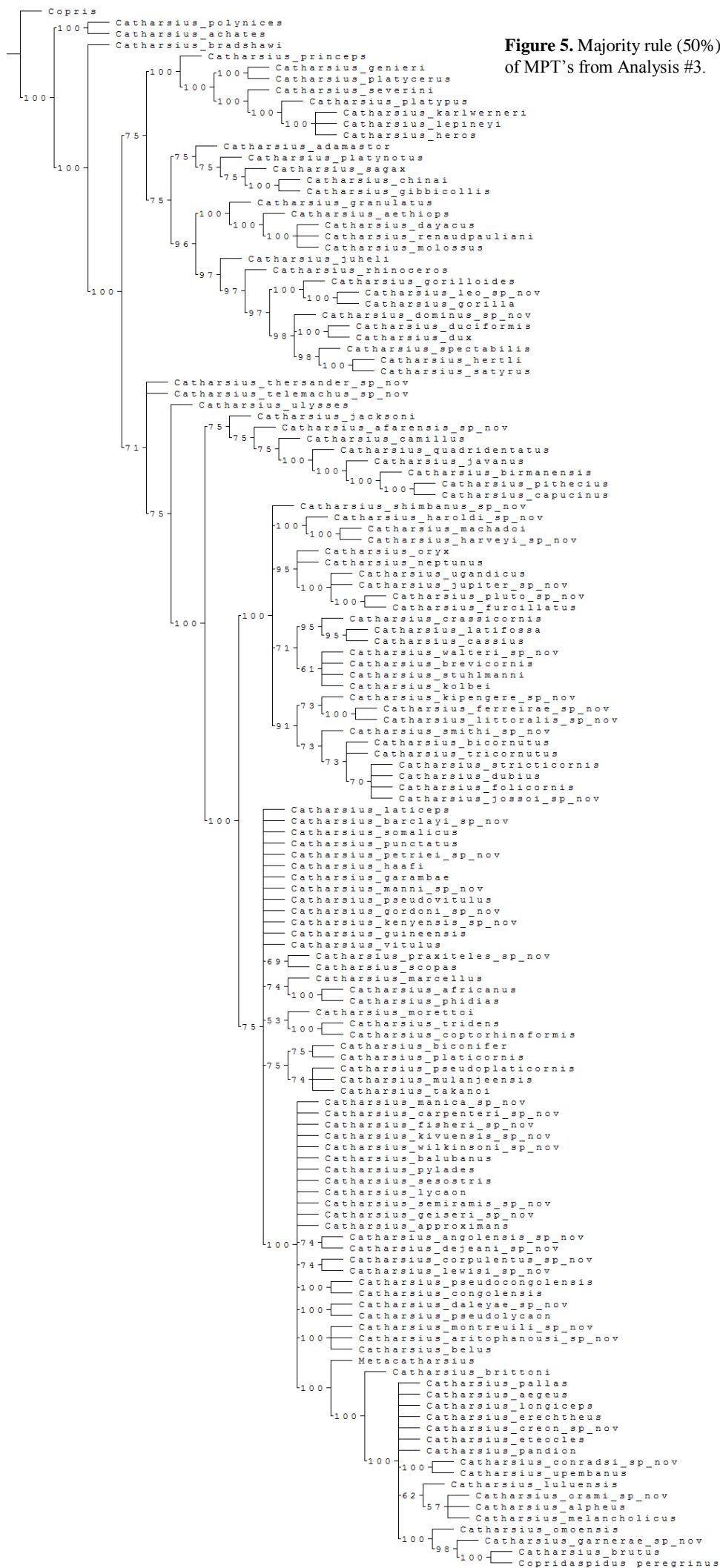
**Figure 2.** Strict consensus of parsimonious trees of the genus *Catharsius*, with Bremer Supports: (A) Analysis #3 and (B) Analysis #4.

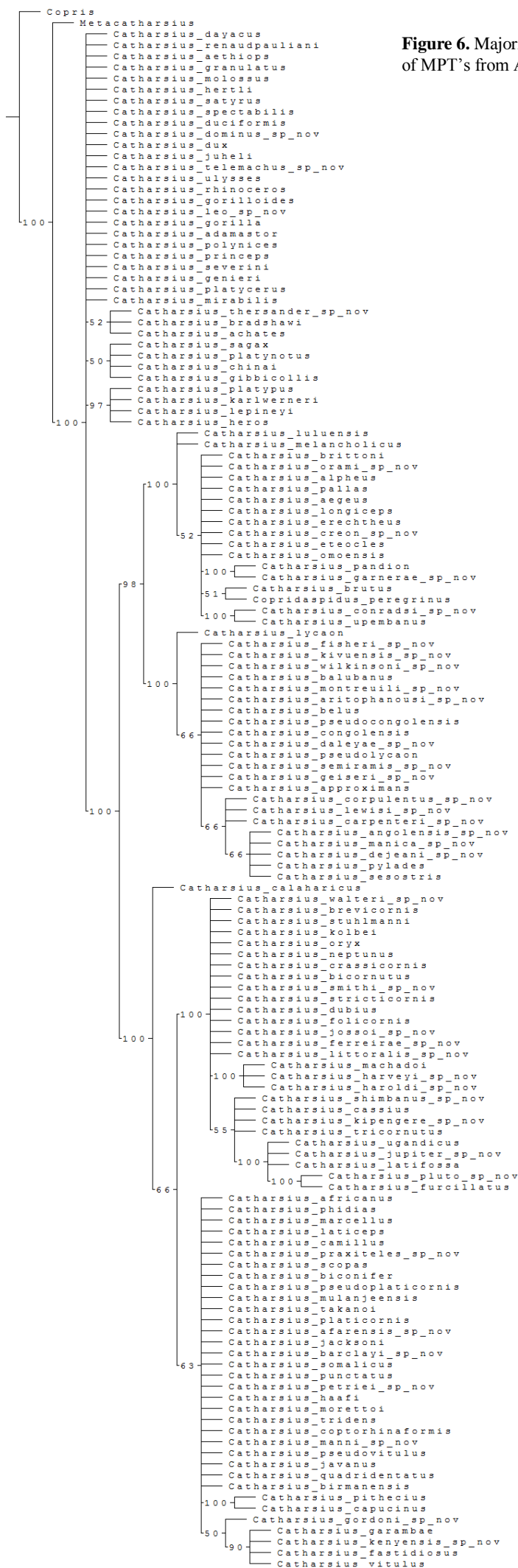


**Figure 3.** Majority rule (50%) consensus of MPT's from Analysis #1.



**Figure 4.** Majority rule (50%) consensus of MPT's from Analysis #2.





**Figure 6.** Majority rule (50%) consensus of MPT's from Analysis #4.

## APPENDIX II - Morphological characters

<b>HEAD</b>	
1	shape of cephalic horn (0: triangular [Fig. 1C]; 1: subconical [Fig. 1A]; 2: rectangular [Fig. 1B])
2	bifurcation of cephalic horn (0: absent; 1: present [Fig. 1B])
3	lateral flattening of the cephalic horn (0: absent; 1: present [Fig. 1E])
4	angled lateral side of cephalic horn (0: absent; 1: present [Fig. 1E])
5	angle of cephalic horn (0: upright, curved forward before bending back on itself [Fig. 1D]; 1: angled forward [Fig. 1I]; 2: perpendicular to clypeus [Fig. 1L]; 3: recurved [Fig. 1O])
6	length of cephalic horn higher than pronotum (0: absent; 1: present [Fig. 1D])
7	orientation of cephalic horn on clypeus (0: centrally [Fig. 1J]; 1: anteriorly [Fig. 1K]; 2: posteriorly [Fig. 1N])
8	smooth microsculpture of cephalic horn (0: absent; 1: present [Fig. 1G])
9	horn carinate laterally, joining genal suture (0: absent; 1: present [Fig. 1M])
10	shape of the anterior margin of clypeus (0: continuous or slightly concave [Fig. 1M]; 1: broad and shallow concavity [Fig. 1H]; 2: deep concavity [Fig. 1G]; 3: broad triangular concavity > 90° medially [Fig. 1J]; 4: sharp triangular concavity < 90° medially [Fig. 1N])
11	anterior margin of clypeus with two sharp tooth-like projections (0: absent; 1: present [Fig. 1N])
12	lateral clypeal margin with upward pointing tooth at genal suture (0: absent; 1: present [Fig. 1D])
13	genae parallel-sided (0: absent; 1: present [Fig. 1K])
14	genae and anterior clypeal margin clearly indented (0: absent; 1: present [Fig. 1K])
15	mentum with concavity (0: absent; 1: present [Fig. 1Q])
16	shape of ventral clypeal tooth (0: sharp and pointed [Fig. 1P]; 1: broad and triangular [Fig. 1R])
17	scape wider at top than base (0: absent; 1: present [Fig. 2A])
<b>FORELEGS</b>	
18	shape of protibia with inner projection (0: absent; 1: present [Fig. 2A])
19	ventral protibial carina fused with insertion point of tarsi (0: absent; 1: present [Fig. 2B])
20	protibial ventral striae (0: absent; 1: present [Fig. 2B])
21	protibia with four teeth laterally (0: absent; 1: present [Fig. 2D])
22	protibial serration (0: absent; 1: present [Fig. 2C])
23	extent of protibial serration (0: < half the length [Fig. 2A]; 1: > half the length [Fig. 2C])
24	serration between protibial teeth (0: absent; 1: present [Fig. 2E])
25	ventral surface granulation (0: absent; 1: present [Fig. 2B])
26	shape of protibial spur (0: rectangular; 1: triangular [Fig. 2D])
27	apex of protibial spur (0: gently curved; 1: hooked [Fig. 2F])
28	inner margin of protibia convex (0: absent; 1: present [Fig. 2E])
29	femur with three complete or incomplete carinae (0: absent; 1: present [Fig. 2G])
<b>PRONOTUM</b>	
30	form of the anterior pronotal disc (0: smooth or with depressions [Fig. 2L]; 1: transversely carinate [Fig. 2I]; 2: with horns [Fig. 2J]; 3: tuberculate [Fig. 2K])
31	transverse carina smooth and gently arcuate (0: absent; 1: present [Fig. 2I])
32	transverse carina straight and serrated (0: absent; 1: present [Fig. 2M])
33	transverse carina with a distinct angle on each side of the midline (0: absent; 1: present [Fig. 2N])
34	transverse carina triangular (0: absent; 1: present [Fig. 3A])
35	transverse carina extended forward laterally (0: absent; 1: present [Fig. 2O])
36	carina gently compressed laterally in frontal view (0: absent; 1: present [Fig. 3B])
37	number of pronotal horns (0: two [Fig. 2J]; 1: three [Fig. 3C]; 2: four [Fig. 3D])
38	position of the two horns on pronotal disc (0: close together, near the midline [Fig. 2J]; 1: far apart, nearer the lateral margin [Fig. 3E])
39	direction of the horns (0: pointing forwards [Fig. 2J]; 1: pointing upwards [Fig. 3F])
40	angle of the horns (0: diverging [Fig. 2J]; 1: parallel [Fig. 3G]; 2: converging [Fig. 3F])
41	tubercles connected by wide V-shaped furrow (0: absent; 1: present [Fig. 3H])
42	sculpture of pronotal disc (0: smooth [Fig. 3K]; 1: granulose [Fig. 3L]; 2: punctate [Fig. 3M])
43	pronotal disc with smooth area wider than long (0: absent; 1: present [Fig. 2E])
44	depression on the dorsal surface of pronotal disc (0: absent; 1: present [Fig. 2M])
45	depressions underneath pronotal carina (0: absent; 1: present [Fig. 3J])
46	large depression on anterior declivity (0: absent; 1: present [Fig. 3I])
47	setae on anterior declivity (0: absent; 1: present [Fig. 1F])
48	angle of anterior declivity perpendicular to head (0: absent; 1: present [Fig. 3Q])
49	sculpture of central part of anterior declivity (0: smooth [Fig. 3N]; 1: fully granulose [Fig. 3O]; 2: punctate [Fig. 3P])
50	smooth region between fovea and latero-anterior margin (0: absent; 1: present [Fig. 4A])
51	anterior margin of pronotum incomplete (0: absent; 1: present [Fig. 3R])
52	centre of anterior margin of pronotum emarginate (0: absent; 1: present [Fig. 2I])
53	lateral pronotal margin concave (0: absent; 1: present [Fig. 3J])

54	latero-anterior angle of pronotum (0: angled [Fig. 3J]; 1: rounded [Fig. 3I])
55	prothoracic pleurae with large smooth region (0: absent; 1: present [Fig. 4C])
56	longitudinal carina of prosternum (0: absent; 1: present [Fig. 4D])
57	setae on prosternum (0: absent; 1: present [Fig. 4D])
58	projection on prosternum (0: absent; 1: present [Fig. 4E])
59	posterior border to pronotal disc (0: absent; 1: present [Fig. 3H])
60	large excavations on pronotal declivity (0: absent; 1: present [Fig. 4B])
	<b>ELYTRUM</b>
61	depth of striae (0: shallow [Fig. 4H]; 1: deep [Fig. 4F])
62	sculpture of interstriae (0: smooth [Fig. 4F]; 1: rugose [Fig. 4J]; 2: alutaceous [Fig. 4H])
63	punctures of interstriae (0: absent or very fine [Fig. 4G]; 1: heavily punctured [Fig. 4F]; 2: granulose [Fig. 4I])
64	9 <sup>th</sup> elytral interstria with carina (0: absent; 1: present [Fig. 4K])
65	presence of pseudoeopleural carina (0: absent; 1: present [Fig. 4K])
66	extent of pseudoeopleural carina (0: < half the length of elytrum [Fig. 4N]; 1: > half the length of elytrum [Fig. 4K])
67	shape of body (0: rounded [Fig. 4L]; 1: triangular [Fig. 4O])
68	scutellum (0: absent; 1: present [Fig. 4M])
	<b>VENTRITE</b>
69	Fifth sternite half the width of sixth sternite (0: absent; 1: present [Fig. 4P])
70	mesepisternal carina (0: absent; 1: present [Fig. 4Q])
71	setae on metasternum (0: absent; 1: present [Fig. 4D])
72	large rounded punctures on apex of metasternum (0: absent; 1: present [Fig. 4R])
	<b>MID/HIND LEGS</b>
73	Outline of posterior apex of mesatibia with undulation (0: absent; 1: present [Fig. 5E])
74	shape of middle femur ovoid (0: absent; 1: present [Fig. 5A])
75	mesa- and metatibial serration (0: absent; 1: present [Fig. 5D])
76	extent of mesa- and metatibial serration (0: < half the length [Fig. 5D]; 1: > half the length [Fig. 2H])
77	broad and expanded first tarsal segment (0: absent; 1: present [Fig. 5F])
78	number of teeth on metatibia (0: one; 1: two [Fig. 5H])
79	shape of metatibial spur (0: curved and pointed [Fig. 5B]; 1: square ended [Fig. 5C])
	<b>AEDEAGUS</b>
80	apex of parameres rounded (0: absent; 1 present [Fig. 5G])
81	angle on parameres (0: absent; 1: present [Fig. 5H])
82	excavation on meatus (0: absent, 1: present [Fig. 6A])
83	small semicircular indentation on paramere (0: absent; 1 present [Fig. 5I])
84	large circular indentation on paramere (0: absent; 1 present [Fig. 5J])
85	large excavation of most of the paramere (0: absent; 1 present [Fig. 5G])
	<b>ENDOPHALLUS</b>
86	AS (0: absent; 1: present [Fig. 1])
87	AS fused to LC (0: absent; 1: present [Fig. 6H])
88	FLP flat with a sclerotised and unsclerotised regions (0: absent; 1: present [Fig. 5K])
89	sclerotised region of FLP fused only medially (0: absent; 1: present [Fig. 5K])
90	sclerotised region of FLP fused along whole length (0: absent; 1: present [Fig. 5L])
91	sclerotised region of FLP fused at base only (0: absent; 1: present [Fig. 5M])
92	lateral margin of FLP notched at the suture between the sclerotised and unsclerotised regions (0: absent; 1: present [Fig. 5H])
93	left raspula (0: absent; 1: present [Fig. 7A])
94	right raspula (0: absent; 1: present [Fig. 7A])
95	A (0: absent; 1: present [Fig. 1])
96	AIS (0: absent; 1: present [Fig. 1])
97	LC (0: absent; 1: present [Fig. 1])
98	shape of LC groundplan 1 (0: absent; 1: present [Fig. 6F])
99	spiral on ventral surface of LC groundplan 1 (0: absent; 1 present [Fig. 6G])
100	LC groundplan 1 bilobed and emarginate centally (0: absent; 1: present [Fig. 6I])
101	shape of LC groundplan 2 (0: absent; 1: present [Fig. 6E])
102	shape of LC groundplan 3 (0: absent; 1: present [Fig. 6B])
103	shape of LC groundplan 4 (0: absent; 1: present [Fig. 6O])
104	lateral edge of LC groundplan 4 tridentate (0: absent; 1: present [Fig. 6D])
105	lateral edge of LC groundplan 4 with long basal protrusion (0: absent; 1: present [Fig. 6C])
106	shape of LC groundplan 5 (0: absent; 1: present [Fig. 6H])
107	base of LC groundplan 5 with weak concavity (0: absent; 1: present [Fig. 6P])
108	shape of LC groundplan 6 (0: absent; 1: present [Fig. 6K])
109	apex of LC groundplan 6 broad and angled (0: absent; 1 present [Fig. 6J])
110	base of LC groundplan 6 with undulation (0: absent; 1 present [Fig. 6R])
111	shape of LC groundplan 7 (0: absent; 1: present [Fig. 6M])

112	sharp projection on left ventral side of LC groundplan 7 (0: absent; 1: present [Fig. 6N])
113	sharp projections on right ventral side of LC groundplan 7 (0: absent; 1: present [Fig. 6N])
114	shape of LC groundplan 8 (0: absent; 1: present [Fig. 6L])
	<b>FEMALE</b>
	<b>HEAD</b>
115	raised clypeal shield (0: absent; 1: present [Fig. 7B])
116	shape of clypeal carina (0: rectangular horn [Fig. 7P]; 1: raised centrally with two tubercles on each side [Fig. 7B]; 2: tridentate, the central point higher than the other two [Fig. 7C]; 3: broad triangular projection [Fig. 7O]; 4: laterally flattened carina slightly raised or with tubercles centrally [Fig. 7K])
	<b>PRONOTUM</b>
117	form of pronotal disc (0: smooth [Fig. 7F]; 1: tuberculate [Fig. 7B]; 2: carinate [Fig. 7J]; 3: with horns [Fig. 7L])
118	position of tubercles (0: close together [Fig. 7J]; 1: far apart [Fig. 7M])
119	pronotal carina projecting and extended forward (0: absent; 1: present [Fig. 7D])
120	pronotal carina shorter than distance between eyes (0: absent; 1: present [Fig. 7H])
121	pronotal carina with an emargination pointing towards the posterior (0: absent; 1: present [Fig. 7C])
122	pronotal carina short, straight and uninterrupted (0: absent; 1: present [Fig. 7H])
123	pronotum with a semicircular carina (0: absent; 1: present [Fig. 7I])
124	pronotum with short angled carina in centre (0: absent; 1: present [Fig. 7E])
125	pronotum with a short carina weakly emarginate centrally (0: absent; 1: present [Fig. 7K])
126	pronotum with short carina as wide as clypeal carina (0: absent; 1: present [Fig. 7D])
127	sulcus between carina and anterior margin of pronotum (0: absent; 1: present [Fig. 7G])
128	pronotum with concave pronotal declivity in lateral view (0: absent; 1: present [Fig. 7N])
129	pronotal disc with indistinct depressions (0: absent; 1: present [Fig. 7F])
130	pronotal disc with smooth area (0: absent; 1: present [Fig. 7K])



### APPENDIX III - Character matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13
Copris	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890	0000011000000001100100	10-002	-----2	-----110000010010010101010000	00001110011000010000	0	-----0	000	-----0	0	0002	000000000000
Metacatharsius	001020201400001101100111010110	-----0	000001000010100100201110011000010110000000100	-----0	001	-----0	0	0030	-----000				
Catharsius_heros	0000200010011011001100	-----0	1000011000101101011011110011010	011000000101100	0	-----111101000	0	0	0	0112	000000000000		
Catharsius_lepineyi	0000200010011011001100	-----0	1000011000101101011011110011010	011000000101100	0	-----111101000	0	0	0	0112	000000000000		
Catharsius_karlwerneri	0000200010011011001100	-----0	1000011000101101011011110011010	011000000101100	0	-----111101000	0	0	0	0112	000000000000		
Catharsius_platypus	2100101000011011001100	-----0	1000011010101101011011110011010	011000000101100	0	-----111101000	0	0	0	0112	000000000000		
Catharsius_mirabilis	010001100000011001100	-----0	10012	-----0001	0	-----1001100000001010110111100111110110000000101100	0	-----111100010	0	0	0013	-----000	
Catharsius_platycerus	210010100000111001100	-----0	10000110101011010100111100111110111000000101100	0	-----111100000	0	0	0	0012	010000000000			
Catharsius_genieri	200010100000111001100	-----0	10000110101011010100111100111110111000000101100	0	-----111100000	0	0	0	0012	000000000000			
Catharsius_severini	000010100000011001100	-----0	100001001010110101201111001110110111000000101100	0	-----111100000	0	0	0	0012	010000000000			
Catharsius_princeps	0000101000001011001100	-----0	1000011000001010100111100111110111000000101100	0	-----111100000	0	0	0	0012	010000000000			
Catharsius_achates	0000101010000011001100	-----0	10100001001000110101001110001111101110100000101100	0	-----111110000	0	0	0	0022	0000000000001			
Catharsius_polynices	000010100000011001100	-----0	1010000100100011010100111000111110111000000101100	0	-----111110000	0	0	0	0022	000000000000			
Catharsius_bradshawi	0000101000001011001100	-----0	10000001001000110100001110001111101110100000101100	0	-----111110000	0	0	0	0022	0100000000001			
Catharsius_gibbicollis	0000101000001111001100	-----0	001011010000110100001110001111101110100000101100	0	-----1110	100	0	0	0	0022	000000000000		
Catharsius_adamastor	0000101000001111001100	-----0	00000110000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	010000000000			
Catharsius_chinai	0000101000001111001100	-----0	000011010000110100001110001111101110100000101100	0	-----1110	100	0	0	0	0022	000000000000		
Catharsius_platynotus	2100101000001111001100	-----0	000001100000110100201110001111101110100000101100	0	-----1110	100	0	0	0	0022	010000000000		
Catharsius_gorilla	000010100000011001100	-----0	01000100010011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	001000000000			
Catharsius_leo_sp_nov	000010100000011001100	-----0	01000100010011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	001000000000			
Catharsius_gorilloides	100010100000011001100	-----0	100100010000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	001000000000			
Catharsius_rhinoceros	1000101000001011001110	-----0	00000100010011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	001000000000			
Catharsius_ulysses	0000200000001011001100	-----0	1000000100000110100201110011111101110100000101100	0	-----111110000	0	0	0	0022	010000000000			
Catharsius_telemachus_sp_nov	0000101000001011001100	-----0	10000000100000110100001110001111101110100000101100	0	-----111100000	0	0	0	0022	010000000000			
Catharsius_thersander_sp_nov	0000101000001011001100	-----0	10000001100000110100001110001111101110100000101100	0	-----111110000	0	0	0	0022	0000000000001			
Catharsius_juheli	000010100000011001110	-----0	00000100000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	010000000000			
Catharsius_dux	000010100000011001110	-----0	00000100000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	011000000000			
Catharsius_dominus_sp_nov	000010100000011001110	-----0	00000100000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	001000000000			
Catharsius_duciformis	000010000000011001110	-----0	00000100000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	011000000000			
Catharsius_spectabilis	000010100000111001110	-----0	00000100000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	000000000000			
Catharsius_satyrs	210010100000011001110	-----0	00000100000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	000000000000			
Catharsius_hertli	210010100000011001110	-----0	00000100000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	000000000000			
Catharsius_molossus	0000101010000011001100	-----0	00000110000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	0010000000000			
Catharsius_sagax	000010100000011001110	-----0	00000100000011010020111000111110111000000101100	0	-----1110	100	0	0	0	0022	000000000000		
Catharsius_granulatus	0000101000000011001100	-----0	00000110000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	000000000000			
Catharsius_aethiops	0000101000000011001100	-----0	00000110000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	001000000000			
Catharsius_renaudpauliani	0000101010000011001100	-----0	00000110000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	001000000000			
Catharsius_dayacus	0000101010000011001100	-----0	00000110000011010020111000111110111000000101100	0	-----111100000	0	0	0	0022	001000000000			
Catharsius_calaharicus	0000101000000011001100	-----0	100000010000001101000011000011101101101000010101000	1110	000	0	0	0	1030	-----001			
Catharsius_birmanensis	0000210010000011001100	-----0	100000001000001101000011000111111011100000010101000	1110	000	0	0	0	1010030	-----010			
Catharsius_quadridentatus	000001001000001100110100010012	-----2	-----000000100000110100001100011111101110000001010100101110	000	0	0	0	0	1110	????????????????			
Catharsius_javanus	000001001000001100110100010013	-----00	000000100000110100201100011111101110000001010100101110	000	0	0	0	0	10100311	-----000			
Catharsius_capucinus	001130211000001100110100010012	-----2	-----10000000100000110100001100011111101110000001010100101110	000	0	0	0	0	1000040	-----011			
Catharsius_pithecius	000001001000001100110100010013	-----011	000000100000110101001100011111101110000001010100101110	000	0	0	0	0	1000030	-----011			
Catharsius_vitulus	001120201000001100110100010013	-----010	0000000000000011010100110000101001011101010010101000	1110	000	0	0	0	1110040	-----001			

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 Catharsius kenyensis\_sp\_nov 001010001000001100110100010013-----01100000000000011010100110000101001011101010010101000-1110-000-0-0-1110040-----011  
 Catharsius gordonii\_sp\_nov 001110001000001100110100010013-----010000000000000110100110000101001011100000010101000-1110-000-0-0-1110040-----011  
 Catharsius pseudovittulus 001010101000001100110100010013-----0110000000000001101002011000110100101110100101010100101110-000-0-0-1110040-----011  
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 Catharsius pluto\_sp\_nov 000010001000001100110100010012-----0002-1100000000000001101112110001111001011101000010101011110-001010-0-0-00410-----0-0  
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 Catharsius ugandicus 010010001000001100110100010012-----0002-0-00000000000001101100110001111001011101000010101011110-001010-0-0-00410-----0-1  
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Catharsius_stuhlmanni	200020001000001100110100010012----	0012-11000000000000110101001100011110010111010000101010101110-001100-0-0-0042-000000011001
Catharsius_brevicornis	010010001000001100110100010012----	0012-11000000000000110101001100011110010111010000101010101110-001100-0-0-0042-000000011001
Catharsius_walteri_sp_nov	000010001000001100110100010012----	0012-11000000000000110101001100011110010111010000101010101110-001100-0-0-0042-000000011001
Catharsius_haroldi_sp_nov	0000100010000011001100-010012----	0100-11000000100000110101001100011110010111010100101010101110-001000-0-0-0042-100000000001
Catharsius_harveyi_sp_nov	0011100010000011001100-010012----	0100-11000000100000110101001100011110010111010100101010101110-001000-0-0-0042-100000000001
Catharsius_machadoi	0010302001000011001100-010012----	0100-11000000100000110101001100011110010111010100101010101110-001000-0-0-0042-100000000001
Catharsius_approximans	001010001000001101110100010013-----	011000000000000011010000110001101001011110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_geiseri_sp_nov	001130001000001101110100010013-----	0110000000000000110101001100011010010111110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_semiramis_sp_nov	001020001000001101110100010013-----	0110000000000000110100001100011010010111110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_lycaon	000000001000001101110100010012----	0101-11000000000000110101201100011010010111010001111001-0-1110-000-110-0-0042-000100000001
Catharsius_pseudolycaon	000010001000001101110100010012----	0101-11000000100000110101001100011010010111110001111001-0-1110-000-110-0-0032-000100000001
Catharsius_daleyae_sp_nov	000010001000001101110100010012----	0101-11000000100000110101001100011010010111110001111001-0-1110-000-110-0-0????????????????
Catharsius_congolensis	000011000000001101110100010012----	2--11000000000000110100001100011010010111110001111001-0-1110-000-110-0-0042-000000000001
Catharsius_pseudocongolensis	000010001000001101110100010012----	2--11000000000000110100001100011010010111110001111001-0-1110-000-110-0-0042-000000000001
Catharsius_belus	001120211000001101110100010013-----	0111000000000000110101201100011010010111110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_aritophanousi_sp_nov	001120211000001101110100010013-----	0111000000000000110101201100011010010111110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_montreuii_sp_nov	001130211000001101110100010013-----	0111000000000000110101201100011010010111110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_sesostris	001020201000001101110100010013-----	00-0000010000000110100201100011010010111110001111001-0-1110-000-100-0-0032-000100000000
Catharsius_pylades	001020201000001101110100010013-----	00-0000000000000110100201100011010010111110001111001-0-1110-000-100-0-0032-000100000000
Catharsius_balubanus	001020201000001101110100010013-----	0110000000000000110100201100011010010111110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_wilkinsoni_sp_nov	000010001000001101110100010013-----	0110000000000000110100001100011010010111110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_kivuensis_sp_nov	000010001000001101110100010013-----	0110000000000000110100201100011010010111110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_fisheri_sp_nov	000010001000001101110100010013-----	0110000000000000110100001100011010010111110001111001-0-1110-000-110-0-0042-000100000001
Catharsius_carpenteri_sp_nov	000010001000001101110100010013-----	0110000000000000110101001100011010010111110001111001-0-1110-000-100-0-0042-000100000001
Catharsius_lewisi_sp_nov	000010001000001101110100010013-----	0110000010000000110100201100011010010111110001111001-0-1110-000-100-0-0042-000100000001
Catharsius_dejeani_sp_nov	001020201000001101110100010013-----	00-0000000000000110101001100011010010111110001111001-0-1110-000-100-0-0032-000100000000
Catharsius_manica_sp_nov	000010001000001101110100010013-----	00-0000000000000110100201100011010010111110001111001-0-1110-000-100-0-0042-000100000000
Catharsius_corpulentus_sp_nov	0000100010000011011100-010013-----	0110000010000000110100001100011010010111110001111001-0-1110-000-100-0-0032-000000000001
Catharsius_angolensis_sp_nov	001120201000001101110100010013-----	00-0000000000000110101201100011010010111110001111001-0-1110-000-100-0-0032-000100000000
Copridaspis_peregrinus	0010202113000010001100-110013-----	011000012000010100001001100111010010110000000101001-0-1110-000-0-1000-00310-----001
Catharsius_upembanus	001130211310101000110100110013-----	2110000000000000110100001100111110010110000000101001-0-1110-000-0-1010-00311-----000
Catharsius_conradsi_sp_nov	001130211310101000110100110013-----	2100000000000000110100001100111110010110000000101001-0-1110-000-0-1010-00310-----000
Catharsius_brutus	000010001300001000110110110013-----	02-000002000000110100211100111110010110000000101001-0-1110-000-0-1000-00310-----001
Catharsius_garnerae_sp_nov	001120011410001000110110110013-----	02-000002000000110100211100111110010110000000101001-0-1110-000-0-1100-00310-----000
Catharsius_omoensis	001120211410001000110110010013-----	02-000002000000110100201100111110010110000000101001-0-1110-000-0-1000-00310-----000
Catharsius_pandion	001130211410001000110110010013-----	20-0000000000000110100211100111110010110000000101001-0-1110-000-0-1100-00310-----000
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Catharsius_luluensis	001130201410001000110100110013-----	20-000001000000011100201100111110010110010000101001-0-1110-000-0-1000-00310-----000
Catharsius_eteocles	001120201410001000110100010013-----	20-0000010000000110100201100111110010110000000101001-0-1110-000-0-1000-00311-----000
Catharsius_creon_sp_nov	001020201410001000110100010013-----	20-0000010000000110100201100111110010110000000101001-0-1110-000-0-1000-00311-----000
Catharsius_erechtheus	001120201410001000110100010013-----	22-000002000000110100201100111110010110000000101001-0-1110-000-0-1000-00311-----000
Catharsius_longiceps	001130211410001000110100010013-----	20-0000000000000110100201100111110010110000000101001-0-1110-000-0-1000-00310-----000
Catharsius_aegeus	001130211410001000110100110013-----	20-0000010000000110100201100111110010110000000101001-0-1110-000-0-1000-00310-----000
Catharsius_pallas	001120211410001000110100010013-----	20-0000010000000110100201100111110010110000000101001-0-1110-000-0-1000-00310-----000
Catharsius_alpheus	000010001410001000110100110013-----	20-0000010000000110100201100111110010110000000101001-0-1110-000-0-1000-00311-----000
Catharsius_orami_sp_nov	000010001410001000110100110013-----	20-0000010000000110100201100111110010110000000101001-0-1110-000-0-1000-00311-----000
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## APPENDIX IV - Character images

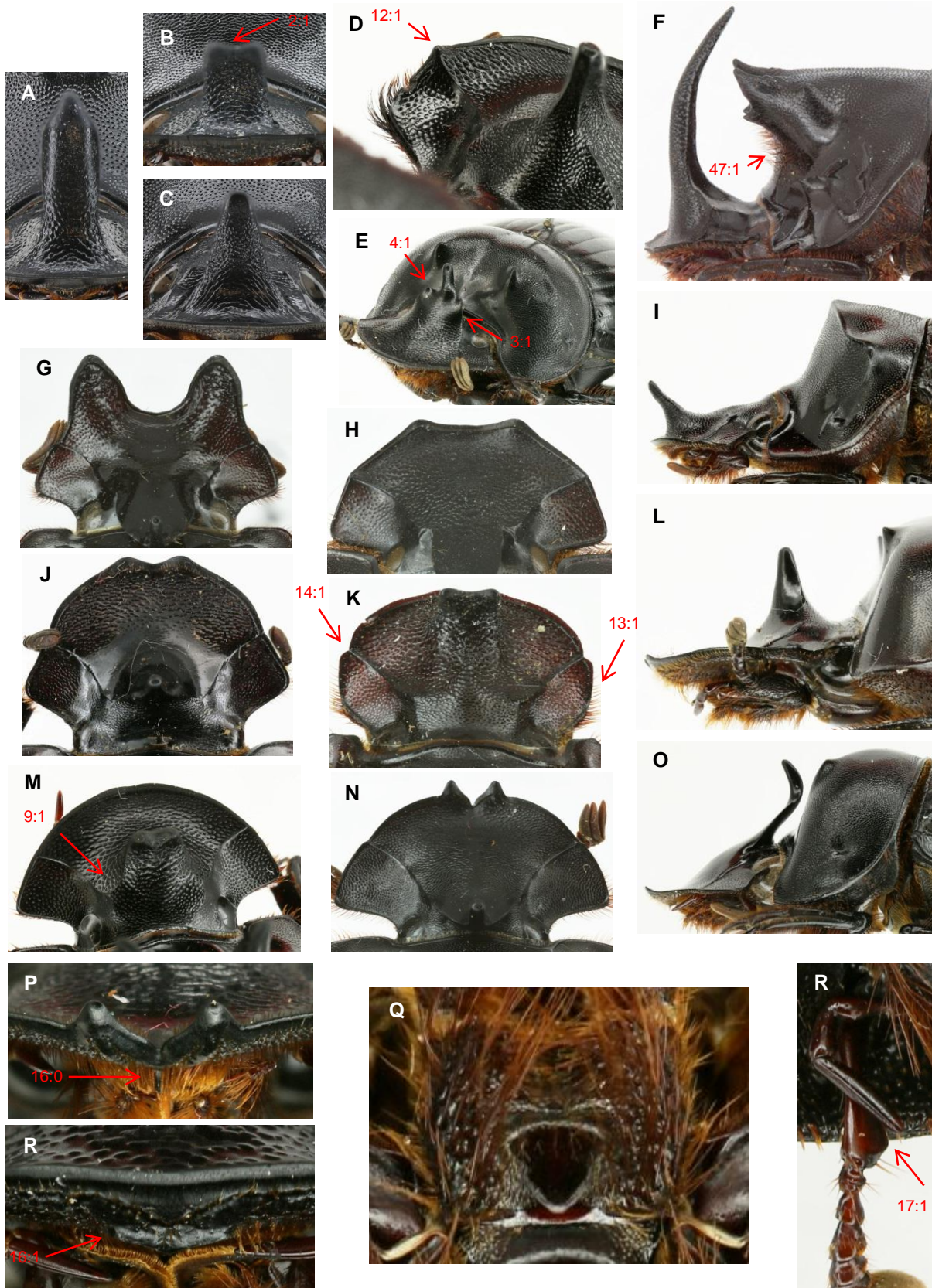


Figure 1: cephalic horn of *C. rhinoceros* (A), *C. platynotus* (B) and *C. bradshawi* (C); head of *C. heros* (D), *C. marcellus* (E & O), *C. mirabilis* (F), *C. coptorhinaformis* (G), *C. machadoi* (H), *C. platycerus* (I), *C. peregrinus* (J & L), *C. platynotus* (K), *C. shimbanus* (M) and *C. luluensis* (N); ventral clypeal tooth of *C. luluensis* (P) and *C. harveyi* (R); mentum of *C. bradshawi* (Q), antennal segments of *Copris* sp. (R).



Figure 2: protibia of *C. lycaon* (A), *C. luluensis* (B), *C. brutus* (C), *C. juheli* (D), *Metacatharsius* sp. (E) and *C. takanoi* (F); profemur of *C. harveyi* (G); mesatibia of *Copris* sp. (H); pronotal disc of *C. platycerus* (I), *C. neptunus* (J), *C. eteocles* (K), *C. calaharicus* (L), *C. heros* (M), *C. bradshawi* (N) and *C. dayacus* (O).

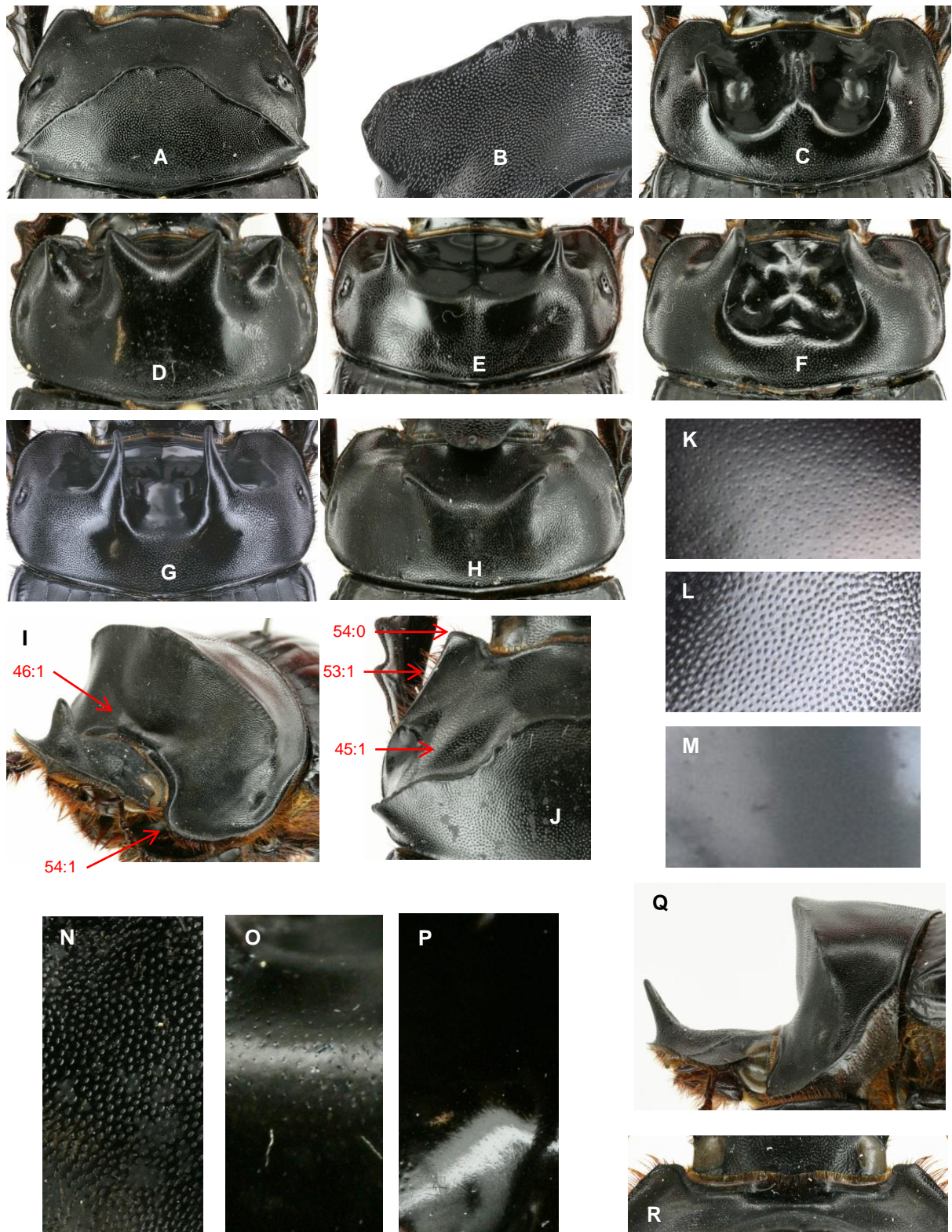


Figure 3: pronotal disc of *C. dux* (A & B), *C. kolbei* (C), *C. jacksoni* (D), *C. harveyi* (E), *C. cassius* (F), *C. smithi* (G), *C. phidias* (H) and *C. gorilla* (J); pronotal anterior declivity of *C. gibbicollis* (I & Q); sculpture of pronotal disc in *C. brutus* (K), *C. alpheus* (L) and *C. harveyi* (M); sculpture of the anterior declivity in *C. gorilla* (N), *C. pandion* (O) and *C. harveyi* (P); anterior pronotal margin of *C. gibbicollis* (R).

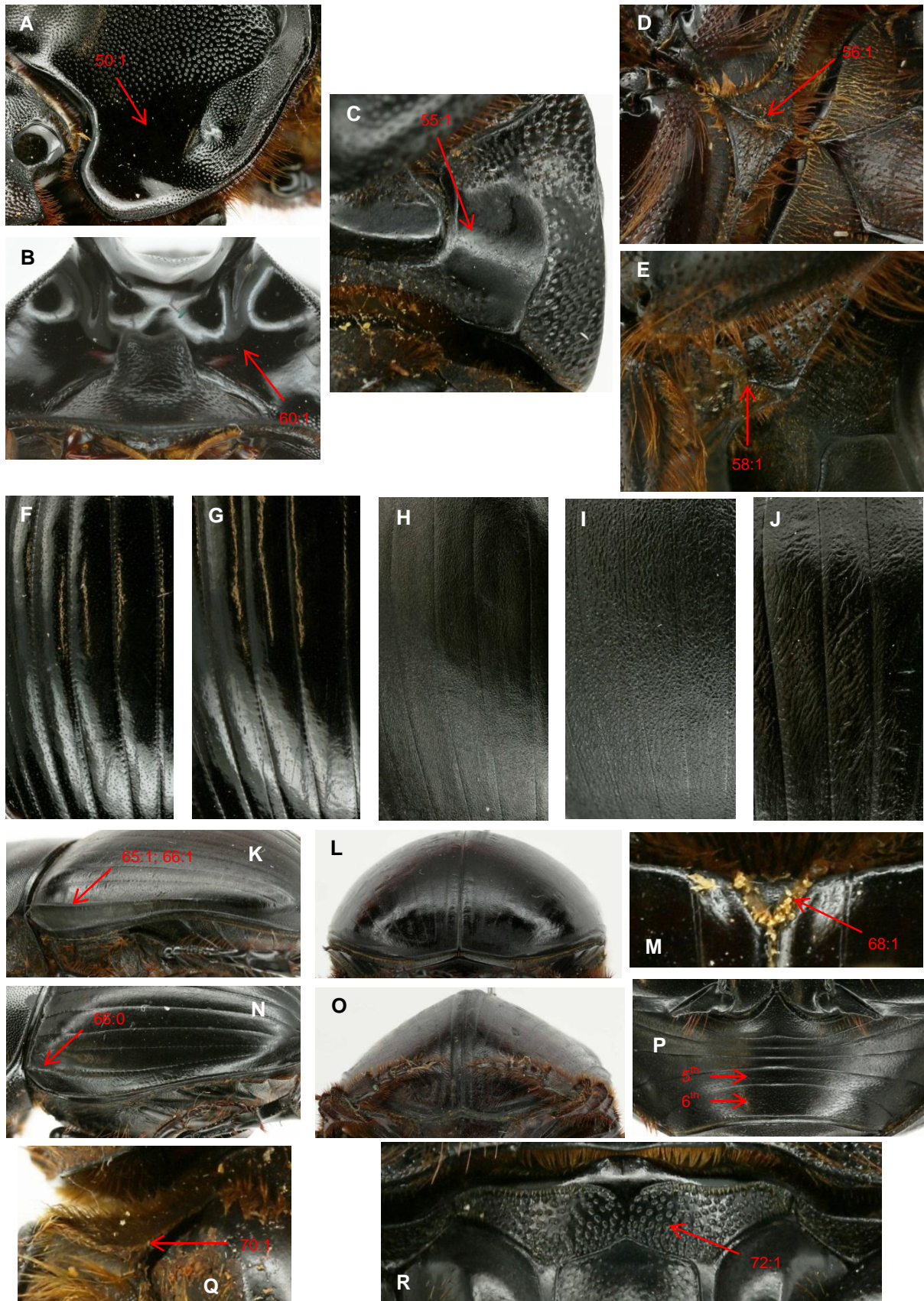


Figure 4: pronotal lateral declivity of *C. platycerus* (A); pronotal anterior declivity of *C. shimbanus* (B); prothoracic pleura of *Copris* sp. (C); prosternum of *C. bradshawi* (D) and *C. luluensis* (E); left elytrum of *C. platycornis* (F), *C. harveyi* (G), *C. dux* (H), *C. rhinoceros* (I) and *C. heros* (J); pseudoepipleural carina of *C. luluensis* (K) and *C. shimbanus* (N); rear-view of *C. dux* (L) & *C. mirabilis* (O); scutellum of *C. peregrinus* (M); sternites of *C. luluensis* (P); mesepisternal carina of *C. jacksoni* (Q); metasternum of *Metacatharsius* sp. (R).

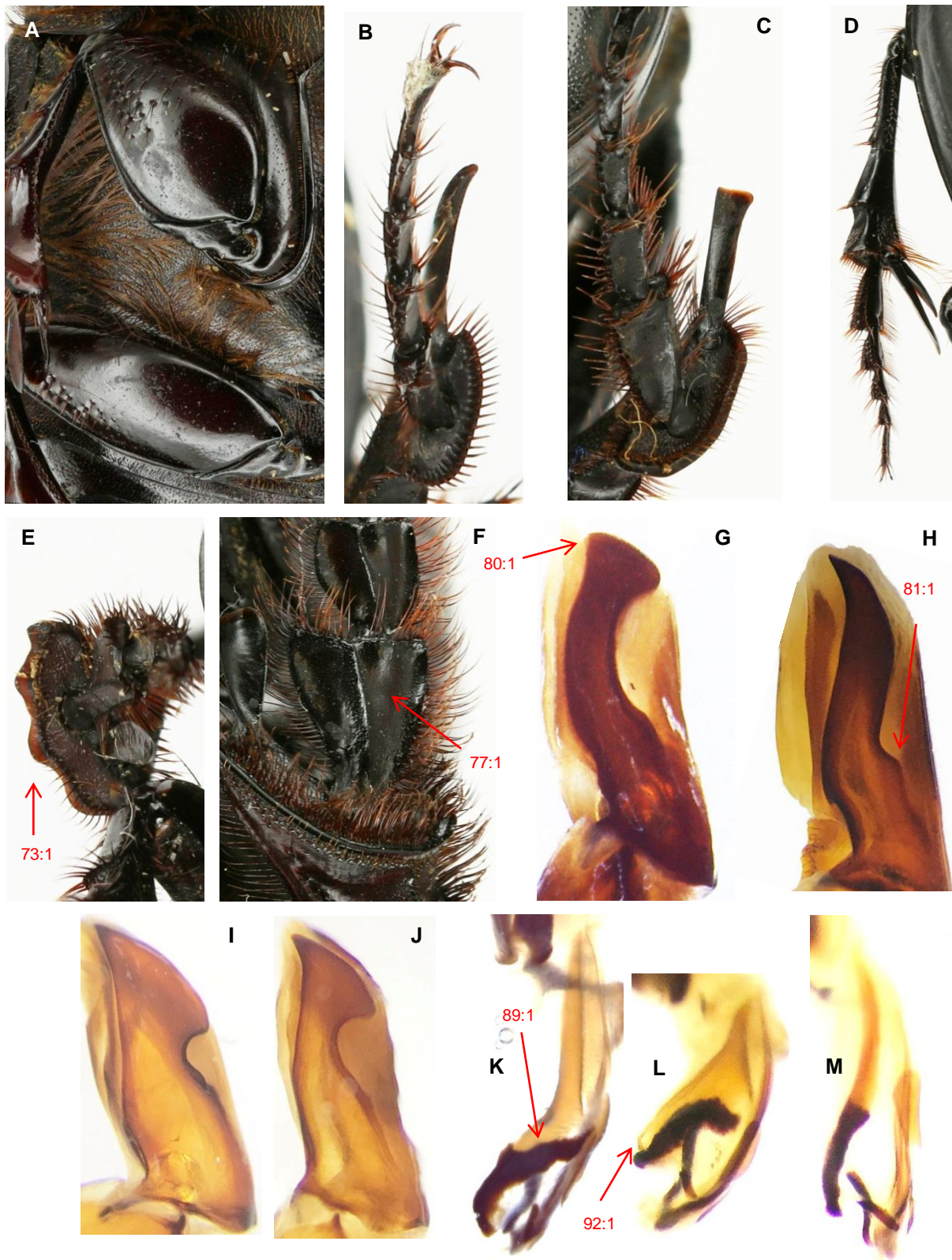


Figure 5: the metasternum, mesafemur and metafemur of *C. bradshawi* (A); metatibial spur of *C. luluensis* (B) and *C. dux* (C); metatibia of *C. luluensis* (D) and *C. dux* (E); first metatarsal segment of *C. heros* (F); parameres of *C. sesostris* (G), *C. telemachus* (H), *C. haroldi* (I) and *C. biconifer* (J); FLP of *C. dux* (K), *C. machadoi* (L) and *C. eteocles* (M).

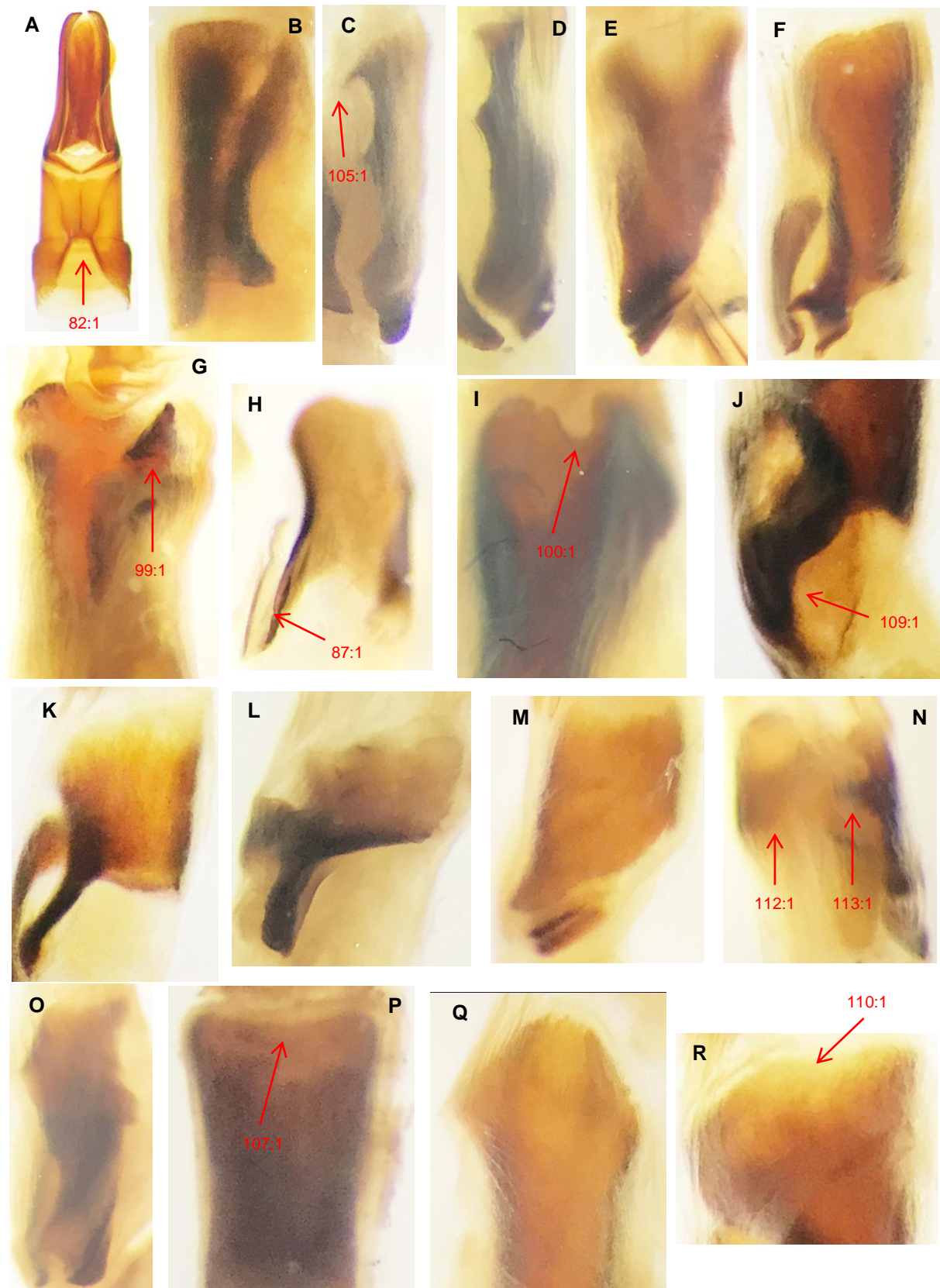


Figure 6: parameres and meatus of *Copris* sp. (ventral view, A); AS and LC of *C. manica* (H); LC of *C. mirabilis* (dorsal view, B), *C. tricornutus* (lateral view, C & dorsal view, O), *C. pluto* (lateral view, D), *C. gibbicollis* (dorsal view, E), *C. adamastor* (dorsal view, F), *C. polynices* (ventral view base, G), *C. heros* (dorsal view base, I), *C. pandion* (dorsal view apex, J), *C. luluensis* (dorsal view, K), *C. calaharicus* (dorsal view, L), *C. vitulus* (dorsal view, M & ventral view, N) *C. daleyae* (dorsal view base, P), *C. dux* (dorsal view base, Q) and *C. upembanus* (dorsal view base, R).

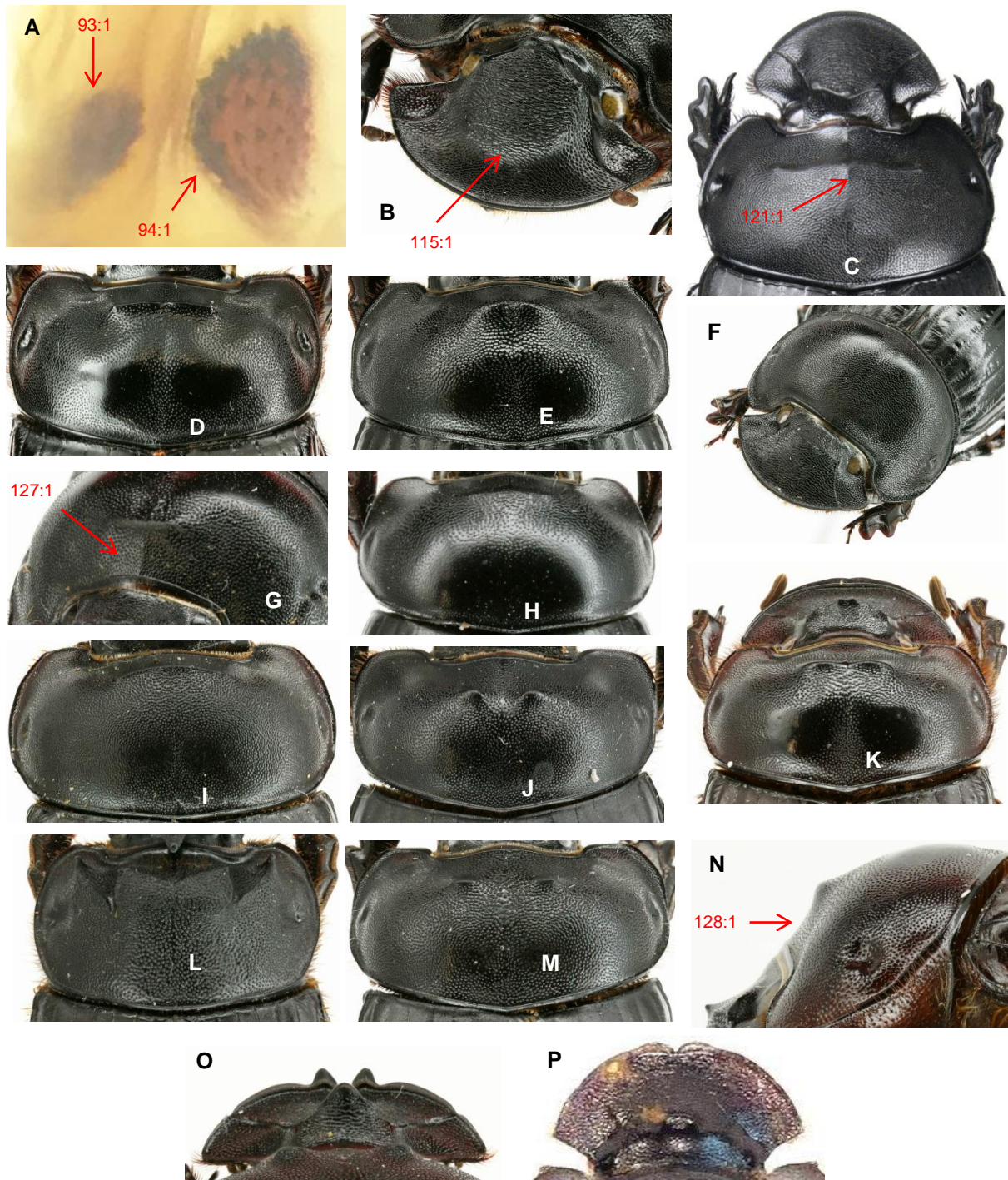
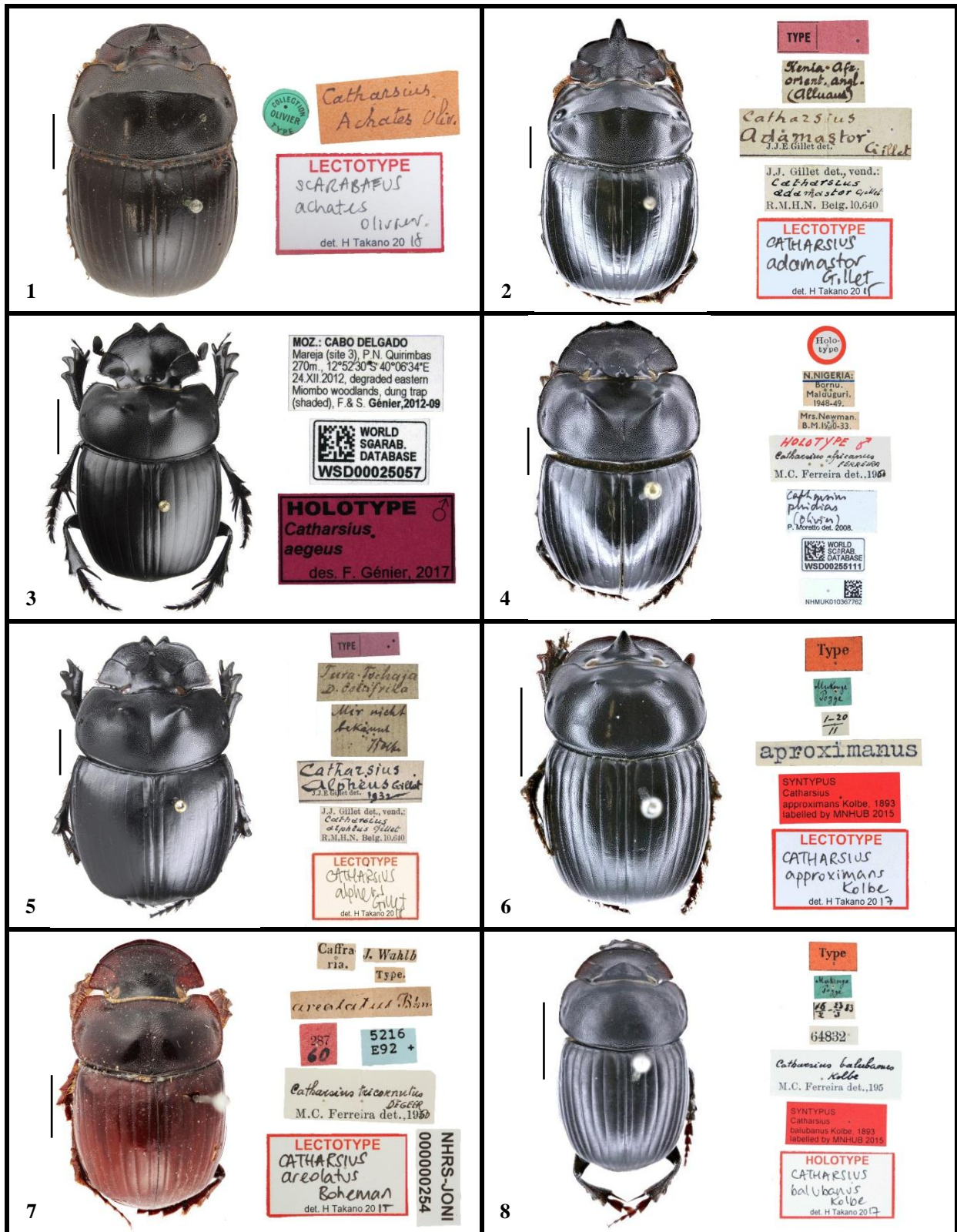


Figure 7: raspulae of *C. pluto* (A); female head of *C. heros* (B), *C. dux* (C), *C. tricornutus* (K & L), *C. eteocles* (O) and *Copris* sp. (P); female pronotum of *C. harveyi* sp. nov. (D), *C. takanoi* (E), *C. vitulus* (F), *C. stuhlmanni* (G), *C. semiramis* (H), *C. phidias* (I), *C. luluensis* (J), *C. mirabilis* (L) and *C. eteocles* (M).



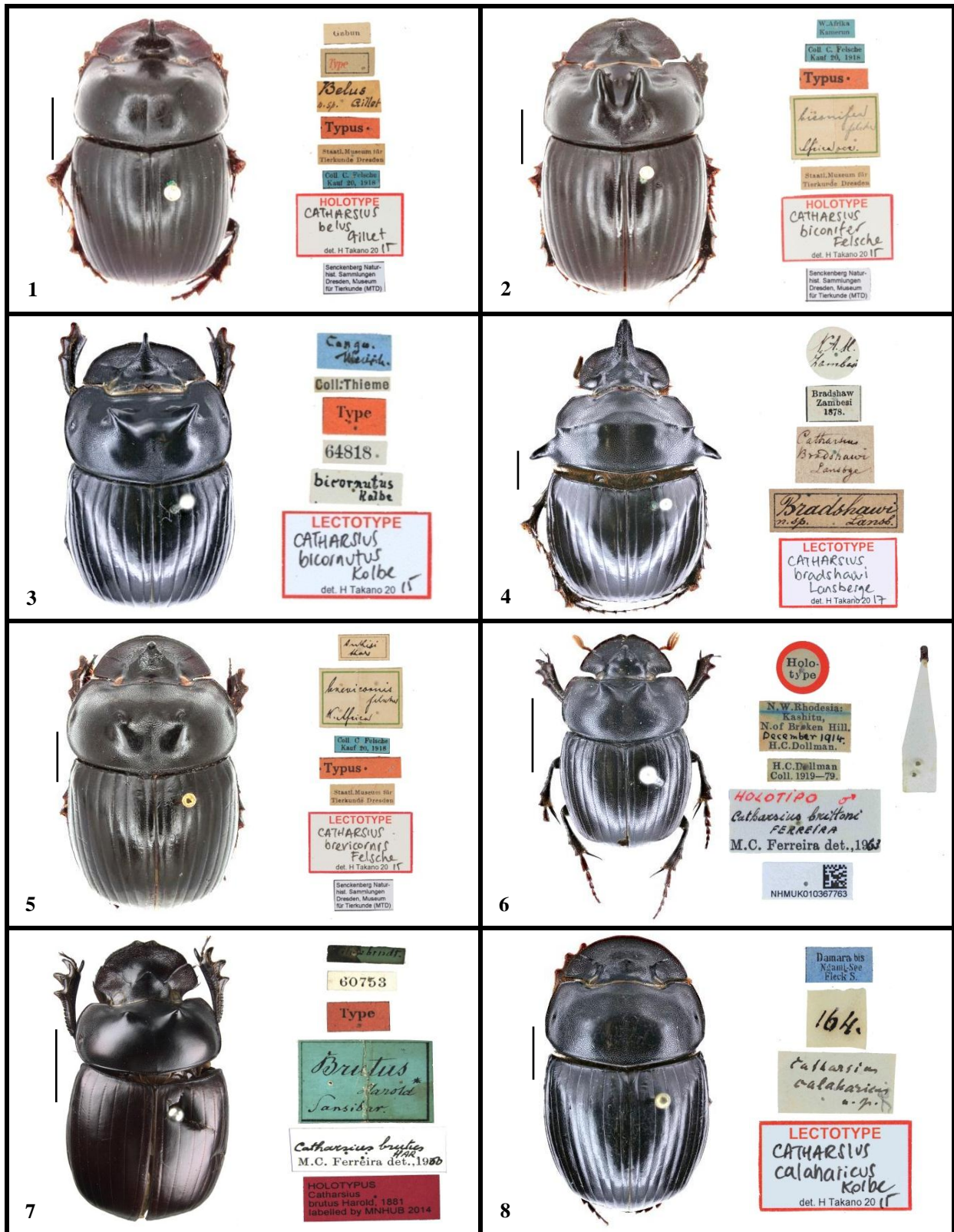
# APPENDIX V - Type specimens

## PLATE 1



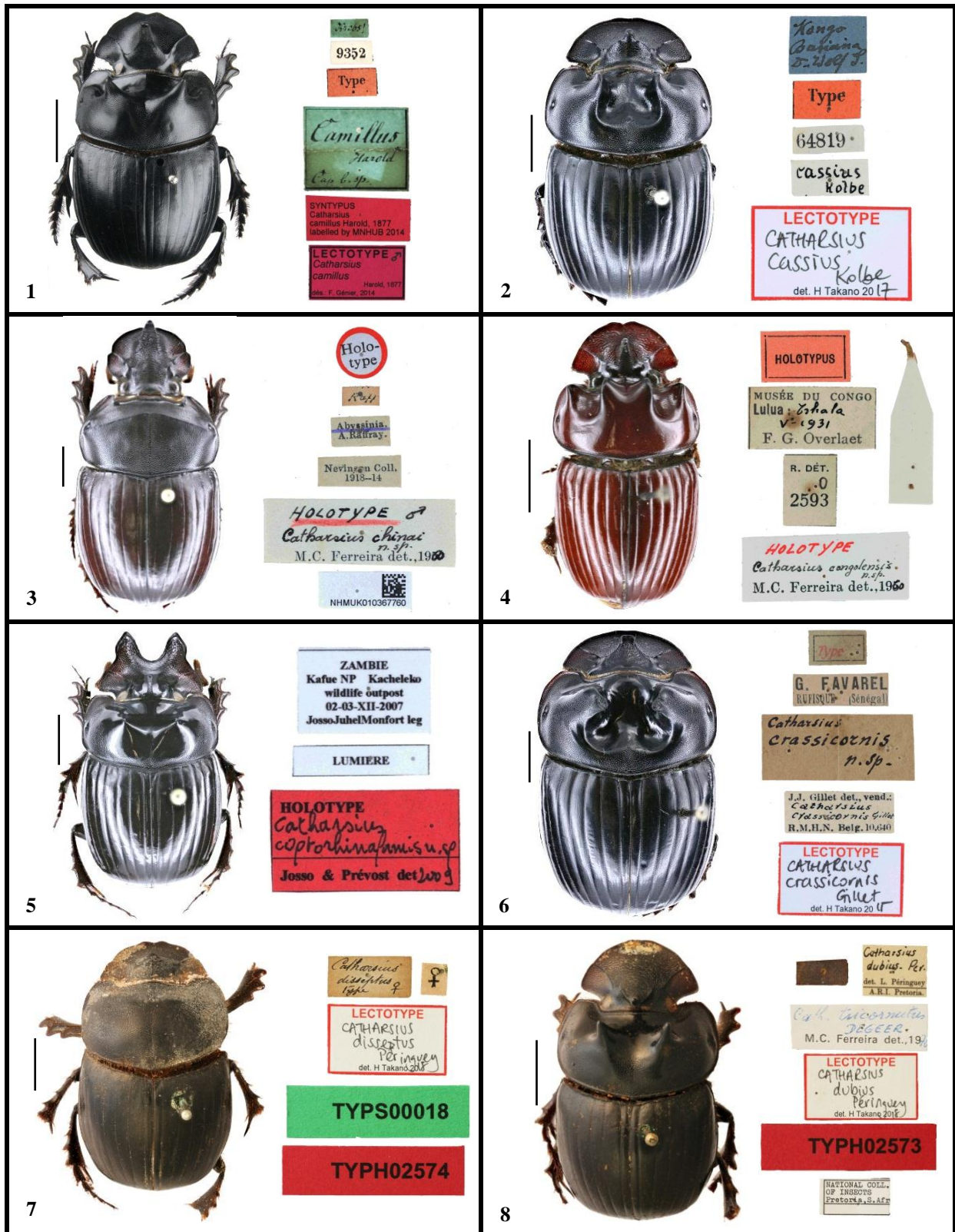
Name-bearing types of *Catharsius* spp. with their labels. 1. *Scarabaeus achates* Olivier (Lectotype); 2. *Catharsius adamastor* Gillet (Lectotype); 3. *Catharsius aegaeus* Génier (Holotype); 4. *Catharsius africanus* Ferreira (Holotype); 5. *Catharsius alphesus* Gillet (Lectotype); 6. *Catharsius approximans* Kolbe (Lectotype); 7. *Catharsius areolatus* Boheman (Lectotype); 8. *Catharsius balubanus* Kolbe (Holotype).

PLATE 2



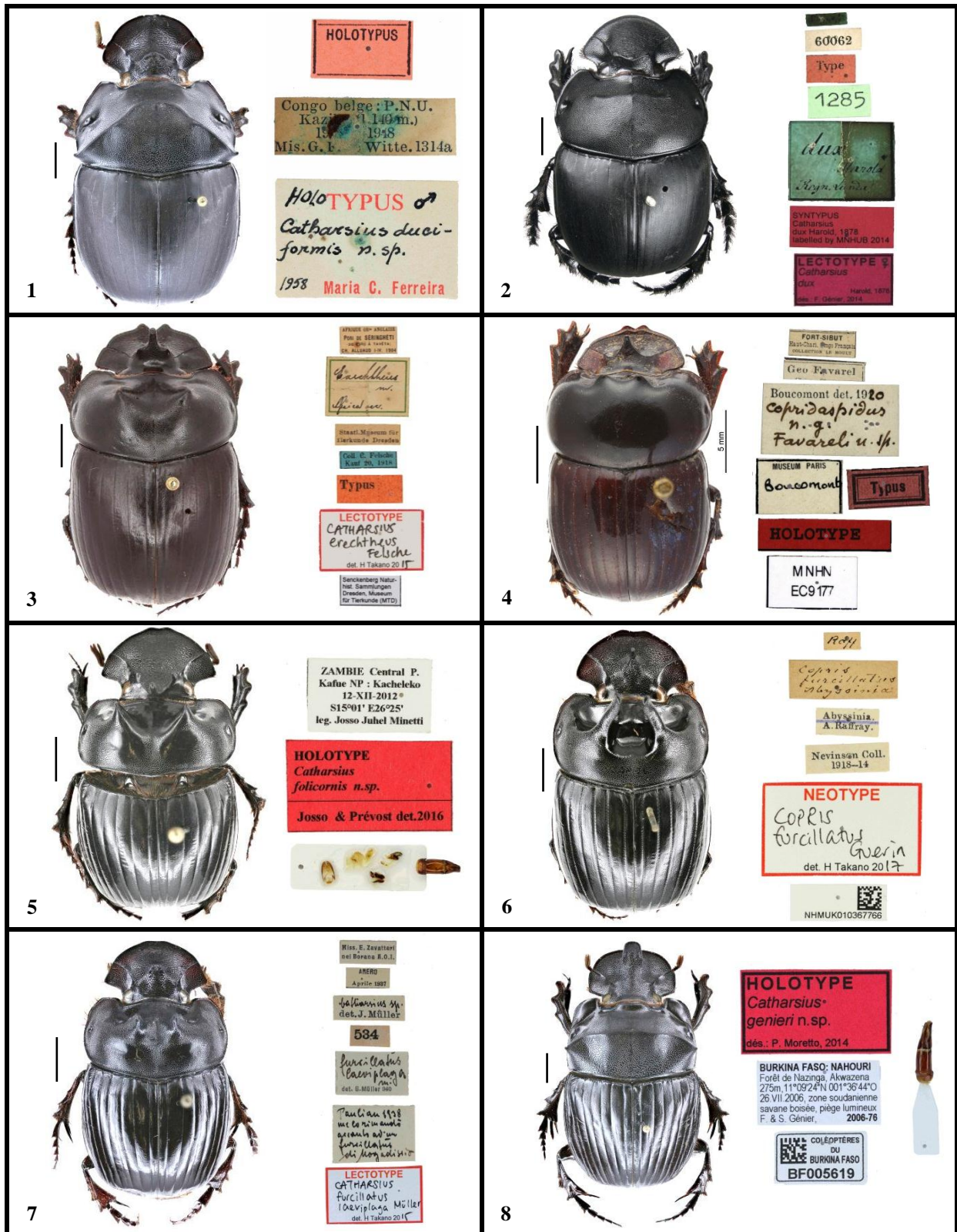
Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius belus* Gillet (Holotype); 2. *Catharsius biconifer* Felsche (Holotype); 3. *Catharsius bicornutus* Kolbe (Lectotype); 4. *Catharsius bradshawi* Lansberge (Lectotype); 5. *Catharsius brevicornis* Felsche (Lectotype); 6. *Catharsius brittoni* Ferreira (Holotype); 7. *Catharsius brutus* Harold (Holotype); 8. *Catharsius calaharicus* Kolbe (Lectotype).

PLATE 3



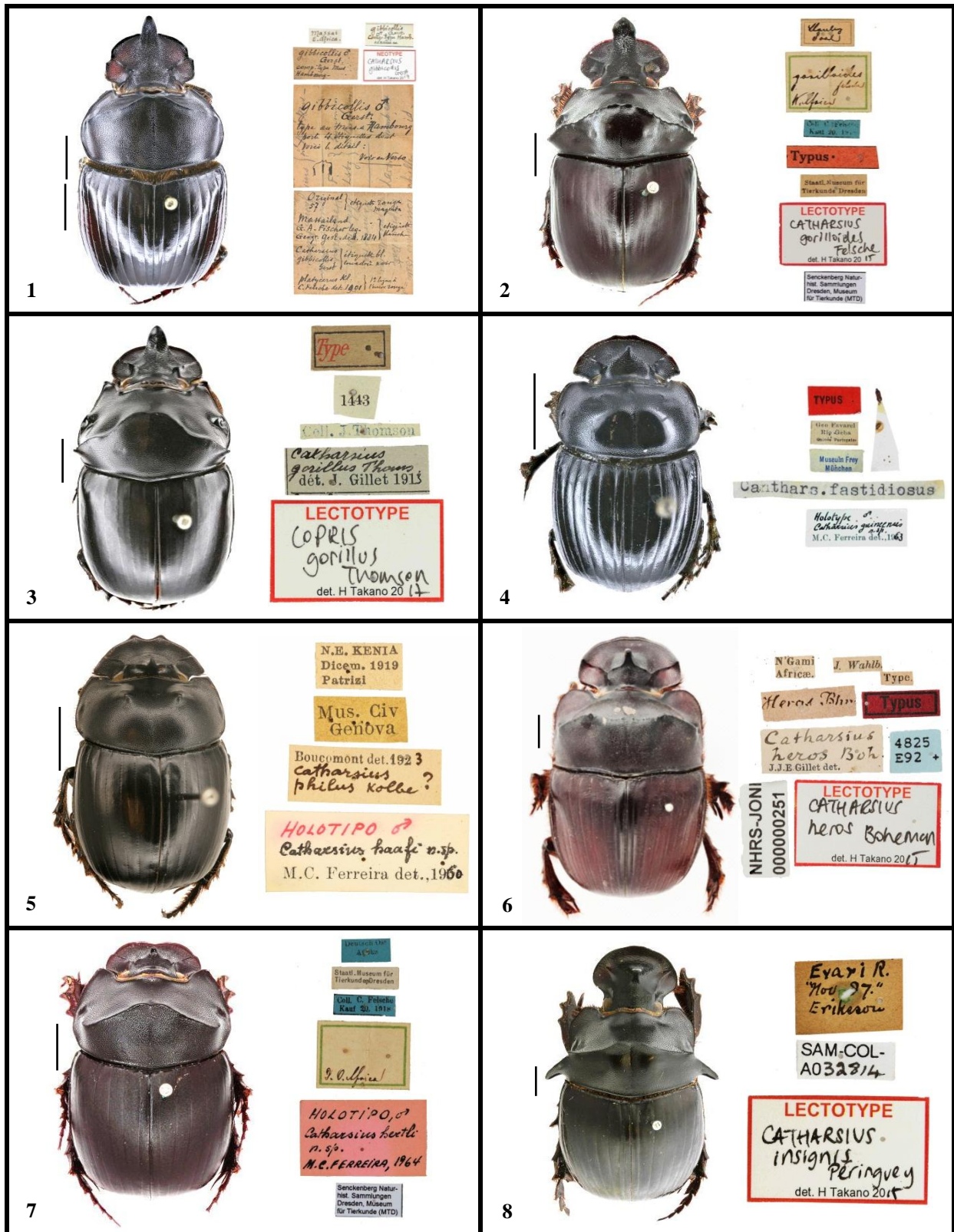
Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius camillus* Harold (Lectotype); 2. *Catharsius cassius* Kolbe (Lectotype); 3. *Catharsius chinai* Ferreira (Holotype); 4. *Catharsius congolensis* Ferreira (Holotype); 5. *Catharsius coptorhinaformis* Josso & Prevost (Holotype); 6. *Catharsius crassicornis* Gillet (Lectotype); 7. *Catharsius disseptus* Péringuey (Lectotype); 8. *Catharsius dubius* Péringuey (Lectotype).

PLATE 4



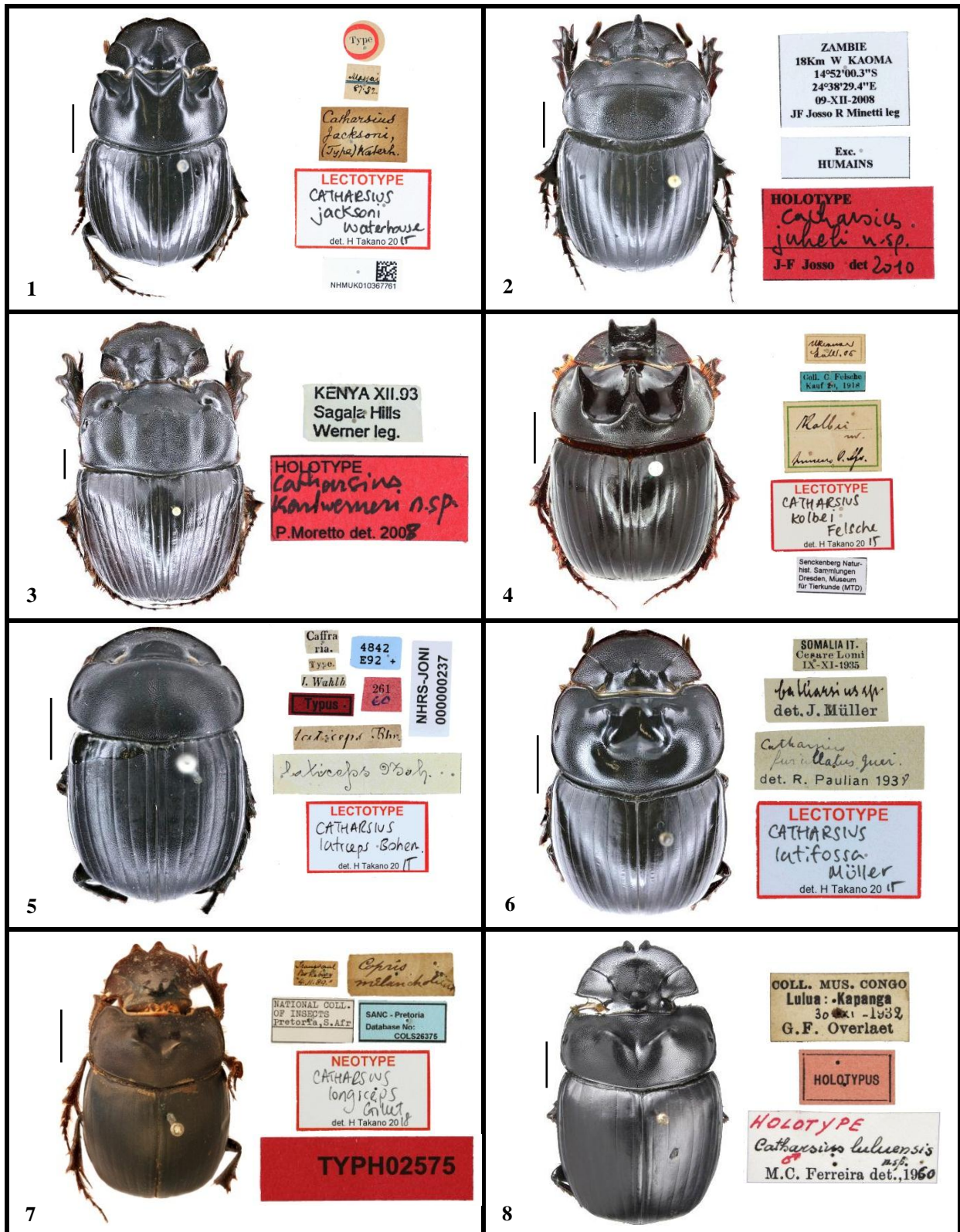
Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius duciformis* Ferreira (Holotype); 2. *Catharsius dux* Harold (Lectotype); 3. *Catharsius erechtheus* Felsche (Lectotype); 4. *Copridaspidus favareli* Boucomont (Holotype); 5. *Catharsius folicornis* Josso & Prevost (Holotype); 6. *Copris furcillatus* Guérin-Méneville (Neotype); 7. *Catharsius furcillatus laevipectus* Müller (Lectotype); 8. *Catharsius genieri* Moretto (Holotype).

PLATE 5



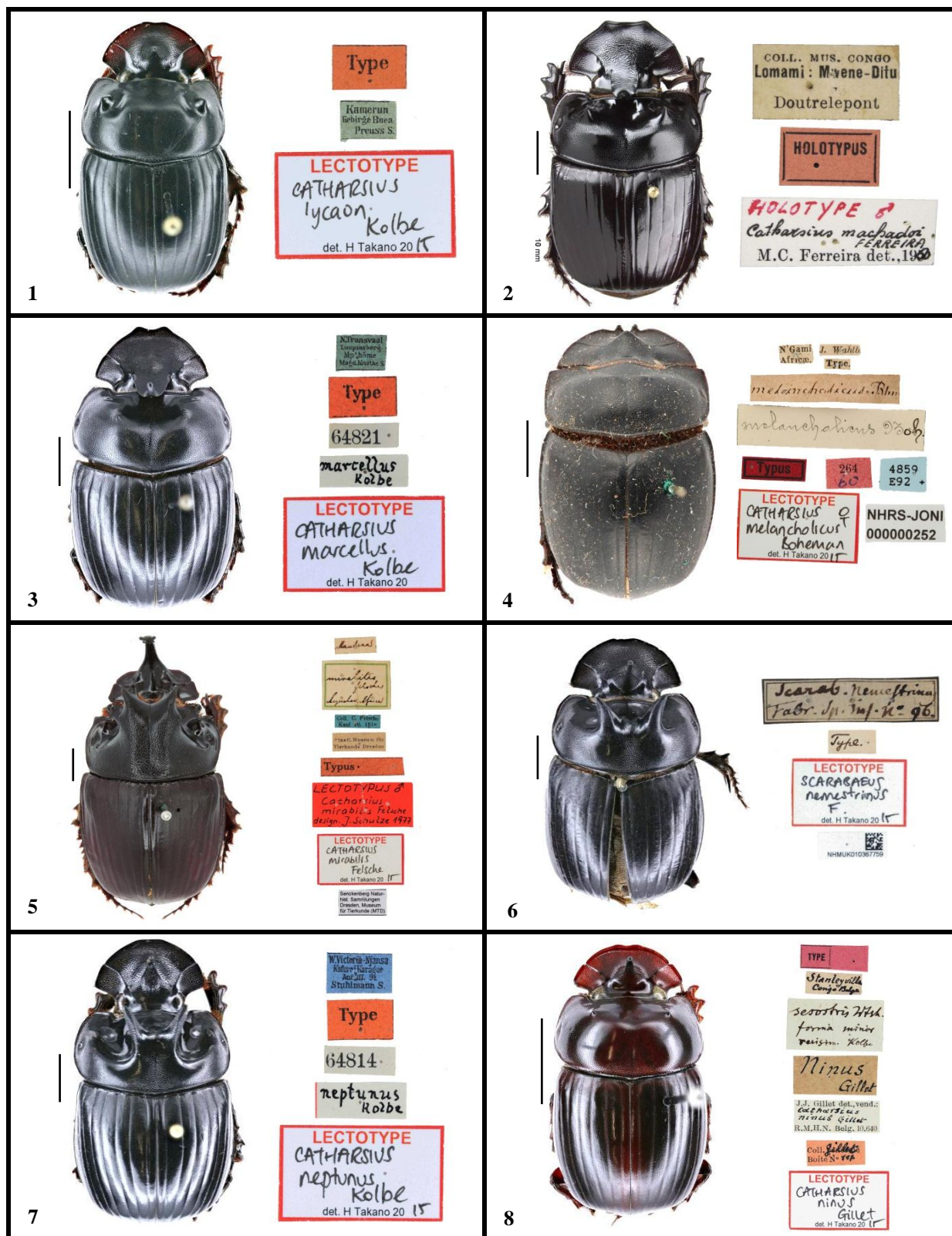
Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius gibbicollis* Gerstaecker (Neotype); 2. *Catharsius gorilloides* Felsche (Lectotype); 3. *Copris gorillus* Thomson (Lectotype); 4. *Catharsius guineensis* Ferreira (Holotype); 5. *Catharsius haafi* Ferreira (Holotype); 6. *Catharsius heros* Boheman (Lectotype); 7. *Catharsius hertli* Ferreira (Holotype); 8. *Catharsius insignis* Péringuey (Lectotype).

PLATE 6



Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius jacksoni* Waterhouse (Lectotype); 2. *Catharsius juheli* Josso (Holotype); 3. *Catharsius karlwerneri* Moretto (Holotype); 4. *Catharsius kolbei* Felsche (Lectotype); 5. *Catharsius laticeps* Boheman (Lectotype); 6. *Catharsius latifossa* Müller (Lectotype); 7. *Catharsius longiceps* Gillet (Neotype); 8. *Catharsius luluensis* Ferreira (Holotype).

PLATE 7



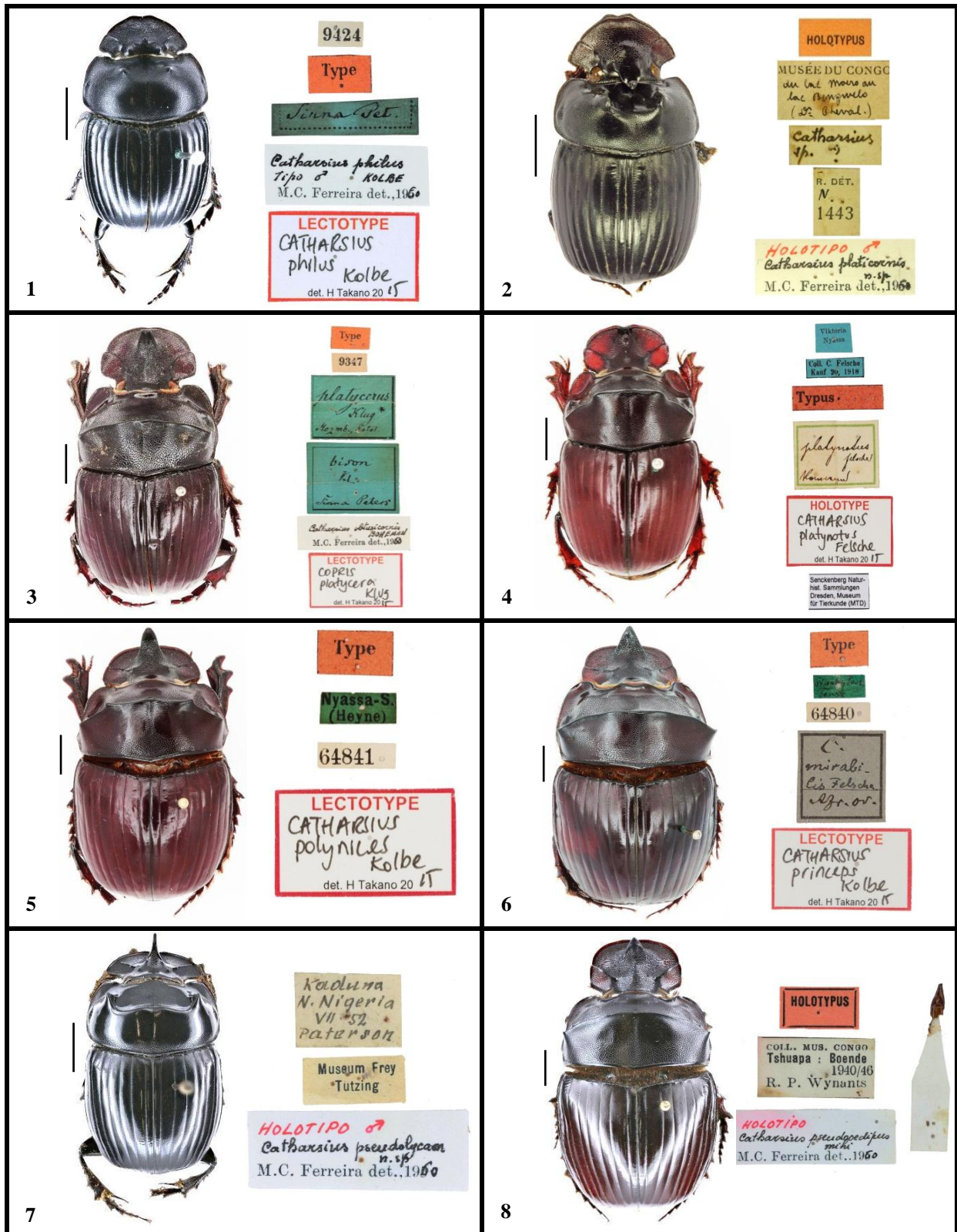
Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius lycaon* Kolbe (Lectotype); 2. *Catharsius machadoi* Ferreira (Holotype); 3. *Catharsius marcellus* Kolbe (Lectotype); 4. *Catharsius melancholicus* Boheman (Lectotype); 5. *Catharsius mirabilis* Felsche (Lectotype); 6. *Scarabaeus nemestrinus* Fabricius (Lectotype); 7. *Catharsius neptunus* Kolbe (Lectotype); 8. *Catharsius ninus* Gillet (Lectotype).

PLATE 8



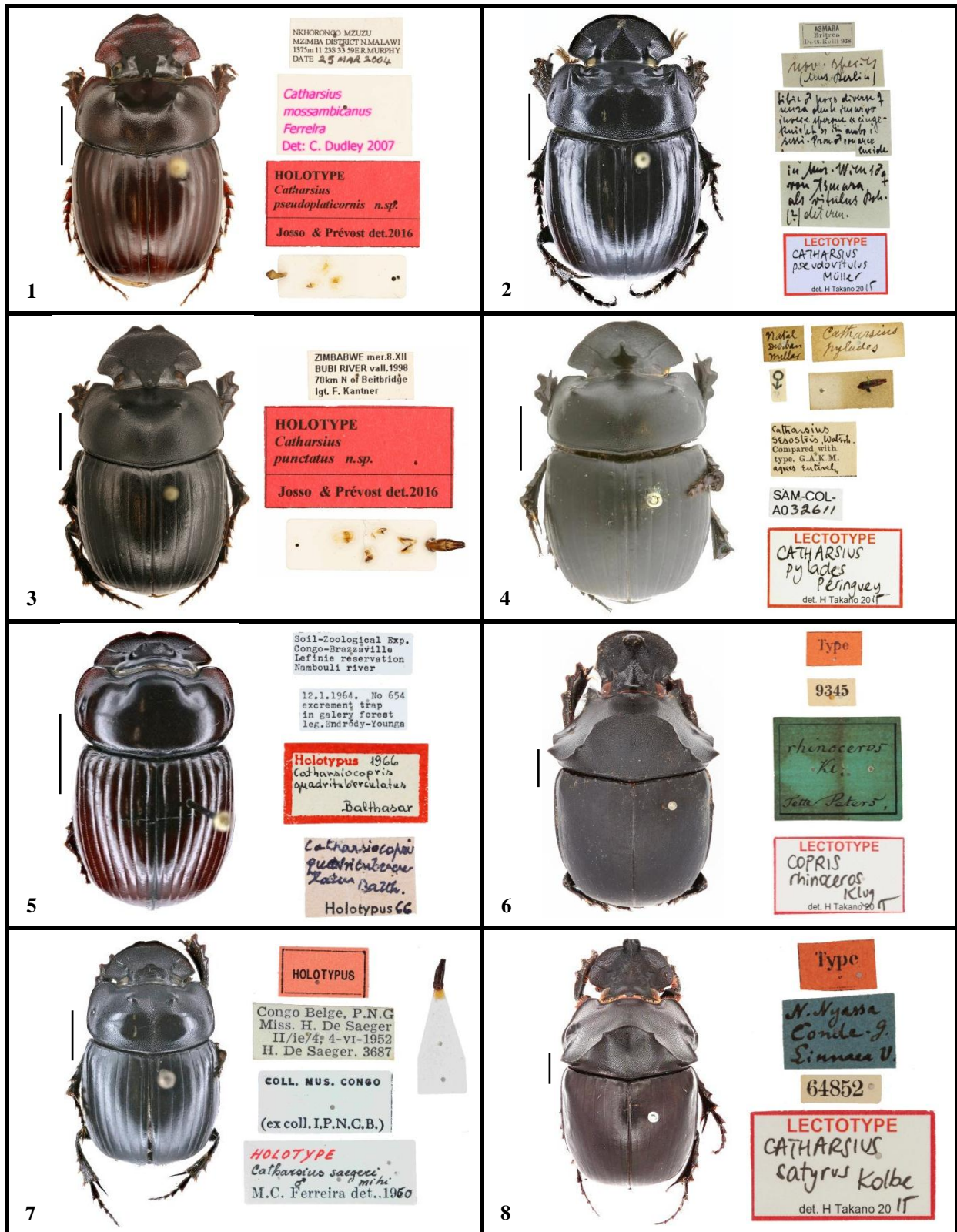
Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius obtusicornis* Boheman (Lectotype); 2. *Catharsius oedipus* Felsche (Lectotype); 3. *Catharsius omoensis* Müller (Lectotype); 4. *Catharsius oryx* Frey (Holotype); 5. *Catharsius pallas* Genier (Holotype); 6. *Catharsius pandion* Harold (Lectotype); 7. *Catharsius peregrinus* Harold (Lectotype); 8. *Scarabaeus phidias* Olivier (Lectotype).

PLATE 9



Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius philus* Kolbe (Lectotype); 2. *Catharsius platycornis* Ferreira (Holotype); 3. *Copris platycera* Klug (Lectotype); 4. *Catharsius platynotus* Felsche (Holotype); 5. *Catharsius polynices* Kolbe (Lectotype); 6. *Catharsius princeps* Kolbe (Lectotype); 7. *Catharsius pseudolycaon* Ferreira (Holotype); 8. *Catharsius pseudoedipus* Ferreira (Holotype).

PLATE 10



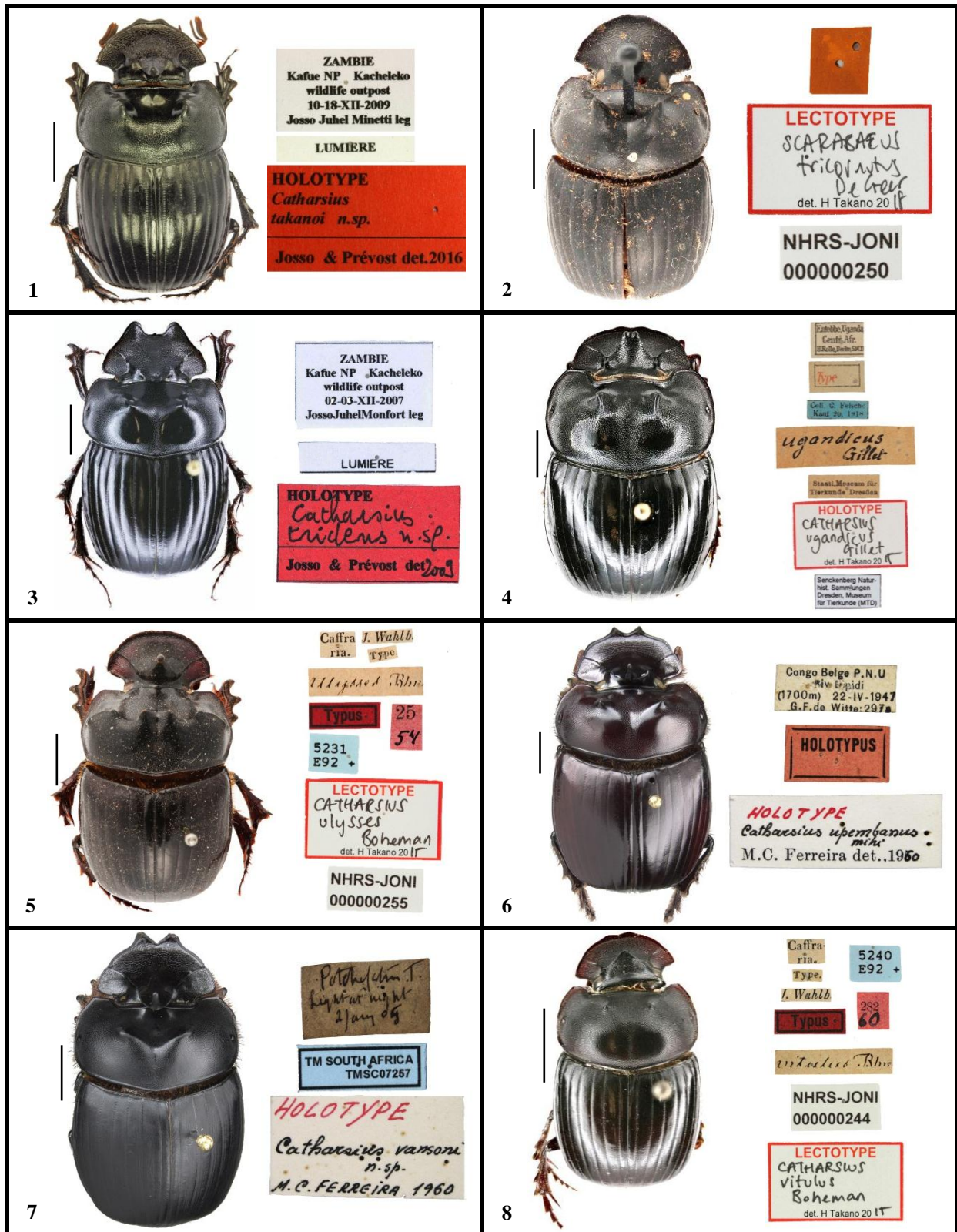
Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius pseudoplasticornis* Josso (Holotype); 2. *Catharsius pseudovitulus* Müller (Lectotype); 3. *Catharsius punctatus* Josso (Holotype); 4. *Catharsius pylades* Péringuey (Lectotype); 5. *Catharsiocopris quadrituberculatus* Balthasar (Holotype); 6. *Copris rhinoceros* Klug (Lectotype); 7. *Catharsius saegeri* Ferreira (Holotype); 8. *Catharsius satyrus* Kolbe (Lectotype).

PLATE 11



Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius scopas* Felsche (Holotype); 2. *Catharsius sesostris* Waterhouse (Holotype); 3. *Catharsius severini* Gillet (Holotype); 4. *Catharsius simillimus* Ferreira (Holotype); 5. *Catharsius spectabilis* Gillet (Neotype); 6. *Catharsius straeleni* Ferreira (Holotype); 7. *Catharsius stricticornis* Josso (Holotype); 8. *Catharsius stuhlmanni* Kolbe (Lectotype).

PLATE 12



Name-bearing types of *Catharsius* spp. with their labels. 1. *Catharsius takanoi* Josso (Holotype); 2. *Scarabaeus tricornutus* De Geer (Lectotype); 3. *Catharsius tridens* Josso & Prévost (Holotype); 4. *Catharsius ugandicus* Gillet (Holotype); 5. *Catharsius ulysses* Boheman (Lectotype); 6. *Catharsius upembanus* Ferreira (Holotype); 7. *Catharsius vansoni* Ferreira (Holotype); 8. *Catharsius vitulus* Boheman (Lectotype).













## APPENDIX VII - Gazetteer of African Localities

ANGOLA	HUAMBO	<b>Bailundo</b>	12°12'S	15°51'E
ANGOLA	BENGUELA	<b>Benguela</b>	12°35'S	13°24'E
ANGOLA	HUILA	<b>Bicuar National Park, camp</b>	15°06'S	14°50'E
ANGOLA	HUAMBO	<b>Bimbi</b>	11°49'S	15°50'E
ANGOLA	HUILA	<b>Caconda</b>	13°44'S	15°04'E
ANGOLA	CUANZA SUL	<b>Calulo</b>	10°00'S	14°54'E
ANGOLA	MALANJE	<b>Cangangala National Park</b>	09°50'S	16°39'E
ANGOLA	BIE	<b>Catabola</b>	12°09'S	17°17'E
ANGOLA	CUANZA SUL	<b>Congulu</b>	10°53'S	14°23'E
ANGOLA	BENGUELA	<b>Cubal</b>	13°02'S	14°15'E
ANGOLA	BIE	<b>Cuemba</b>	12°09'S	18°05'E
ANGOLA	HUAMBO	<b>Cuima</b>	13°15'S	15°38'E
ANGOLA	LUNDA NORTE	<b>Dundo</b>	07°23'S	20°50'E
ANGOLA	BIE	<b>Ebanga</b>	12°44'S	14°44'E
ANGOLA	CUNENE	<b>Evale</b>	16°33'S	15°45'E
ANGOLA	CUNENE	<b>Evuri River [=Evale]</b>		
ANGOLA	CUNENE	<b>Kahama</b>	16°17'S	14°18'E
ANGOLA	BIE	<b>Kambuecho</b>	12°35'S	17°00'E
ANGOLA	BIE	<b>Kuemba [=Cuemba]</b>		
ANGOLA	CABINDA	<b>Landana</b>	05°14'S	12°09'E
ANGOLA	LUANDA	<b>Luanda</b>	08°49'S	13°14'E
ANGOLA	MALANJE	<b>Malange [=Malanje]</b>		
ANGOLA	MALANJE	<b>Malanje</b>	09°33'S	16°21'E
ANGOLA	CABINDA	<b>Malongo</b>	05°23'S	12°12'E
ANGOLA	ZAIRE	<b>M'banza-Kongo</b>	06°16'S	14°14'E
ANGOLA	HUAMBO	<b>Menga</b>	12°02'S	15°22'E
ANGOLA	HUILA	<b>Mukoti</b>	14°12'S	15°48'E
ANGOLA	CUANDA CUBANGO	<b>Muleke [=Tombole]</b>		
ANGOLA	CUNENE	<b>Namacunde</b>	17°18'S	15°50'E
ANGOLA	HUILA	<b>Negola</b>	14°08'S	14°30'E
ANGOLA	HUILA	<b>Nova Moncao</b>	13°27'S	15°20'E
ANGOLA	CUNENE	<b>Omrora</b>	17°00'S	16°00'E
ANGOLA	CUANZA SUL	<b>Quarenta</b>	10°12'S	16°08'E
ANGOLA	CUANZA SUL	<b>Quirimbo</b>	10°38'S	14°20'E
ANGOLA	CUANZA NORTE	<b>Salazar, Instituto de Investigacao Agronomica</b>	09°18'S	14°55'E
ANGOLA	ZAIRE	<b>San Salvador [=M'banza-Kongo]</b>		
ANGOLA	CUANDA CUBANGO	<b>Santa Cruz</b>	16°19'S	22°02'E
ANGOLA	CUANDA CUBANGO	<b>Tombole</b>	14°33'S	16°32'E
BENIN	ATLANTIQUE	<b>Attongon, Foret de Niamouli</b>	06°44'N	02°08'E
BENIN	ATAKORA	<b>Batia</b>	10°53'N	01°29'E
BENIN	ZOU	<b>Bohicon</b>	07°11'N	02°04'E
BENIN	BORGOU	<b>Borgou</b>	09°32'N	02°47'E
BENIN	DONGA	<b>Djougou-Kouande</b>	10°03'N	01°42'E
BENIN	DONGA	<b>Goutansoukpa</b>	09°13'N	01°50'E

BENIN	ALIBORI	Mammasi Gourma	12°03'N	03°08'E
BENIN	DONGA	Penelan	09°15'N	01°31'E
BOTSWANA	NORTH-WEST	Bakwena	17°48'S	25°14'E
BOTSWANA	NORTH-WEST	Caprivi Gate, Chobe Game Reserve	17°56'S	24°44'E
BOTSWANA	CENTRAL	Central Magkadikgadi National Park	20°47'S	25°28'E
BOTSWANA	NORTH-WEST	Chobe Game Lodge	17°51'S	25°05'E
BOTSWANA	CENTRAL	Francistown	21°10'S	27°31'E
BOTSWANA	SOUTH-EAST	Gabarone	24°39'S	25°54'E
BOTSWANA	GHANZI	Ghanzi	21°42'S	21°39'E
BOTSWANA	NORTH-WEST	Island Safari Lodge	19°55'S	23°30'E
BOTSWANA	GHANZI	Kalkfontein [=Tshootsha]		
BOTSWANA	KGALAGADI	Kang	23°40'S	22°47'E
BOTSWANA	NORTH-WEST	Kanyu	20°05'S	24°37'E
BOTSWANA	NORTH-WEST	Kasane	17°48'S	25°10'E
BOTSWANA	KGALAGADI	Kgalagadi Transfrontier Park	26°20'S	20°45'E
BOTSWANA	CENTRAL	Khumaga	20°28'S	24°31'E
BOTSWANA	GHANZI	Kuke Pan	23°18'S	24°29'E
BOTSWANA	SOUTHERN	Kukong	24°21'S	23°07'E
BOTSWANA	CENTRAL	Lake Makadikadi	20°47'S	25°28'E
BOTSWANA	NORTH-WEST	Lake Ngami	20°28'S	22°42'E
BOTSWANA	CENTRAL	Mahalapye	23°06'S	26°50'E
BOTSWANA	NORTH-WEST	Maun	20°00'S	23°25'E
BOTSWANA	KWENENG	Molepabelo [=Molepolole]		
BOTSWANA	KWENENG	Molepolole	24°24'S	25°30'E
BOTSWANA	NORTH-WEST	Moremi Game Reserve	19°22'S	23°03'E
BOTSWANA	CENTRAL	Mount Serowe	22°20'S	26°43'E
BOTSWANA	CENTRAL	Nata	20°13'S	26°11'E
BOTSWANA	NORTH-WEST	Okavango Swamps, Chief's Island	19°24'S	23°05'E
BOTSWANA	CENTRAL	Planet Baobab Camp	20°11'S	25°18'E
BOTSWANA	NORTH-WEST	Sehithwa	20°28'S	22°42'E
BOTSWANA	NORTH-WEST	Sehitwe [=Sehithwa]		
BOTSWANA	SOUTHERN	Sekhuma	24°31'S	23°55'E
BOTSWANA	NORTH-WEST	Senyati Safari Camp	17°52'S	25°14'E
BOTSWANA	CENTRAL	Serowe	22°23'S	26°43'E
BOTSWANA	CENTRAL	Serue [=Serowe]		
BOTSWANA	NORTH-EAST	Tati [=Francistown]		
BOTSWANA	NORTHWEST	Thamalakane River	19°53'S	23°33'E
BOTSWANA	NORTH-EAST	Tsessebe	20°45'S	27°34'E
BOTSWANA	KGALAGADI	Tshabong	26°01'S	22°24'E
BOTSWANA	GHANZI	Tshootsha	22°09'S	20°52'E
BURKINA FASO	BOUCLE DE MOUHOUN	Bekui	11°38'N	03°53'W
BURKINA FASO	HAUTS-BASSINS	Bobo-Dioulasso	11°10'N	04°18'W
BURKINA FASO	SAHEL	Dori	14°02'N	00°03'W
BURKINA FASO	HAUTS-BASSINS	Foret de Kou	11°11'N	04°26'W
BURKINA FASO	CENTRE-SUD	Foret de Nazinga, Akwazena	11°09'N	01°37'W
BURKINA FASO	CENTRE-SUD	Foret de Nazinga, Naguio	11°08'N	01°35'W
BURKINA FASO	CENTRE-OUEST	Foret de Sorobouli	11°48'N	02°53'W
BURKINA FASO	SAHEL	Gorom-Gorom, Essakane	14°23'N	00°06'E

BURKINA FASO	CENTRE-EST	<b>Koupela</b>	12°11'N	00°21'W
BURKINA FASO	SAHEL	<b>N'djong</b>	14°04'N	00°03'W
BURKINA FASO	CENTRE	<b>Ouagadougou</b>	12°22'N	01°31'W
BURKINA FASO	CENTRE	<b>Pabre</b>	12°30'N	01°34'W
BURKINA FASO	CENTRE-SUD	<b>Pama</b>	11°05'N	01°18'W
BURKINA FASO	CENTRE-SUD	<b>Po</b>	11°09'N	01°09'W
BURKINA FASO	BOUCLE DE MOUHOUN	<b>Pondou</b>	12°12'N	03°35'W
BURKINA FASO	BOUCLE DE MOUHOUN	<b>Pundu [=Pondou]</b>		
BURKINA FASO	NORD	<b>Toulfe</b>	13°53'N	01°57'W
BURKINA FASO	NORD	<b>Yako</b>	12°57'N	02°16'W

BURUNDI	BUJUMBURA-MAIRIE	<b>Bujumbura</b>	03°23'S	29°22'E
BURUNDI	BURURI	<b>Bururi</b>	03°57'S	29°37'E
BURUNDI	GITEGA	<b>Gitega</b>	03°45'S	30°10'E
BURUNDI	GITEGA	<b>Kitega [=Gitega]</b>		
BURUNDI	NGOZI	<b>Ngozi</b>	02°54'S	29°49'E

CAMEROON	SOUTH	<b>Akoafim</b>	02°19'N	12°45'E
CAMEROON	SOUTH	<b>Akonangi</b>	02°12'N	11°21'E
CAMEROON	LITTORAL	<b>Babimbi</b>	04°14'N	10°37'E
CAMEROON	ADAMAWA	<b>Baboua</b>	06°59'N	14°15'E
CAMEROON	ADAMAWA	<b>Babua [=Baboua]</b>		
CAMEROON	NORTHWEST	<b>Bafut</b>	06°05'N	10°07'E
CAMEROON	SOUTHWEST	<b>Bakassi</b>	04°37'N	08°36'E
CAMEROON	NORTHWEST	<b>Bali</b>	05°53'N	10°00'E
CAMEROON	NORTHWEST	<b>Baliland [=Bali]</b>		
CAMEROON	NORTHWEST	<b>Bamenda</b>	05°58'N	10°09'E
CAMEROON	WEST	<b>Bamum [=Foumban]</b>		
CAMEROON	WEST	<b>Bandjoun</b>	05°22'N	10°25'E
CAMEROON	WEST	<b>Banjun [=Bandjoun]</b>		
CAMEROON	LITTORAL	<b>Bare</b>	05°01'N	09°58'E
CAMEROON	SOUTHWEST	<b>Barombi</b>	04°39'N	09°25'E
CAMEROON	SOUTH	<b>Batanga</b>	02°51'N	09°53'E
CAMEROON	EAST	<b>Batouri</b>	04°26'N	14°22'E
CAMEROON	SOUTH	<b>Bipindi</b>	03°05'N	10°25'E
CAMEROON	LITTORAL	<b>Dibongo</b>	03°42'N	10°01'E
CAMEROON	EAST	<b>Dja</b>	03°15'N	13°30'E
CAMEROON	LITTORAL	<b>Douala</b>	04°02'N	09°44'E
CAMEROON	WEST	<b>Dschang</b>	05°27'N	10°03'E
CAMEROON	LITTORAL	<b>Edea</b>	03°47'N	10°08'E
CAMEROON	CENTRE	<b>Eseka</b>	03°38'N	10°47'E
CAMEROON	SOUTHWEST	<b>Esosung</b>	04°52'N	09°44'E
CAMEROON	LITTORAL	<b>Etamba</b>	05°11'N	09°59'E
CAMEROON	LITTORAL	<b>Etombo [=Etamba]</b>		
CAMEROON	WEST	<b>Foumban</b>	05°44'N	10°54'E
CAMEROON	ADAMAWA	<b>Galim</b>	07°06'N	12°28'E
CAMEROON	NORTH	<b>Garoua</b>	09°19'N	13°24'E
CAMEROON	NORTH	<b>Garua [=Garoua]</b>		
CAMEROON	FAR NORTH	<b>Goufey [=Gouffey]</b>		
CAMEROON	FAR NORTH	<b>Gouffey</b>	12°23'N	14°54'E

CAMEROON	ADAMAWA	Goungel	07°16'N	11°51'E
CAMEROON	LITTORAL	Japoma	04°02'N	09°49'E
CAMEROON	CENTRE	Jaunde-station [=Yaounde]		
CAMEROON	SOUTHWEST	Johann Albrechtshohe	04°39'N	09°25'E
CAMEROON	CENTRE	Joko [=Yoko]		
CAMEROON	FAR NORTH	Kousseri	12°05'N	15°01'E
CAMEROON	SOUTH	Kribi	02°57'N	09°55'E
CAMEROON	SOUTHWEST	Kumba	04°38'N	09°27'E
CAMEROON	ADAMAWA	Lake Baledjam	07°08'N	13°52'E
CAMEROON	SOUTH	Lolodorf	03°14'N	10°44'E
CAMEROON	SOUTH	Londji	?	
CAMEROON	SOUTHWEST	Malende	04°20'N	09°26'E
CAMEROON	SOUTHWEST	Mamfe	05°45'N	09°19'E
CAMEROON	NORTH	Maroua	10°36'N	14°19'E
CAMEROON	EAST	Mimpala	03°25'N	13°09'E
CAMEROON	CENTRE	Mont Kala	03°58'N	11°24'E
CAMEROON	LITTORAL	Mont Manengouba	05°00'N	09°51'E
CAMEROON	SOUTHWEST	Mucli Nordseite	04°23'N	09°07'E
CAMEROON	WEST	Ndzi'e [=Ndziih]		
CAMEROON	WEST	Ndziih	05°35'N	10°07'E
CAMEROON	ADAMAWA	Ngaoundaba	07°08'N	13°42'E
CAMEROON	ADAMAWA	Ngaoundere	07°19'N	13°35'E
CAMEROON	ADAMAWA	Ngaoundere, Bini Dang	07°25'N	13°32'E
CAMEROON	NORTHWEST	Nkambe	06°35'N	10°42'E
CAMEROON	CENTRE	Nkolbisson	03°52'N	11°27'E
CAMEROON	CENTRE	Nkolebae	03°20'N	11°26'E
CAMEROON	LITTORAL	Nkongsamba	04°58'N	06°56'E
CAMEROON	SOUTH	Obem	02°42'N	11°31'E
CAMEROON	CENTRE	Region de Samba	03°22'N	11°01'E
CAMEROON	NORTH	Rei Buba [=Rey-Bouba]		
CAMEROON	NORTH	Rey-Bouba	08°40'N	14°11'E
CAMEROON	SOUTHWEST	Rio del Rey	04°34'N	08°44'E
CAMEROON	CENTRE	Tina	05°29'N	12°23'E
CAMEROON	SOUTHWEST	Victoria	04°00'N	09°13'E
CAMEROON	FAR NORTH	Waza	11°24'N	14°34'E
CAMEROON	FAR NORTH	Waza National Park	11°20'N	14°40'E
CAMEROON	CENTRE	Yaounde	03°51'N	11°31'E
CAMEROON	CENTRE	Yoko	05°32'N	12°19'E
CAMEROON	SOUTH	Yop	03°04'N	11°25'E

CENTRAL AFRICAN REPUBLIC	OUAKA	Bambari	05°46'N	20°40'E
CENTRAL AFRICAN REPUBLIC	OMBELLA-M'POKO	Bangui	04°23'N	18°33'E
CENTRAL AFRICAN REPUBLIC	SANGHA-MBAERE	Bayanga	02°55'N	16°16'E
CENTRAL AFRICAN REPUBLIC	KEMO	Bessou [=Djoukou]		
CENTRAL AFRICAN REPUBLIC	OUHAM-PENDE	Bossum [=Bozoum]	06°19'N	16°22'E
CENTRAL AFRICAN REPUBLIC	NANA-MAMBERE	Bouar	05°57'N	15°36'E
CENTRAL AFRICAN REPUBLIC	OUHAM	Bouca	06°30'N	18°17'E
CENTRAL AFRICAN REPUBLIC	OMBELLA-M'POKO	Bozo	05°08'N	18°29'E
CENTRAL AFRICAN REPUBLIC	KEMO	Djoukou	05°08'N	19°24'E
CENTRAL AFRICAN REPUBLIC	NANA-GREBIZI	Fort Crampel	06°59'N	19°11'E

CENTRAL AFRICAN REPUBLIC	KEMO	Fort Sibut	05°44'N	19°05'E
CENTRAL AFRICAN REPUBLIC	LOBAYE	La Maboke	03°51'N	17°51'E
CENTRAL AFRICAN REPUBLIC	SANGHA-MBAERE	Parc National Ndoki	02°29'N	19°13'E
CENTRAL AFRICAN REPUBLIC	MBOMOU	Rafai	04°58'N	23°56'E
CENTRAL AFRICAN REPUBLIC	BAMINGUI-BANGORAN	Sangba	07°34'N	20°25'E
CENTRAL AFRICAN REPUBLIC	SANGHA-MBAERE	Sangha	03°30'N	16°05'E
CENTRAL AFRICAN REPUBLIC	MBOMOU	Sankiri	05°20'N	22°15'E
CENTRAL AFRICAN REPUBLIC	HAUT-MBOMOU	Semnio [=Zemio]		
CENTRAL AFRICAN REPUBLIC	HAUT-KOTTO	Yalinga	06°31'N	23°15'E
CENTRAL AFRICAN REPUBLIC	HAUT-MBOMOU	Zemio	05°02'N	25°08'E

CHAD	OUDDAI	Abeche	13°50'N	20°50'E
CHAD	SILA	Am Dam	12°46'N	20°28'E
CHAD	LOGONE ORIENTAL	Bebedija	08°40'N	16°34'E
CHAD	LAC	Bol	13°28'N	14°43'E
CHAD	HADJER-HAMIS	Djintilo	12°50'N	14°35'E
CHAD	MOYEN-CHARI	Fort Archambault [=Sarh]		
CHAD	N'DJAMENA	Fort Lamy [=N'Djamena]		
CHAD	LOGONE ORIENTAL	Kome	08°28'N	16°42'E
CHAD	LOGONE OCCIDENTAL	Moundou	08°34'N	16°05'E
CHAD	N'DJAMENA	N'Djamena	12°07'N	15°03'E
CHAD	LAC	Ngouri	13°38'N	15°22'E
CHAD	MOYEN-CHARI	Sarh	09°09'N	18°23'E

CONGO	BRAZZAVILLE	Brazzaville	04°16'S	15°15'E
CONGO	CUVETTE-OUEST	Diba	00°20'N	14°47'E
CONGO	CUVETTE	Diele	01°41'S	14°45'E
CONGO	KOUILOU	Hinda	04°34'S	12°05'E
CONGO	LEKOUMOU	IRHO, Sibiti	03°40'S	13°20'E
CONGO	NIARI	Kola	03°51'S	12°04'E
CONGO	PLATEAUX	Lefinie Reservation, Mpo	02°24'S	15°30'E
CONGO	PLATEAUX	Lefinie Reservation, Nambouli River	02°30'S	15°29'E
CONGO	POOL	Lesio-Louna	03°17'S	15°29'E
CONGO	BOUENZA	Louboulou	03°56'S	13°39'E
CONGO	BOUENZA	Luxulu [=Louboulou]		
CONGO	POOL	Mah	03°21'S	15°29'E
CONGO	NIARI	Mayoko	02°24'S	12°54'E
CONGO	POOL	Musana [=Mousana]	04°33'S	14°41'E
CONGO	KOUILOU	Nzambi	03°58'S	11°17'E
CONGO	CUVETTE	Odzala	00°16'N	15°44'E
CONGO	BRAZZAVILLE	ORSTOM Park, Brazzaville	04°11'S	15°10'E
CONGO	KOUILOU	Thoumby [=Toumbi]		
CONGO	KOUILOU	Toumbi	04°36'S	11°55'E
CONGO	NIARI	Tsingidi	02°24'S	12°58'E
CONGO	POOL	Voka	04°40'S	14°40'E
CONGO	NIARI	Vouka	02°35'S	12°45'E
CONGO	KOUILOU	Zambi [=Nzambi]		

DJIBOUTI	TADJOURAH	Maro [=Malho]	12°05'N	42°14'E
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D.R. CONGO	HAUT-UELE	Abimva	03°09'N	29°50'E
D.R. CONGO	HAUT-UELE	Arebi	02°49'N	29°34'E
D.R. CONGO	ITURI	Aru	02°52'N	30°50'E
D.R. CONGO	BAS-UELE	Bambesa	03°27'N	25°41'E
D.R. CONGO	TSHOPO	Banalia	01°33'N	25°19'E
D.R. CONGO	KONGO CENTRAL	Banana	05°59'S	12°23'E
D.R. CONGO	ITURI	Banzville [=Mobayi-Mbongo]		
D.R. CONGO	TSHOPO	Barumbu	01°15'N	23°29'E
D.R. CONGO	TANGANYIKA	Baudouinville [=Kirungu]		
D.R. CONGO	MAI-NDOMBE	Bena-Bendi	04°18'S	20°21'E
D.R. CONGO	NORD-KIVU	Beni	00°30'N	29°27'E
D.R. CONGO	MAI-NDOMBE	Beni Bendi [=Bena-Bendi]	04°17'N	20°22'E
D.R. CONGO	LUALABA	Biano	10°13'S	26°04'E
D.R. CONGO	TSHUAPA	Boende	00°17'S	20°53'E
D.R. CONGO	MAI-NDOMBE	Bokoro	02°48'S	18°14'E
D.R. CONGO	MAI-NDOMBE	Bolobo	02°09'S	16°14'E
D.R. CONGO	KONGO CENTRAL	Boma	05°51'S	13°03'E
D.R. CONGO	KINSHASA	Bombo-Lumene	04°25'S	16°00'E
D.R. CONGO	MONGALA	Bopoto	02°08'N	21°30'E
D.R. CONGO	TSHUAPA	Bosekele	01°18'N	22°32'E
D.R. CONGO	ITURI	Bunia	01°33'N	30°15'E
D.R. CONGO	EQUATEUR	Busira	00°15'N	18°59'E
D.R. CONGO	BAS-UELE	Buta	02°48'N	24°45'E
D.R. CONGO	KONGO CENTRAL	Cattier	05°26'S	14°45'E
D.R. CONGO	KONGO CENTRAL	Congo da Lemba	05°42'S	13°40'E
D.R. CONGO	KASAI	Dekese	03°29'S	21°23'E
D.R. CONGO	SANKURU	Djeka	03°17'S	23°59'E
D.R. CONGO	HAUT-UELE	Doruma	04°43'N	27°41'E
D.R. CONGO	HAUT-UELE	Dungu	03°36'N	28°34'E
D.R. CONGO	EQUATEUR	Eala	00°03'N	18°19'E
D.R. CONGO	HAUT-KATANGA	Elizabethville [=Lubumbashi]		
D.R. CONGO	TSHUAPA	Etata	00°14'S	20°42'E
D.R. CONGO	HAUT-UELE	Faradje	03°44'N	29°43'E
D.R. CONGO	EQUATEUR	Flandria	00°12'S	19°00'E
D.R. CONGO	MAI-NDOMBE	Galli-Koko	02°14'S	19°10'E
D.R. CONGO	LOMAMI	Gandajika	06°44'S	23°57'E
D.R. CONGO	HAUT-UELE	Gangala na Bodio	03°42'N	29°17'E
D.R. CONGO	ITURI	Geti	01°13'N	30°11'E
D.R. CONGO	KWANGO	Goa	05°42'S	16°36'E
D.R. CONGO	KINSHASA	Guma	04°07'S	15°40'E
D.R. CONGO	LULUA	Hemptinne St-Benoit	06°18'S	22°31'E
D.R. CONGO	BAS-UELE	Ibembo	02°38'N	23°37'E
D.R. CONGO	TSHUAPA	Ikela	01°03'S	23°22'E
D.R. CONGO	HAUT-LOMAMI	Ilebo	04°20'S	20°35'E
D.R. CONGO	KWILU	Ipamu	04°10'S	19°38'E
D.R. CONGO	LUALABA	Kabamba	09°31'S	22°51'E
D.R. CONGO	LOMAMI	Kabinda	06°08'S	24°29'E
D.R. CONGO	LUALABA	Kabomba [=Kabamba]		
D.R. CONGO	HAUT-LOMAMI	Kabongo	07°21'S	25°35'E
D.R. CONGO	LUALABA	Kafakumba	09°40'S	23°46'E

D.R. CONGO	LUALABA	<b>Kalani River</b>	?	
D.R. CONGO	HAUT-LOMAMI	<b>Kaluli-Nord [=Kalule-Nord]</b>	09°47'S	26°00'E
D.R. CONGO	LOMAMI	<b>Kambaye</b>	06°53'S	23°44'E
D.R. CONGO	HAUT-LOMAMI	<b>Kamina</b>	08°44'S	25°00'E
D.R. CONGO	LULUA	<b>Kananga</b>	05°54'S	22°25'E
D.R. CONGO	HAUT-LOMAMI	<b>Kaniama</b>	07°31'S	24°10'E
D.R. CONGO	LUALABA	<b>Kapanga</b>	08°21'S	22°39'E
D.R. CONGO	HAUT-UELE	<b>Kapili</b>	03°42'S	27°53'E
D.R. CONGO	HAUT-KATANGA	<b>Kapiri</b>	09°42'S	27°13'E
D.R. CONGO	MANIEMA	<b>Kasongo</b>	04°26'S	26°40'E
D.R. CONGO	HAUT-KATANGA	<b>Kasumbalesa</b>	12°14'S	27°48'E
D.R. CONGO	KASAI-OCCIDENTAL	<b>Katoka</b>	05°40'S	22°24'E
D.R. CONGO	LOMAMI	<b>Katoto</b>	06°44'S	23°50'E
D.R. CONGO	LULUA	<b>Kele</b>	06°55'S	23°11'E
D.R. CONGO	HAUT-LOMAMI	<b>Kiabukwa</b>	08°45'S	24°50'E
D.R. CONGO	KWILU	<b>Kikwit</b>	05°02'S	18°48'E
D.R. CONGO	KWILU	<b>Kimbao</b>	05°08'S	17°37'E
D.R. CONGO	KWILU	<b>Kimbau [=Kimbao]</b>		
D.R. CONGO	HAUT-LOMAMI	<b>Kinda</b>	09°18'S	25°03'E
D.R. CONGO	MANIEMA	<b>Kindu</b>	02°57'S	25°55'E
D.R. CONGO	KWILU	<b>Kingungi</b>	05°25'S	17°56'E
D.R. CONGO	KONGO CENTRAL	<b>Kiniati</b>	05°20'S	12°56'E
D.R. CONGO	KINSHASA	<b>Kinshasa</b>	04°21'S	15°18'E
D.R. CONGO	HAUT-KATANGA	<b>Kipopo</b>	11°39'S	27°27'E
D.R. CONGO	HAUT-KATANGA	<b>Kipushya</b>	12°58'S	29°30'E
D.R. CONGO	TANGANYIKA	<b>Kirungu</b>	07°05'S	29°44'E
D.R. CONGO	HAUT-LOMAMI	<b>Kisamba</b>	07°21'S	24°02'E
D.R. CONGO	TSHOPO	<b>Kisangani</b>	00°31'N	25°11'E
D.R. CONGO	KONGO CENTRAL	<b>Kisantu</b>	05°08'S	15°05'E
D.R. CONGO	SANKURU	<b>Kole</b>	03°28'S	22°27'E
D.R. CONGO	LUALABA	<b>Kolwezi</b>	10°43'S	25°30'E
D.R. CONGO	SANKURU	<b>Kondue</b>	04°58'S	23°19'E
D.R. CONGO	LUALABA	<b>Koni</b>	10°46'S	25°41'E
D.R. CONGO	HAUT-KATANGA	<b>Kundelungu</b>	10°37'S	27°50'E
D.R. CONGO	MAI-NDOMBE	<b>Kwamouth</b>	03°11'S	16°12'E
D.R. CONGO	ITURI	<b>Lac Albert, Kasenyi</b>	01°24'N	30°26'E
D.R. CONGO	HAUT-LOMAMI	<b>Lac Upemba</b>	08°36'S	26°22'E
D.R. CONGO	KONGO CENTRAL	<b>Lemfu</b>	05°18'S	15°13'E
D.R. CONGO	KINSHASA	<b>Leopoldville [=Kinshasa]</b>		
D.R. CONGO	KWILU	<b>Leverville [=Lusanga]</b>		
D.R. CONGO	SUD-UBANGI	<b>Libenge</b>	03°39'N	18°38'E
D.R. CONGO	HAUT-KATANGA	<b>Likasi</b>	10°59'S	26°44'E
D.R. CONGO	KASAI	<b>Lodima [=Ludima]</b>		
D.R. CONGO	SANKURU	<b>Lodja</b>	03°31'S	23°36'E
D.R. CONGO	LUALABA	<b>Luashi</b>	10°56'S	23°37'E
D.R. CONGO	HAUT-KATANGA	<b>Lubumbashi</b>	11°40'S	27°29'E
D.R. CONGO	KASAI	<b>Ludima</b>	04°55'S	21°01'E
D.R. CONGO	KASAI	<b>Luebo</b>	05°21'S	21°25'E
D.R. CONGO	EQUATEUR	<b>Lukolela</b>	01°04'S	17°11'E
D.R. CONGO	KONGO CENTRAL	<b>Lukula</b>	05°24'S	12°57'E

D.R. CONGO	LULUA	Lula	07°25'S	22°33'E
D.R. CONGO	LULUA	Luluabourg [=Kananga]		
D.R. CONGO	ITURI	Luma	02°35'N	30°35'E
D.R. CONGO	SANKURU	Lusambo	04°58'S	23°26'E
D.R. CONGO	KWILU	Lusanga	04°50'S	18°43'E
D.R. CONGO	BANDUNDU	Luswe?	03°00'S	16°00'E
D.R. CONGO	KWILU	Madibi	04°18'S	18°25'E
D.R. CONGO	ITURI	Mahagi a Niarembe	02°16'N	31°04'E
D.R. CONGO	KONGO CENTRAL	Matadi	05°50'S	13°27'E
D.R. CONGO	ITURI	Mawambi	01°04'N	28°34'E
D.R. CONGO	KONGO CENTRAL	Mayidi	05°11'S	15°09'E
D.R. CONGO	KONGO CENTRAL	Mayumbe	05°27'S	12°52'E
D.R. CONGO	KONGO CENTRAL	Mbanza-Ngungu	05°15'S	14°51'E
D.R. CONGO	KINSHASA	Menkao, Plateau Bateke	04°12'S	15°42'E
D.R. CONGO	ITURI	Mobayi-Mbongo	04°18'N	21°11'E
D.R. CONGO	SUD-UBANGI	Molanda	02°29'N	20°48'E
D.R. CONGO	TANGANYIKA	Moliro	08°13'S	30°34'E
D.R. CONGO	HAUT-UELE	Moto	02°54'N	29°25'E
D.R. CONGO	SUD-UBANGI	M'Paka, Libenge	03°39'N	18°38'E
D.R. CONGO	KONGO CENTRAL	Mpese	05°14'S	15°33'E
D.R. CONGO	LULUA	Mukenge	06°01'S	22°19'E
D.R. CONGO	KWILU	Mukila	05°01'S	16°59'E
D.R. CONGO	HAUT-LOMAMI	Mukishi	08°30'S	24°43'E
D.R. CONGO	HAUT-LOMAMI	Muteba	06°11'S	21°34'E
D.R. CONGO	KONGO CENTRAL	Mvuangu	05°32'S	12°43'E
D.R. CONGO	LOMAMI	Mwene-Ditu	07°01'S	23°27'E
D.R. CONGO	HAUT-UELE	Niangara [=Nyangara]		
D.R. CONGO	ITURI	Niarembe	02°15'N	31°07'E
D.R. CONGO	ITURI	Nioka	02°06'N	30°37'E
D.R. CONGO	HAUT-UELE	Nyangara	03°41'N	27°54'E
D.R. CONGO	MANIEMA	Nyangwe	04°17'S	26°15'E
D.R. CONGO	HAUT-UELE	Nzoro	03°20'N	29°30'E
D.R. CONGO	TSHOPO	Opala	00°31'S	24°14'E
D.R. CONGO	KWANGO	Panzi	07°12'S	17°57'E
D.R. CONGO	NORD-KIVU	Parc National Albert, Kalinga	00°51'S	29°20'E
D.R. CONGO	NORD-KIVU	Parc National Albert, Katanda	00°50'S	29°22'E
D.R. CONGO	NORD-KIVU	Parc National Albert, Kikyo pres Kalonge	00°20'N	29°48'E
D.R. CONGO	NORD-KIVU	Parc National Albert, Mabenga	01°01'S	29°21'E
D.R. CONGO	NORD-KIVU	Parc National Albert, Ndeko	00°52'S	29°16'E
D.R. CONGO	NORD-KIVU	Parc National Albert, NE Rutshuru, Binza	00°52'S	29°23'E
D.R. CONGO	NORD-KIVU	Parc National Albert, Rwindi	00°47'S	29°18'E
D.R. CONGO	NORD-KIVU	Parc National Albert, Secteur Nord, Riviere Ngokoi	00°19'N	29°45'E
D.R. CONGO	NORD-KIVU	Parc National Albert, Semliki Plain	00°06'S	29°34'E
D.R. CONGO	NORD-KIVU	Parc National Albert, Tshambi	00°44'S	29°14'E
D.R. CONGO	HAUT-UELE	Parc National de la Garamba, Cellule II	03°53'N	29°24'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba	08°50'S	26°50'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Kabwe sur Muye	08°50'S	26°50'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Kalumegongo	08°57'S	27°02'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Kankunda	08°50'S	26°45'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Kaswabilenga	09°09'S	26°42'E

D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Kateke	08°56'S	26°42'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Kaziba	09°10'S	26°50'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Kimilombo	08°55'S	27°11'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Lusinga	08°50'S	27°12'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Mabwe	08°39'S	26°31'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Mubale	08°45'S	26°54'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Mukana	09°15'S	27°12'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Munoi	09°16'S	26°46'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Riviere Dipidi	09°04'S	26°40'E
D.R. CONGO	HAUT-LOMAMI	Parc National de l'Upemba, Riviere Ntumbwa	08°56'S	27°03'E
D.R. CONGO	ITURI	Plaine Semliki	00°54'N	30°10'E
D.R. CONGO	KINSHASA	Pool Malebo	04°17'S	12°29'E
D.R. CONGO	HAUT-LOMAMI	Port-Francqui [=Ilebo]		
D.R. CONGO	HAUT-KATANGA	Pweto-Kilwa	08°49'S	28°35'E
D.R. CONGO	BAS-UELE	Region de Sassa	05°05'N	25°30'E
D.R. CONGO	LUALABA	Sandoa [=Sanduwa]		
D.R. CONGO	LUALABA	Sanduwa	09°42'S	22°53'E
D.R. CONGO	KINSHASA	Stanley Pool [=Pool Malebo]		
D.R. CONGO	TSHOPO	Stanleyville [=Kisangani]		
D.R. CONGO	KONGO CENTRAL	Thysville [=Mbanza-Ngungu]		
D.R. CONGO	LUALABA	Tshala	08°47'S	22°40'E
D.R. CONGO	LULUA	Tshibala	06°22'S	21°52'E
D.R. CONGO	LUALABA	Tshibalaka	08°36'S	23°03'E
D.R. CONGO	HAUT-LOMAMI	Tshibamba	08°12'S	24°21'E
D.R. CONGO	HAUT-LOMAMI	Tshikapa	06°26'S	20°47'E
D.R. CONGO	LUALABA	Tshipaza	08°34'S	22°24'E
D.R. CONGO	HAUT-UELE	Tuku	02°24'N	27°54'E
D.R. CONGO	HAUT-UELE	Van Kerkhovenville [=Nzoro]		
D.R. CONGO	HAUT-UELE	Watsa	03°02'N	29°32'E
D.R. CONGO	MONGALA	Yambata	02°26'N	21°58'E
D.R. CONGO	TSHOPO	Yangambi	00°48'N	24°27'E
D.R. CONGO	HAUT-UELE	Yebo Moto	02°54'N	29°25'E
D.R. CONGO	KWILU	Zaba	04°20'S	18°15'E
D.R. CONGO	LUALABA	Zilo	10°31'S	25°28'E
EGYPT	CAIRO	Al Maadi	29°58'N	31°16'E
EGYPT	ASWAN	Assuan [=Aswan]		
EGYPT	ASWAN	Assouan [=Aswan]		
EGYPT	ASWAN	Aswan	24°05'N	32°54'E
EGYPT	CAIRO	Cairo	30°03'N	31°14'E
EGYPT	CAIRO	Cairo, Pyramids	29°59'N	31°08'E
EGYPT	NEW VALLEY	Edfou	24°59'N	32°52'E
EGYPT	LUXOR	Luxor	25°41'N	32°38'E
EGYPT	CAIRO	Meadia [=Al Maadi]		
EGYPT	PORT SAID	Port Said	31°16'N	32°18'E
EQUATORIAL GUINEA	BIOKO-SUR	Bahia de San Carlos [=Luba]		
EQUATORIAL GUINEA	LITORAL	Benito [=Mbini]		
EQUATORIAL GUINEA	BIOKO-NORTE	Casa Banana	03°40'N	08°52'E
EQUATORIAL GUINEA	BIOKO-SUR	Lake Loreto	03°24'N	08°40'E

EQUATORIAL GUINEA	BIOKO-SUR	<b>Luba</b>	03°27'N	08°33'E
EQUATORIAL GUINEA	LITORAL	<b>Makomo</b>	01°44'N	09°46'E
EQUATORIAL GUINEA	LITORAL	<b>Mbini</b>	01°35'N	09°37'E
EQUATORIAL GUINEA	BIOKO-SUR	<b>Moka</b>	03°21'N	08°40'E
EQUATORIAL GUINEA	LITORAL	<b>Mongo</b>	01°52'N	10°10'E
EQUATORIAL GUINEA	BIOKO-SUR	<b>Musola</b>	03°26'N	08°38'E
EQUATORIAL GUINEA	CENTRO-SUR	<b>Nkolentangan</b>	01°35'N	10°30'E
EQUATORIAL GUINEA	LITORAL	<b>San-Benito [=Mbini]</b>		
EQUATORIAL GUINEA	LITORAL	<b>Uelleburg [=Mbini]</b>		

ETHIOPIA	AMHARA	<b>Abbat</b>	10°38'N	37°46'E
ETHIOPIA	OROMIA	<b>Adaba</b>	07°00'N	39°23'E
ETHIOPIA	OROMIA	<b>Adama</b>	08°32'N	39°16'E
ETHIOPIA	ADDIS ABABA	<b>Addis Ababa</b>	09°00'N	38°45'E
ETHIOPIA	OROMIA	<b>Agere Maryam [=Hagere Maryam]</b>		
ETHIOPIA	OROMIA	<b>Akaki River</b>	09°03'N	38°41'E
ETHIOPIA	TIGRAY	<b>Aksum</b>	14°08'N	38°45'E
ETHIOPIA	OROMIA	<b>Ambo</b>	08°58'N	37°52'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Arba Minch</b>	06°02'N	37°33'E
ETHIOPIA	OROMIA	<b>Arero</b>	04°43'N	38°46'E
ETHIOPIA	OROMIA	<b>Assela</b>	07°58'N	39°08'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Awara</b>	08°13'N	38°39'E
ETHIOPIA	SOMALI	<b>Aware?</b>	08°15'N	44°09'E
ETHIOPIA	OROMIA	<b>Badditu</b>	06°00'N	38°00'E
ETHIOPIA	AMHARA	<b>Bahir Dar</b>	11°34'N	37°22'E
ETHIOPIA	OROMIA	<b>Bedele</b>	08°27'N	36°21'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Bonghe</b>	06°03'N	37°23'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Codjeb River [=Gojeb River]</b>		
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Dalle [=Yirga Alem]</b>	06°45'N	38°25'E
ETHIOPIA	AMHARA	<b>Dessie</b>	11°08'N	39°38'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Dilla</b>	06°25'N	38°18'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Dime</b>	06°16'N	36°20'E
ETHIOPIA	DIRE DAWA	<b>Dire Dawa</b>	09°36'N	41°51'E
ETHIOPIA	OROMIA	<b>Djem-Djem Forest</b>	09°03'N	38°09'E
ETHIOPIA	OROMIA	<b>Dodola</b>	06°59'N	39°11'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Dorze</b>	06°11'N	37°35'E
ETHIOPIA	OROMIA	<b>Doukham</b>	08°48'N	38°54'E
ETHIOPIA	OROMIA	<b>Ejere-dorf</b>	09°55'N	38°31'E
ETHIOPIA	GAMBELLA	<b>Gambela</b>	08°15'N	34°35'E
ETHIOPIA	OROMIA	<b>Gimbi</b>	09°11'N	35°50'E
ETHIOPIA	OROMIA	<b>Gimma [=Jimma]</b>		
ETHIOPIA	OROMIA	<b>Goba</b>	07°01'N	38°59'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Gojeb River</b>	07°20'N	37°20'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Gojeb Valley</b>	07°14'N	36°54'E
ETHIOPIA	OROMIA	<b>Goro</b>	06°59'N	40°29'E
ETHIOPIA	OROMIA	<b>Gudar</b>	08°58'N	37°46'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	<b>Gughe Mountains</b>	06°12'N	37°34'E
ETHIOPIA	OROMIA	<b>Habe</b>	07°49'N	39°47'E
ETHIOPIA	OROMIA	<b>Hagere Maryam</b>	05°38'N	38°14'E
ETHIOPIA	OROMIA	<b>Harairobi-See [=Lake Koka]</b>		

ETHIOPIA	HARARI	Harar	09°19'N	42°07'E
ETHIOPIA	BENISHANGUL-GUMUZ	Hora	10°08'N	34°39'E
ETHIOPIA	OROMIA	Hora Daka [=Lake Abijatta]		
ETHIOPIA	OROMIA	Hora Oitu [=Lake Chitu]		
ETHIOPIA	OROMIA	Hora Salla [=Lake Shala]		
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Hosaena	07°33'N	37°52'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Irgalem [=Yirga Alem]		
ETHIOPIA	OROMIA	Jima [=Jimma]		
ETHIOPIA	OROMIA	Jimma	07°40'N	36°50'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Key Afer	05°31'N	36°44'E
ETHIOPIA	OROMIA	Kibre Mengist	05°35'N	38°59'E
ETHIOPIA	OROMIA	Kofele	07°04'N	38°47'E
ETHIOPIA	OROMIA	Lake Abijatta	07°36'N	38°36'E
ETHIOPIA	OROMIA	Lake Chitu	07°24'N	38°25'E
ETHIOPIA	OROMIA	Lake Haramaiya	09°24'N	42°00'E
ETHIOPIA	OROMIA	Lake Koka	08°23'N	39°05'E
ETHIOPIA	OROMIA	Lake Shala	07°28'N	38°31'E
ETHIOPIA	OROMIA	Lake Zway [=Ziway]		
ETHIOPIA	OROMIA	Langano	07°32'N	38°48'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Malghe-Wando farm, Awasa-Meer	07°06'N	38°30'E
ETHIOPIA	OROMIA	Managasha [=Menagesha]	09°03'N	38°34'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Maraco [=Marequo]		
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Maraquo [=Marequo]		
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Marequo	07°58'N	38°33'E
ETHIOPIA	AMHARA	Mecha	11°30'N	37°00'E
ETHIOPIA	OROMIA	Menagesha	09°03'N	38°34'E
ETHIOPIA	OROMIA	Metahara [=Metehara]		
ETHIOPIA	OROMIA	Metehara	08°54'N	39°55'E
ETHIOPIA	OROMIA	Mount Antoto [=Mount Entoto]		
ETHIOPIA	OROMIA	Mount Entoto	09°07'N	38°46'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Murle	05°09'N	36°13'E
ETHIOPIA	OROMIA	Nazret [=Adama]		
ETHIOPIA	OROMIA	Negele	05°20'N	39°34'E
ETHIOPIA	OROMIA	Neghelli [=Negele]		
ETHIOPIA	TIGRAY	Okule-Kasai, Aksoum [=Aksum]		
ETHIOPIA	OROMIA	Shakiso	05°46'N	38°55'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Soddo [=Sodu]		
ETHIOPIA	OROMIA	Sodere	08°24'N	39°23'E
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Sodu	06°51'N	37°46'E
ETHIOPIA	OROMIA	Wabe Shebele Hotel, Lake Langano	07°39'N	38°42'E
ETHIOPIA	OROMIA	Yabelo	04°54'N	38°06'E
ETHIOPIA	GAMBELLA	Yambela [=Gambela]		
ETHIOPIA	OROMIA	Yambo [=Ambo]		
ETHIOPIA	OROMIA	Yavello [=Yabelo]		
ETHIOPIA	SOUTHERN NATIONS, NATIONALITIES & PEOPLE	Yirga Alem	06°45'N	38°25'E
ETHIOPIA	OROMIA	Ziway	07°56'N	38°43'E
ERITREA	DEBUB	Acrur	15°06'N	39°14'E
ERITREA	DEBUB	Adi Keyh	14°51'N	39°22'E
ERITREA	DEBUB	Adi-Caic [=Adi Keyh]		

ERITREA	MAEKEL	Asmara	15°19'N	38°56'E
ERITREA	GASH-BARKA	Barentu	15°06'N	37°35'E
ERITREA	MAEKEL	Dorfu	15°26'N	38°58'E
ERITREA	ANSEBA	Ghaleb [=Gheleb]		
ERITREA	ANSEBA	Gheleb	15°47'N	38°48'E
ERITREA	ANSEBA	Hagaz	15°42'N	38°16'E
ERITREA	NORTHERN RED SEA	Karora	17°42'N	38°22'E
ERITREA	ANSEBA	Keren	15°47'N	38°27'E
ERITREA	ANSEBA	Vallee de l'Anseba	16°34'N	38°06'E

GABON	OGOOUE-IVINDO	Belinga	00°08'N	13°07'E
GABON	OGOOUE-MARITIME	Bongo	02°10'S	10°12'E
GABON	OGOOUE-IVINDO	Booue	00°06'S	11°57'E
GABON	OGOOUE-LOLO	Dilo	00°01'S	13°02'E
GABON	OGOOUE-MARITIME	Fernan Vaz	01°36'S	09°26'E
GABON	ESTUAIRE	Fort de la Mondah	00°35'N	09°20'E
GABON	OGOOUE-IVINDO	Ipassa	00°31'S	12°48'E
GABON	OGOOUE-MARITIME	Kivoro	02°17'S	10°09'E
GABON	NGOUNIE	Koumba	01°48'S	11°59'E
GABON	OGOOUE-MARITIME	Lambarene	00°42'S	10°14'E
GABON	OGOOUE-LOLO	Lastoursville	00°49'S	12°44'E
GABON	ESTUAIRE	Libreville	00°20'N	09°29'E
GABON	OGOOUE-IVINDO	Makokou	00°34'N	12°51'E
GABON	NYANGA	Malembe	03°29'S	10°51'E
GABON	OGOOUE-MARITIME	Mandji [=Port Gentil]		
GABON	OGOOUE-MARITIME	Milango	00°24'S	09°38'E
GABON	ESTUAIRE	Monts de Cristal, Tchimbele	00°37'N	10°24'E
GABON	NGOUNIE	Mouila	01°52'S	11°03'E
GABON	HAUT-OGOOUE	Mounana	01°24'S	13°09'E
GABON	OGOOUE-IVINDO	Mpassa [=Ipassa]		
GABON	OGOOUE-IVINDO	Ndjole	00°11'S	10°46'E
GABON	OGOOUE-MARITIME	Ndougou	01°39'S	09°40'E
GABON	OGOOUE-IVINDO	N'jole [=Ndjole]		
GABON	WOLEM-NTEM	Oyem	01°36'N	11°34'E
GABON	OGOOUE-IVINDO	Parc National Lope	00°27'S	11°38'E
GABON	OGOOUE-MARITIME	Port Gentil	00°42'S	08°44'E
GABON	OGOOUE-MARITIME	Sette Cama	02°32'S	09°46'E
GABON	NGOUNIE	Sindara	01°02'S	10°39'E
GABON	NYANGA	Tchibanga	02°56'S	11°00'E
GABON	NGOUNIE	Waka	01°04'S	11°00'E
GABON	OGOOUE-MARITIME	Wonga-Wongue	00°29'S	09°18'E

GAMBIA	CENTRAL RIVER	Ballanghar	13°40'N	15°24'W
GAMBIA	BANJUL	Fajara	13°28'N	16°41'W
GAMBIA	CENTRAL RIVER	Georgetown [=Janjanbureh]		
GAMBIA	CENTRAL RIVER	Janjanbureh	13°32'N	14°46'W
GAMBIA	CENTRAL RIVER	Kuntaur Agricultural Station	13°40'N	14°53'W
GAMBIA	CENTRAL RIVER	McCarthy Island	13°32'N	14°46'W
GAMBIA	WEST COAST	Tanji	13°21'N	16°47'W
GAMBIA	WEST COAST	Tanji Bird Reserve	13°22'N	16°46'W

GAMBIA	WEST COAST	Yundum Agricultural Station	13°20'N	16°40'W
GHANA	GREATER ACCRA	Accra	05°33'N	00°12'W
GHANA	GREATER ACCRA	Achimota	05°37'N	00°14'W
GHANA	NORTHERN	Banda Nkwanta	08°22'N	02°08'W
GHANA	NORTHERN	Damongo	09°05'N	01°49'W
GHANA	VOLTA	Kete-Krachi	07°48'N	00°03'E
GHANA	VOLTA	Kete-Kratji [=Kete-Krachi]		
GHANA	VOLTA	Kpando	07°00'N	00°17'E
GHANA	VOLTA	Kyabobo National Park, Laboum Outpost	08°19'N	00°33'E
GHANA	NORTHERN	Nakpanduri	10°38'N	00°32'W
GHANA	UPPER EAST	Zuarungu	10°47'N	00°48'E
GUINEA	CONAKRY	Camayenne	09°32'N	13°41'W
GUINEA	MAMOU	Dalaba	10°41'N	12°15'W
GUINEA	MAMOU	Ditinn	10°53'N	12°11'W
GUINEA	SEREDOU	Foret de Ziama	08°11'N	09°16'W
GUINEA	KANKAN	Kankan	10°23'N	09°18'W
GUINEA	KINDIA	Kindia	10°03'N	12°51'W
GUINEA	FARANAH	Kisidougou	09°11'N	10°06'W
GUINEA	KINDIA	Kolanguelle	10°49'N	13°01'W
GUINEA	LABE	Labe	11°19'N	12°17'W
GUINEA	KINDIA	Mont Gangan	10°05'N	12°54'W
GUINEA	NZÉRÉKORÉ	Nzérékoré	07°45'N	08°49'W
GUINEA	SEREDOU	Seredou	08°22'N	09°17'W
GUINEA-BISSAU	CACHEU	Bambora [=Barraca Bambore]		
GUINEA-BISSAU	CACHEU	Barraca Bambore	12°27'N	16°13'W
GUINEA-BISSAU	BOLAMA	Bolama	11°35'N	15°29'W
GUINEA-BISSAU	CACHEU	Calequisse	12°04'N	16°13'W
GUINEA-BISSAU	CACHEU	Calikis [=Calequisse]		
GUINEA-BISSAU	BAFATA	Chime [=Xime]		
GUINEA-BISSAU	QUINARA	Costa de Baixa	11°24'N	15°27'W
GUINEA-BISSAU	BIOMBO	Ile de Bissao [=Ilha de Bissau]		
GUINEA-BISSAU	CACHEU	Ile de Piscis [=Ilha de Pecixe]		
GUINEA-BISSAU	BIOMBO	Ilha de Bissau	11°53'N	15°46'W
GUINEA-BISSAU	CACHEU	Ilha de Pecixe	11°49'N	16°05'W
GUINEA-BISSAU	BAFATA	Rio Geba	11°58'N	14°59'W
GUINEA-BISSAU	BAFATA	Xime	11°58'N	14°56'W
IVORY COAST	ABIDJAN	Abidjan	05°19'N	04°02'W
IVORY COAST	LAGUNES	Adiopodoume	05°20'N	04°08'W
IVORY COAST	LAGUNES	Akoupe	05°29'N	04°09'W
IVORY COAST	COMOE	Assinie	05°09'N	03°19'W
IVORY COAST	ABIDJAN	Banco Forest	05°23'N	04°03'W
IVORY COAST	LAGUNES	Bingerville	05°21'N	03°52'W
IVORY COAST	VALLEE DU BANDAMA	Bouake	07°42'N	05°02'W
IVORY COAST	LACS	Bringakro	06°26'N	05°05'W
IVORY COAST	ZANZAN	Comoe	08°37'N	03°47'W
IVORY COAST	ZANZAN	Comoe National Park	08°37'N	03°47'W

IVORY COAST	NZI-COMOE	<b>Dimbokro</b>	06°39'N	04°43'W
IVORY COAST	KEDOUGOU	<b>Dindefelo</b>	12°23'N	13°40'W
IVORY COAST	KEDOUGOU	<b>Dinnedefelou [=Dindefelo]</b>		
IVORY COAST	ZANZAN	<b>Kakpin</b>	08°37'N	03°47'W
IVORY COAST	SAVANES	<b>Koko</b>	08°09'N	06°07'W
IVORY COAST	ZANZAN	<b>Kolomabira</b>	08°29'N	03°45'W
IVORY COAST	LAGUNES	<b>Lamto</b>	06°13'N	05°02'W
IVORY COAST	SAVANES	<b>M'banto</b>	09°34'N	06°41'W
IVORY COAST	MONTAGNES	<b>Mont Tonkoui</b>	07°27'N	07°38'W
IVORY COAST	DENGUELE	<b>Niamasso</b>	09°29'N	07°41'W
IVORY COAST	VALLEE DU BANDAMA	<b>Ounantiekaha</b>	08°22'N	05°10'W
IVORY COAST	ZANZAN	<b>Parc National de la Comoe, Lola-Camp</b>	08°45'N	03°49'W
IVORY COAST	MOYEN-CAVALLY	<b>Research Station, Tai National Park</b>	05°50'N	07°21'W
IVORY COAST	SAVANES	<b>Senguekele</b>	09°30'N	06°07'W
IVORY COAST	ZANZAN	<b>Zamou</b>	08°35'N	03°46'W

KENYA	KAJIADO	<b>Amboseli National Park</b>	02°40'S	37°17'E
KENYA	KILIFI	<b>Arabuko Forest</b>	03°15'S	39°58'E
KENYA	ISIOLO	<b>Archers Post</b>	00°38'N	37°40'E
KENYA	SAMBURU	<b>Baragoi</b>	01°47'S	36°47'E
KENYA	NANDI	<b>Baraton Animal Husbandry Research Station</b>	00°15'N	35°05'E
KENYA	NANDI	<b>Baraton, University College of East Africa</b>	00°15'N	35°05'E
KENYA	ISIOLO	<b>Buffalo Springs Game Reserve, Uaso Nyiro River</b>	00°37'N	37°38'E
KENYA	TAITA-TAVETA	<b>Bungule</b>	03°51'S	38°40'E
KENYA	TAITA-TAVETA	<b>Bura</b>	03°27'S	38°19'E
KENYA	KAJIADO	<b>campsites near Ol Tukai</b>	02°41'S	37°16'E
KENYA	TURKANA	<b>Central Island, Lake Rudolf [=Turkana]</b>	03°30'N	36°02'E
KENYA	NANDI	<b>Chemiesia [=Chomisia]</b>	00°15'N	35°01'E
KENYA	MAKUENI	<b>Chyulu Hills</b>	02°47'S	37°57'E
KENYA	KWALE	<b>Diani Beach</b>	04°17'S	39°35'E
KENYA	TRANS-NZOIA	<b>East Surrey Estates</b>	01°09'N	35°02'E
KENYA	UASIN GISHU	<b>Eldoret</b>	00°31'N	35°17'E
KENYA	MAKUENI	<b>Emali Range, Sultan Hamud</b>	02°01'S	37°22'E
KENYA	MURANGA	<b>Fort Hall [=Muranga]</b>	00°43'S	37°09'E
KENYA	KILIFI	<b>Galana Game Ranch, Headquarters</b>	03°04'S	39°20'E
KENYA	KILIFI	<b>Galana Game Ranch, Koromodo</b>	03°02'S	39°25'E
KENYA	TANA RIVER	<b>Galana Game Ranch, Lali Hills area</b>	03°01'S	39°16'E
KENYA	TANA RIVER	<b>Galana Game Ranch, Sala Gate</b>	03°04'S	39°13'E
KENYA	GARISSA	<b>Garissa</b>	00°27'S	39°39'E
KENYA	TANA RIVER	<b>Garsen</b>	02°16'S	40°07'E
KENYA	MARSABIT	<b>Gof Bongole</b>	02°12'S	37°56'E
KENYA	NAROK	<b>Guaso Nyiro</b>	01°10'S	35°57'E
KENYA	NAKURU	<b>Hell's Gate National Park</b>	00°53'S	36°18'E
KENYA	TANA RIVER	<b>Hola [=Bura]</b>	02°16'S	40°07'E
KENYA	KITUI	<b>Ikuta [=Ikutha]</b>	02°04'S	38°11'E
KENYA	NAKURU	<b>Joan Root's Shamba</b>	00°49'S	36°23'E
KENYA	VHIGA	<b>Kaimosi</b>	00°07'N	34°51'E
KENYA	KAKAMEGA	<b>Kakamega</b>	00°17'N	34°45'E
KENYA	KAKAMEGA	<b>Kakamega Forest</b>	00°16'N	34°52'E
KENYA	NANDI	<b>Kapsemoite [=Kipsamoite]</b>	00°19'S	35°00'E

KENYA	KERICHO	Kapsoit	00°19'N	35°13'E
KENYA	NAIROBI	Karura Forest	01°14'S	36°50'E
KENYA	TAITA-TAVETA	Kasigau	03°50'S	38°40'E
KENYA	TAITA-TAVETA	Kedai	38°22'E	38°22'E
KENYA	KAJIADO	Kedong Valley	01°10'S	36°30'E
KENYA	NAROK	Keekorok	01°35'S	35°14'E
KENYA	KERICHO	Kericho	00°22'S	35°17'E
KENYA	MAKUENI	Kibwezi	02°25'S	37°58'E
KENYA	KIAMBU	Kijabe	00°57'S	36°36'E
KENYA	TAITA-TAVETA	Kilaguni Lodge	02°54'S	38°04'E
KENYA	KILIFI	Kilifi	03°30'S	39°55'E
KENYA	TRANS-NZOIA	Kitale	01°01'N	35°00'E
KENYA	TANA RIVER	Kora	00°12'S	38°44'E
KENYA	KWALE	Kwale	04°10'S	39°27'E
KENYA	KAKAMEGA	Kwishero [=Khwisero]	00°10'N	34°36'E
KENYA	NAKURU	Lake Elementaita	00°27'S	36°15'E
KENYA	TAITA-TAVETA	Lake Jipe	03°36'S	37°47'E
KENYA	NAIROBI	Langata	01°22'S	36°44'E
KENYA	TAITA-TAVETA	Lion Hill near Voi	03°21'S	38°25'E
KENYA	NAROK	Lolgorien	01°14'S	34°49'E
KENYA	KERICHO	Lombwua [=Lumbwa]	00°12'S	35°28'E
KENYA	MACHAKOS	Machakos	01°31'S	37°16'E
KENYA	KWALE	Mackinnon Road	03°43'S	39°02'E
KENYA	KWALE	Makadara Forest	04°14'S	39°23'E
KENYA	MURANGA	Makindi	00°58'S	37°06'E
KENYA	MURANGA	Makuyu	00°54'S	37°11'E
KENYA	KILIFI	Malindi	03°13'S	40°07'E
KENYA	LAMU	Manda Island, Takwa	02°17'S	40°58'E
KENYA	KIAMBU	Mangu	01°04'S	37°03'E
KENYA	KAJIADO	Mara area	01°24'S	36°26'E
KENYA	VHIGA	Maragoli	00°05'N	34°43'E
KENYA	SAMBURU	Maralal	01°06'N	36°42'E
KENYA	KILIFI	Mariakani Research Station	03°51'N	39°27'E
KENYA	MARSABIT	Marsabit	02°20'N	37°59'E
KENYA	MARSABIT	Marsabit campsite	02°19'N	37°59'E
KENYA	NAROK	Masai Mara	01°28'S	35°02'E
KENYA	KWALE	Mbungu	04°05'S	39°23'E
KENYA	TAITA-TAVETA	Mbuyuni	03°24'S	37°53'E
KENYA	MERU	Meru National Park	00°13'N	38°10'E
KENYA	MERU	Meru National Park, Headquarters	00°16'N	38°08'E
KENYA	MERU	Meru National Park, Mulika Lodge	00°13'N	38°10'E
KENYA	MERU	Meru National Park, Mulika Plains	00°10'N	38°12'E
KENYA	MERU	Meru National Park, Tana River area	00°04'S	38°23'E
KENYA	KILIFI	Mnarani	03°39'S	39°51'E
KENYA	MOMBASA	Mombasa	04°03'S	39°40'E
KENYA	MURANGA	Mont Kinangop	00°40'S	36°49'E
KENYA	BUNGOMA	Mount Elgon	01°08'N	34°42'E
KENYA	NYERI	Mount Kenya	00°09'S	37°18'E
KENYA	MAKUENI	Mtito Andei	02°41'S	38°10'E
KENYA	MOMBASA	Mtwapa	03°57'S	39°45'E

KENYA	KIAMBU	Muguga	01°15'S	36°39'E
KENYA	KIAMBU	Muguga Research Station	01°13'S	36°39'E
KENYA	KAKAMEGA	Mumias	00°20'N	34°29'E
KENYA	KITUI	Mutha	01°48'S	38°26'E
KENYA	KITUI	Mwingi	00°56'S	38°04'E
KENYA	NAIROBI	Nairobi	01°19'S	36°50'E
KENYA	NAKURU	Naivasha	00°43'S	36°26'E
KENYA	NAKURU	Nakuru	00°17'S	36°04'E
KENYA	LAIKIPIA	Naro Moru	00°10'S	37°01'E
KENYA	NAROK	Narok	01°05'S	35°52'E
KENYA	SIAYA	Ndori	00°01'S	34°26'E
KENYA	KAJIADO	Ngong	01°21'S	36°40'E
KENYA	TAITA-TAVETA	Ngulia Lodge	03°01'S	38°13'E
KENYA	KITUI	Nguni	01°31'S	37°57'E
KENYA	NYERI	Nyeri	00°26'S	36°57'E
KENYA	KAJIADO	Ol Tukai	02°40'S	37°16'E
KENYA	KILIFI	Rabai	03°56'S	39°43'E
KENYA	MIGORI	Rongo	00°45'S	34°36'E
KENYA	TAITA-TAVETA	Sagala Hills	03°28'S	38°35'E
KENYA	SAMBURU	Samburu	00°37'N	37°32'E
KENYA	SAMBURU	Samburu Game Reserve	00°37'N	37°38'E
KENYA	SAMBURU	Samburu Lodge	00°34'N	37°34'E
KENYA	ISIOLO	Samburu-Isiolo Game Reserve	00°35'N	37°28'E
KENYA	KWALE	Shimba Hills	04°15'S	39°23'E
KENYA	KILIFI	Sokoke Forest	03°25'S	39°53'E
KENYA	KITUI	Sosoma	00°53'N	38°40'E
KENYA	NAROK	South Masai Reserve, near Mara River	01°28'S	35°02'E
KENYA	NAKURU	Soy Sambu Estates	00°28'S	36°04'E
KENYA	KAJIADO	Suswa	01°11'S	36°22'E
KENYA	TAITA-TAVETA	Taveta	03°24'S	37°40'E
KENYA	TAITA-TAVETA	Teita [=Taita]	03°22'S	38°22'E
KENYA	KIAMBU	Thika	01°02'S	37°05'E
KENYA	KWALE	Tiwi	04°15'S	39°36'E
KENYA	TAITA-TAVETA	Tsavo	03°00'S	38°28'E
KENYA	TAITA-TAVETA	Tsavo East National Park, Aruba	03°20'S	38°50'E
KENYA	TAITA-TAVETA	Tsavo East National Park, Aruba Road	03°21'S	38°39'E
KENYA	TAITA-TAVETA	Tsavo East National Park, Buchuma	03°40'S	38°56'E
KENYA	TAITA-TAVETA	Tsavo East National Park, Dida Harea	03°35'S	38°50'E
KENYA	TAITA-TAVETA	Tsavo East National Park, Lugard's Falls	03°02'S	38°42'E
KENYA	TAITA-TAVETA	Tsavo East National Park, Mudanda Rock	03°12'S	38°31'E
KENYA	TAITA-TAVETA	Tsavo East National Park, Ndara	03°42'S	38°43'E
KENYA	TAITA-TAVETA	Tsavo East National Park, Voi Safari Lodge	03°21'S	38°35'E
KENYA	TAITA-TAVETA	Tsavo National Park, Manyani	03°06'S	38°30'E
KENYA	TAITA-TAVETA	Tsavo National Park, Mzinga	03°21'S	38°39'E
KENYA	TAITA-TAVETA	Tsavo Park	02°45'S	38°49'E
KENYA	TAITA-TAVETA	Tsavo West National Park, Murka area	03°22'S	37°56'E
KENYA	TAITA-TAVETA	Tsavo West National Park, Ngulia	03°01'S	38°13'E
KENYA	LAIKIPIA	Uaso Nyiro	00°10'N	36°53'E
KENYA	KITUI	Ukazzi Hill [=Ukasi Hill]	00°49'S	38°33'E
KENYA	TAITA-TAVETA	Voi	03°24'S	38°33'E

KENYA	KITUI	Wamata	02°26'S	38°27'E
KENYA	LAMU	Witu	02°23'S	40°26'E
LESOTHO	MASERU	Maseru	29°21'S	27°31'E
LIBERIA	LOFA	Foya Proposed Protected Area	07°57'N	10°17'W
LIBERIA	LOFA	Mount Wologizi	08°07'N	09°58'W
MALAWI	CENTRAL	Bua River	12°47'S	34°12'E
MALAWI	SOUTHERN	Bvumbwe	15°56'S	35°05'E
MALAWI	NORTHERN	Chelinda	10°35'S	33°48'E
MALAWI	SOUTHERN	Chiromo	16°33'S	35°08'E
MALAWI	NORTHERN	Chisasira	11°54'S	34°04'E
MALAWI	NORTHERN	Chiwenga	09°25'S	32°58'E
MALAWI	SOUTHERN	Cholo	16°04'S	35°09'E
MALAWI	CENTRAL	Dzalanyama Forest Reserve	14°20'S	33°31'E
MALAWI	NORTHERN	Jembya Forest Reserve	10°08'S	33°27'E
MALAWI	NORTHERN	Likoma	12°04'S	34°44'E
MALAWI	NORTHERN	Livingstonia	10°36'S	34°06'E
MALAWI	SOUTHERN	Lujeri	16°02'S	35°40'E
MALAWI	NORTHERN	Misuku Hills	09°40'S	33°33'E
MALAWI	SOUTHERN	Mlanje [=Mulanje]		
MALAWI	NORTHERN	Mughese Forest Reserve	09°39'S	33°33'E
MALAWI	SOUTHERN	Mulanje	16°01'S	35°31'E
MALAWI	NORTHERN	Mzuzu	11°27'S	34°01'E
MALAWI	CENTRAL	Nkhata Bay	11°37'S	34°18'E
MALAWI	NORTHERN	Nkhorongo	11°23'S	33°59'E
MALAWI	CENTRAL	Ntchisi	13°22'S	33°55'E
MALAWI	CENTRAL	Ntchisi Forest Reserve	13°22'S	34°01'E
MALAWI	CENTRAL	Nyamadzane [=Nyamazani]		
MALAWI	CENTRAL	Nyamazani	14°16'S	33°55'E
MALAWI	NORTHERN	Rhumpi	11°01'S	33°51'E
MALAWI	NORTHERN	Rumphi [=Rhumpi]		
MALAWI	NORTHERN	Viphya Forest Reserve	12°07'S	33°43'E
MALAWI	NORTHERN	Vwaza Game Reserve, Kazuni Camp	11°08'S	33°39'E
MALAWI	NORTHERN	Vwaza Marsh Wildlife Reserve	10°53'S	33°26'E
MALAWI	SOUTHERN	Zomba	15°23'S	35°19'E
MALI	BAMAKO	Bamako	12°38'N	08°00'W
MALI	GAO	Bandiakara	16°24'N	00°03'W
MALI	MOPTI	Douentza	15°00'N	02°57'W
MALI	KAYES	Kayes	14°26'N	11°27'W
MALI	KAYES	Khayes [=Kayes]		
MALI	KAYES	Kita	13°02'N	09°29'W
MALI	SEGOU	Manimpe	14°09'N	05°31'W
MALI	SEGOU	Moninpe [=Manimpe]		
MALI	KOULIKORO	Nara	15°10'N	07°17'W
MALI	SEGOU	Segou	13°26'N	06°15'W
MALI	MOPTI	Sevare	14°32'N	04°06'W
MALI	SIKASSO	Sikasso	11°19'N	05°41'W

MAURITANIA	BRAKNA	Boghé	16°36'N	14°16'W
MAURITANIA	TRARZA	Garak	16°33'N	15°46'W
MAURITANIA	GUIDIMAKA	Guidimaka	15°14'N	12°15'W
MAURITANIA	TRARZA	Rosso	16°31'N	15°48'W
MAURITANIA	NOUAKCHOTT	Nouakchott	18°05'N	15°58'W
MAURITANIA	TRARZA	Tounguen	16°31'N	15°46'W
MOZAMBIQUE	MANICA	Amatongas	19°15'S	33°50'E
MOZAMBIQUE	MANICA	Bandula	19°02'S	33°09'E
MOZAMBIQUE	SOFALA	Beira	19°50'S	34°50'E
MOZAMBIQUE	MAPUTO	Bela Vista	26°21'S	32°40'E
MOZAMBIQUE	SOFALA	Caia	17°50'S	35°20'E
MOZAMBIQUE	SOFALA	Chemba	17°10'S	34°53'E
MOZAMBIQUE	TETE	Chifumbasi	14°22'S	32°56'E
MOZAMBIQUE	MANICA	Chimoio	19°08'S	33°28'E
MOZAMBIQUE	ZAMBEZIA	Chinde	18°35'S	36°28'E
MOZAMBIQUE	SOFALA	Chinizua	18°57'S	35°08'E
MOZAMBIQUE	SOFALA	Chironde Camp	18°23'S	35°33'E
MOZAMBIQUE	MANICA	Chupanga	18°02'S	35°37'E
MOZAMBIQUE	MAPUTO	Delagoa [=Maputo Bay]		
MOZAMBIQUE	MAPUTO	Delagoabai [=Maputo Bay]		
MOZAMBIQUE	SOFALA	Dondo	19°37'S	34°44'E
MOZAMBIQUE	ZAMBEZIA	E of Chipirone, Valley of Kola River	16°29'S	35°46'E
MOZAMBIQUE	MANICA	Espungabera	20°27'S	32°47'E
MOZAMBIQUE	MANICA	Gondola	19°05'S	33°39'E
MOZAMBIQUE	SOFALA	Gorongosa Mountain	18°24'S	34°04'E
MOZAMBIQUE	SOFALA	Gorongosa National Park	18°49'S	34°30'E
MOZAMBIQUE	SOFALA	Gorongosa National Park, Chitengo	18°58'S	34°22'E
MOZAMBIQUE	MANICA	Inhacoro [=Tambara]		
MOZAMBIQUE	SOFALA	Inhanconde Forest	18°23'S	34°10'E
MOZAMBIQUE	GAZA	João Belo [=Xai-Xai]		
MOZAMBIQUE	CABO DELGADO	Kionga [=Quionga]		
MOZAMBIQUE	MAPUTO	Lourenço Marques [=Maputo]		
MOZAMBIQUE	MAPUTO	Maputo	25°58'S	32°35'E
MOZAMBIQUE	MAPUTO	Maputo Bay	25°58'S	32°34'E
MOZAMBIQUE	CABO DELGADO	Mareja (Site 1), Parque Nacional das Quirimbas	12°51'S	40°11'E
MOZAMBIQUE	CABO DELGADO	Mareja (Site 2), Parque Nacional das Quirimbas	12°52'S	40°10'E
MOZAMBIQUE	CABO DELGADO	Mareja (Site 3), Parque Nacional das Quirimbas	12°52'S	40°07'E
MOZAMBIQUE	MAPUTO	Marracuene	25°44'S	32°40'E
MOZAMBIQUE	SOFALA	Marromeu	18°18'S	35°56'E
MOZAMBIQUE	INHAMBANE	Morrumbene	23°39'S	35°20'E
MOZAMBIQUE	SOFALA	Muda	19°23'S	34°24'E
MOZAMBIQUE	CABO DELGADO	Namaluco (Site 1), Parque Nacional das Quirimbas	12°19'S	40°17'E
MOZAMBIQUE	CABO DELGADO	Namaluco (Site 2), Parque Nacional das Quirimbas	12°19'S	40°17'E
MOZAMBIQUE	CABO DELGADO	Namaluco (Site 3), Parque Nacional das Quirimbas	12°19'S	40°16'E
MOZAMBIQUE	CABO DELGADO	Namaluco (Site 4), Parque Nacional das Quirimbas	12°19'S	40°15'E
MOZAMBIQUE	CABO DELGADO	Namaluco (Site 5), Parque Nacional das Quirimbas	12°18'S	40°15'E
MOZAMBIQUE	CABO DELGADO	Pemba	12°58'S	40°29'E
MOZAMBIQUE	MAPUTO	Pessene	25°42'S	32°21'E

MOZAMBIQUE	INHAMBANE	Pomene	22°59'S	35°32'E
MOZAMBIQUE	CABO DELGADO	Porto Amelia [=Pemba]		
MOZAMBIQUE	SOFALA	Pungwe Bay	19°47'S	34°47'E
MOZAMBIQUE	CABO DELGADO	Quionga	10°36'S	40°30'E
MOZAMBIQUE	CABO DELGADO	Ravia (Site 1), Parque Nacional das Quirimbas	12°40'S	39°25'E
MOZAMBIQUE	CABO DELGADO	Ravia (Site 2), Parque Nacional das Quirimbas	12°40'S	39°26'E
MOZAMBIQUE	CABO DELGADO	Ravia (Site 3), Parque Nacional das Quirimbas	12°40'S	39°26'E
MOZAMBIQUE	CABO DELGADO	Ravia (Site 4), Parque Nacional das Quirimbas	12°40'S	39°27'E
MOZAMBIQUE	CABO DELGADO	Ravia (Site 5), Parque Nacional das Quirimbas	12°41'S	39°27'E
MOZAMBIQUE	CABO DELGADO	Ravia (Site 6), Parque Nacional das Quirimbas	12°31'S	39°19'E
MOZAMBIQUE	MAPUTO	Rikatla	25°44'S	32°34'E
MOZAMBIQUE	SOFALA	Sena	17°27'S	35°02'E
MOZAMBIQUE	SOFALA	Senna [=Sena]		
MOZAMBIQUE	MANICA	Tambarara	16°44'S	34°15'E
MOZAMBIQUE	CABO DELGADO	Taratibu (Site 1), Parque Nacional das Quirimbas	12°49'S	39°42'E
MOZAMBIQUE	CABO DELGADO	Taratibu (Site 2), Parque Nacional das Quirimbas	12°49'S	39°42'E
MOZAMBIQUE	CABO DELGADO	Taratibu (Site 3), Parque Nacional das Quirimbas	12°48'S	39°42'E
MOZAMBIQUE	CABO DELGADO	Taratibu (Site 4), Parque Nacional das Quirimbas	12°48'S	39°42'E
MOZAMBIQUE	CABO DELGADO	Taratibu (Site 5), Parque Nacional das Quirimbas	12°47'S	39°42'E
MOZAMBIQUE	CABO DELGADO	Taratibu (Site 6), Parque Nacional das Quirimbas	12°50'S	39°42'E
MOZAMBIQUE	CABO DELGADO	Taratibu (Site 7), Parque Nacional das Quirimbas	12°48'S	39°42'E
MOZAMBIQUE	TETE	Tete	16°10'S	33°36'E
MOZAMBIQUE	ZAMBEZIA	Tshinde [=Chinde]		
MOZAMBIQUE	MAPUTO	West Gate, Maputo Special Reserve	26°30'S	32°43'E
MOZAMBIQUE	GAZA	Xai-Xai	25°03'S	33°40'E
NAMIBIA	OTJOZONDJUPA	Abachaus, Otjiwarongo District	20°26'S	16°39'E
NAMIBIA	ZAMBEZI	B8 Road, Caprivi Strip	17°46'S	23°19'E
NAMIBIA	HARDAP	Bergus	24°05'S	19°25'E
NAMIBIA	OSHIKOTO	Dobe border control	19°35'S	20°59'E
NAMIBIA	OSHIKOTO	Etosha National Park, Namutoni/Andoni	28°39'S	16°53'E
NAMIBIA	KUNENE	Fransfontein	20°13'S	15°01'E
NAMIBIA	OMAHEKE	Gam	20°14'S	20°49'E
NAMIBIA	ERONGO	Gobabeb	23°34'S	15°02'E
NAMIBIA	OMAHEKE	Gobabis	22°27'S	18°58'E
NAMIBIA	HARDAP	Gochas	24°52'S	18°48'E
NAMIBIA	OTJOZONDJUPA	Grooifontein	19°34'S	18°06'E
NAMIBIA	OTJOZONDJUPA	Hochfeld	21°29'S	17°51'E
NAMIBIA	KHOMAS	Hoffnung	22°32'S	17°12'E
NAMIBIA	KAVANGO	Immelman Runway, West Caprivi Park	17°47'S	21°18'E
NAMIBIA	KHOMAS	Khomashochland, Farm Hohenheim	23°20'S	16°20'E
NAMIBIA	KUNENE	Khwarib Schlucht	19°16'S	13°53'E
NAMIBIA	OTJOZONDJUPA	Klein Karas	27°34'S	18°05'E
NAMIBIA	KARAS	Kleinbegin	27°58'S	19°01'E
NAMIBIA	KARAS	Koes	25°56'S	19°07'E
NAMIBIA	ZAMBEZI	Kongola	17°49'S	23°23'E
NAMIBIA	OMAHEKE	Kuzikus Wildlife Reserve	23°14'S	18°23'E
NAMIBIA	ZAMBEZI	Kwando	18°02'S	23°20'E
NAMIBIA	KHOMAS	Leutwein	22°45'S	17°04'E
NAMIBIA	KHOMAS	Lichtenstein-Süd	22°46'S	16°59'E

NAMIBIA	KHOMAS	Mecklenburg	22°10'S	17°39'E
NAMIBIA	KAVANGO	Mile 46 Agricultural Station, Sovo	18°16'S	19°15'E
NAMIBIA	KAVANGO	Mururani	18°47'S	18°56'E
NAMIBIA	OSHIKOTO	Mushara Waterhole, Etosha National Park	18°36'S	16°55'E
NAMIBIA	KHOMAS	Namibgrems Farm	23°37'S	16°14'E
NAMIBIA	KHOMAS	Nauchas	23°39'S	16°18'E
NAMIBIA	KAVANGO	Nawasha Pan	19°10'S	20°54'E
NAMIBIA	OTJOZONDJUPA	Neudamm	22°30'S	17°22'E
NAMIBIA	KAVANGO	Nova, West Caprivi Park	18°12'S	21°46'E
NAMIBIA	KUNENE	Ohopoho [=Opuwo]		
NAMIBIA	OTJOZONDJUPA	Okahandja	21°59'S	16°59'E
NAMIBIA	ERONGO	Omaruru	21°25'S	15°57'E
NAMIBIA	KAVANGO	Omega	18°02'S	22°12'E
NAMIBIA	OSHIKOTO	Ondangua [=Ondangwa]		
NAMIBIA	OSHIKOTO	Ondangwa	17°54'S	15°59'E
NAMIBIA	KUNENE	Opuwo	18°03'S	13°51'E
NAMIBIA	OSHANA	Oshakati	17°47'S	15°42'E
NAMIBIA	OTJOZONDJUPA	Osire	21°04'S	17°22'E
NAMIBIA	OTJOZONDJUPA	Otavi	19°38'S	17°20'E
NAMIBIA	OMAHEKE	Otjituuo	19°38'S	18°36'E
NAMIBIA	OTJOZONDJUPA	Otjiwarongo	20°27'S	16°40'E
NAMIBIA	OMAHEKE	Otjijyarwa	12°18'S	19°23'E
NAMIBIA	KUNENE	Outjo	20°07'S	16°10'E
NAMIBIA	HARDAP	Rehoboth	23°19'S	17°05'E
NAMIBIA	HARDAP	Rietmond	24°34'S	18°11'E
NAMIBIA	KUNENE	Sesfontein Basin	19°08'S	13°36'E
NAMIBIA	KAVANGO	Soncana, Kaudom Game Reserve	18°56'S	20°43'E
NAMIBIA	OMAHEKE	Talismani	21°55'S	20°44'E
NAMIBIA	OSHIKOTO	Tsumeb	19°15'S	17°44'E
NAMIBIA	KHOMAS	Windhoek	22°34'S	17°04'E
NAMIBIA	KHOMAS	Windhoek Airport	22°19'S	17°29'E
NAMIBIA	OMAHEKE	Witvlei	22°24'S	18°30'E
NIGER	TILLABÉRI	Ayorou	14°44'N	00°55'E
NIGER	ZINDER	Dengas	13°04'N	09°21'E
NIGER	ZINDER	Dungass [=Dengas]		
NIGER	MARADI	Gona Aja	14°07'N	08°23'E
NIGER	MARADI	Maradi	13°30'N	07°06'E
NIGER	NIAMEY	Niamey	13°32'N	02°07'E
NIGER	AGADEZ	Tatei	15°11'N	09°31'E
NIGER	TILLABÉRI	Tillabéri	14°12'N	01°27'E
NIGERIA	NASARAWA	Abuja	09°03'N	07°38'E
NIGERIA	FEDERAL CAPITAL TERRITORY	Abuja	09°04'N	07°27'E
NIGERIA	BAUCHI	Azare	11°40'N	10°12'E
NIGERIA	BAUCHI	Bauchi	10°19'N	09°51'E
NIGERIA	JIGAWA	Birnin Kudu	11°27'N	09°29'E
NIGERIA	SOKOTO	Boka	12°35'N	05°19'E
NIGERIA	CROSS RIVER	Calabar	04°57'N	08°20'E
NIGERIA	RIVERS	Degema	04°46'N	06°46'E

NIGERIA	KADUNA	<b>Dogon Kurmi</b>	09°18'N	07°18'E
NIGERIA	TARABA	<b>Gembu General Hospital</b>	06°43'N	11°15'E
NIGERIA	KEBBI	<b>Illela</b>	12°31'N	04°49'E
NIGERIA	KWARA	<b>Ilorin</b>	08°29'N	04°33'E
NIGERIA	KWARA	<b>Jebba</b>	09°07'N	04°50'E
NIGERIA	PLATEAU	<b>Jos</b>	09°56'N	08°53'E
NIGERIA	KADUNA	<b>Kaduna</b>	10°31'N	07°26'E
NIGERIA	KADUNA	<b>Kafanchan</b>	09°35'N	08°18'E
NIGERIA	KANO	<b>Kano</b>	12°00'N	08°32'E
NIGERIA	KATSINA	<b>Katsina</b>	12°59'N	07°36'E
NIGERIA	NIGER	<b>Kontagora</b>	10°24'N	05°28'E
NIGERIA	LAGOS	<b>Lagos</b>	06°27'N	03°24'E
NIGERIA	KANO	<b>Lama-Bura Game Reserve [=Lame-Burra]</b>	11°05'N	08°37'E
NIGERIA	BORNO	<b>Maiduguri</b>	11°50'N	13°07'E
NIGERIA	TARABA	<b>Mambilla Plateau, Gembu</b>	06°43'N	11°15'E
NIGERIA	PLATEAU	<b>Mangu</b>	09°23'N	09°09'E
NIGERIA	NIGER	<b>Minna</b>	09°35'N	06°33'E
NIGERIA	NIGER	<b>Mokwa</b>	09°18'N	05°03'E
NIGERIA	CROSS RIVER	<b>Oban</b>	05°13'N	08°33'E
NIGERIA	CROSS RIVER	<b>Ogoja</b>	06°39'N	08°48'E
NIGERIA	CROSS RIVER	<b>Old Calabar</b>	04°57'N	08°20'E
NIGERIA	ONDO	<b>Ondo</b>	07°05'N	04°50'E
NIGERIA	LAGOS	<b>Oni</b>	06°32'N	04°14'E
NIGERIA	ANAMBRA	<b>Onitsha</b>	06°08'N	06°47'E
NIGERIA	KADUNA	<b>Samaru</b>	11°10'N	07°38'E
NIGERIA	LAGOS	<b>Yaba</b>	06°30'N	03°22'E
NIGERIA	BAUCHI	<b>Yankari Game Reserve</b>	09°51'N	10°18'E
NIGERIA	NIGER	<b>Zungeru</b>	09°49'N	06°09'E
RWANDA	EASTERN	<b>Bugesera</b>	02°14'S	30°09'E
RWANDA	EASTERN	<b>Cabiro [=Gabiro]</b>		
RWANDA	WESTERN	<b>Cyangugu</b>	02°29'S	28°55'E
RWANDA	EASTERN	<b>Gabiro</b>	01°33'S	30°24'E
RWANDA	NORTHERN	<b>Gikondo</b>	01°59'S	30°04'E
RWANDA	NORTHERN	<b>Gikongo [=Gikondo]</b>		
RWANDA	EASTERN	<b>Kagera National Park</b>	01°36'S	30°43'E
RWANDA	KIGALI CITY	<b>Kigali</b>	01°58'S	30°06'E
RWANDA	EASTERN	<b>Lac Ihema</b>	01°53'S	30°45'E
RWANDA	WESTERN	<b>Mutara</b>	00°41'S	30°06'E
RWANDA	SOUTHERN	<b>Nyanza</b>	02°21'S	29°45'E
SENEGAL	DIORBEL	<b>Bambey</b>	14°42'N	16°27'W
SENEGAL	ZIGUINCHOR	<b>Boukitimgo</b>	12°28'N	16°34'W
SENEGAL	DAKAR	<b>Cap-Vert</b>	14°44'N	17°27'W
SENEGAL	SAINT-LOUIS	<b>Dagana</b>	16°31'N	15°30'W
SENEGAL	DAKAR	<b>Dakar</b>	14°46'N	17°22'W
SENEGAL	DIORBEL	<b>Dialakar [=Dialaker]</b>		
SENEGAL	DIORBEL	<b>Dialaker</b>	14°49'N	15°44'W
SENEGAL	DIORBEL	<b>Diourbel</b>	14°39'N	16°14'W
SENEGAL	FATICK	<b>Diouroup</b>	14°21'N	16°32'W

SENEGAL	DIORBEL	Djourbel [=Diourbel]		
SENEGAL	KOLDA	Foret de Bakor	12°55'N	14°48'W
SENEGAL	KOLDA	Foret de Balmadou	12°41'N	15°20'W
SENEGAL	KOLDA	Foret de Bammadou	12°41'N	15°20'W
SENEGAL	FATICK	Foret de Fathala	13°39'N	16°27'W
SENEGAL	DAKAR	Gorée	14°40'N	17°24'W
SENEGAL	KAOLAK	Kaolak	14°10'N	16°04'W
SENEGAL	LOUGA	Linguere	15°24'N	15°07'W
SENEGAL	DIORBEL	M'Bambey [=Bambey]		
SENEGAL	THIES	Mbour	14°25'N	16°58'W
SENEGAL	KAOLAK	Nioro du Rip	13°45'N	15°46'W
SENEGAL	DIORBEL	Palmarin	14°01'N	16°46'W
SENEGAL	TAMBACOUNDA	Parc National Niokolo-Koba, Dienoundialla	13°13'N	13°07'W
SENEGAL	TAMBACOUNDA	Parc National Niokolo-Koba, Mont Assirik	13°48'N	13°35'W
SENEGAL	SAINT-LOUIS	Richard Toll	16°28'N	15°41'W
SENEGAL	DAKAR	Rufisque	14°43'N	17°16'W
SENEGAL	SAINT-LOUIS	Saint-Louis	16°02'N	16°29'W
SENEGAL	SEDHIOU	Sedhiou	12°42'N	15°34'W
SENEGAL	TAMBACOUNDA	Tambacounda	13°46'N	13°40'W
SENEGAL	THIES	Thies	14°47'N	16°56'W
SENEGAL	NORD	Toulfe	13°53'N	01°57'W
SENEGAL	KOLDA	Velingara	13°09'N	14°06'W
SENEGAL	ZIGUINCHOR	Ziguinchor	12°35'N	16°16'W
SIERRA LEONE	NORTHERN	Kaballa [=Kabala]	09°35'N	11°33'W
SIERRA LEONE	NORTHERN	Loma Mountains	09°08'N	11°05'W
SIERRA LEONE	EASTERN	Tiwai Island	07°33'N	11°21'W
SOMALIA	SHABEELLAHA HOOSE	Afgoi [=Afgoye]		
SOMALIA	SHABEELLAHA HOOSE	Afgol [=Afgoye]		
SOMALIA	SHABEELLAHA HOOSE	Afgoye	02°08'N	45°07'E
SOMALIA	LOWER JUBA	Badaada	01°02'N	41°30'E
SOMALIA	BAY	Baidoa	03°07'N	43°39'E
SOMALIA	WOQOQOYI GALBEED	Berbera	10°26'N	45°00'E
SOMALIA	JUBBADA DHEXE	Bidi	01°03'N	42°40'E
SOMALIA	TOGDHEER	Buramo [=Burao]		
SOMALIA	TOGDHEER	Burao	09°31'N	45°32'E
SOMALIA	LOWER JUBA	Chisimaio [=Kismayo]		
SOMALIA	LOWER SHEBELLE	Genale [=Janale]		
SOMALIA	HIRSHABELLE	Giohar [=Jowhaar]		
SOMALIA	LOWER JUBA	Gumbo	00°15'N	42°37'E
SOMALIA	LOWER SHEBELLE	Janale	01°48'N	44°42'E
SOMALIA	HIRSHABELLE	Jowhaar	02°47'N	45°30'E
SOMALIA	LOWER JUBA	Kismayo	00°07'S	42°32'E
SOMALIA	BANAADIR	Mogadishu	02°02'N	45°19'E
SOMALIA	JUBBADA DHEXE	Scionde	01°02'N	42°37'E
SOUTH AFRICA	GAUTENG	Abe Bailey Nature Reserve	26°19'S	27°17'E
SOUTH AFRICA	EASTERN CAPE	Aliwal North	30°42'S	26°43'E
SOUTH AFRICA	LIMPOPO	Amatola Scott Farm	22°56'S	29°23'E

SOUTH AFRICA	KWAZULU-NATAL	Amazulu Lodge	28°23'S	32°24'E
SOUTH AFRICA	GAUTENG	Andalucia	26°01'S	28°04'E
SOUTH AFRICA	NORTHERN CAPE	Askham	26°59'S	20°47'E
SOUTH AFRICA	MPUMALANGA	Badplaas	25°57'S	30°34'E
SOUTH AFRICA	MPUMALANGA	Barberton	25°47'S	31°03'E
SOUTH AFRICA	LIMPOPO	Beaufort, Farm Levubu	23°10'S	30°16'E
SOUTH AFRICA	LIMPOPO	Bela-Bela	24°53'S	28°17'E
SOUTH AFRICA	MPUMALANGA	Belfast	25°41'S	30°02'E
SOUTH AFRICA	NORTHERN CAPE	Benfontein Nature Reserve	28°49'S	24°49'E
SOUTH AFRICA	KWAZULU-NATAL	Berbice	27°12'S	31°09'E
SOUTH AFRICA	MPUMALANGA	Bergen	27°10'S	30°40'E
SOUTH AFRICA	MPUMALANGA	Berg-en-Daal, Kruger National Park	25°25'S	31°27'E
SOUTH AFRICA	KWAZULU-NATAL	Bergville	28°44'S	29°21'E
SOUTH AFRICA	MPUMALANGA	Berlin Forest	25°33'S	30°44'E
SOUTH AFRICA	FREE STATE	Bloemfontein	29°07'S	26°12'E
SOUTH AFRICA	NORTH WEST	Bloemhof	27°39'S	25°36'E
SOUTH AFRICA	LIMPOPO	Blouberg	23°05'S	28°51'E
SOUTH AFRICA	LIMPOPO	Blouberg, Motlakeng	23°07'S	28°59'E
SOUTH AFRICA	LIMPOPO	Bluegumspoort	23°00'S	29°43'E
SOUTH AFRICA	GAUTENG	Boekenhoutskloof	25°33'S	28°24'E
SOUTH AFRICA	GAUTENG	Boksburg	26°14'S	28°15'E
SOUTH AFRICA	WESTERN CAPE	Bontebok National Park	34°04'S	20°28'E
SOUTH AFRICA	GAUTENG	Bordeaux	26°06'S	28°01'E
SOUTH AFRICA	NORTH WEST	Borokalolo Game Reserve	25°10'S	27°43'E
SOUTH AFRICA	MPUMALANGA	Boshokrand	24°50'S	31°10'E
SOUTH AFRICA	KWAZULU-NATAL	Boschberg Farm	28°14'S	29°47'E
SOUTH AFRICA	MPUMALANGA	Botanical Garden, Nelspruit	25°31'S	30°32'E
SOUTH AFRICA	KWAZULU-NATAL	Bothas Hill	29°45'S	30°45'E
SOUTH AFRICA	FREE STATE	Bothaville	27°23'S	26°37'E
SOUTH AFRICA	NORTH WEST	Broedersput	26°49'S	25°07'E
SOUTH AFRICA	WESTERN CAPE	Buffels Bay	34°05'S	22°58'E
SOUTH AFRICA	LIMPOPO	Buffelsdoorn	25°22'S	27°55'E
SOUTH AFRICA	LIMPOPO	Buffelsdrift Gate	25°12'S	28°31'E
SOUTH AFRICA	MPUMALANGA	Cairn	25°30'S	30°52'E
SOUTH AFRICA	WESTERN CAPE	Caledon	34°14'S	19°26'E
SOUTH AFRICA	EASTERN CAPE	Cantoos River [=Gamtoosrivier]		
SOUTH AFRICA	WESTERN CAPE	Cape Town	33°55'S	18°25'E
SOUTH AFRICA	KWAZULU-NATAL	Cape Vidal	28°07'S	32°33'E
SOUTH AFRICA	MPUMALANGA	Carolina	26°01'S	30°17'E
SOUTH AFRICA	GAUTENG	Castle Gorge	25°50'S	27°37'E
SOUTH AFRICA	EASTERN CAPE	Cathcart	32°18'S	27°08'E
SOUTH AFRICA	KWAZULU-NATAL	Cathedral Peak Forest	28°57'S	29°12'E
SOUTH AFRICA	WESTERN CAPE	Ceres	33°22'S	19°19'E
SOUTH AFRICA	KWAZULU-NATAL	Champagne Castle	29°05'S	29°12'E
SOUTH AFRICA	KWAZULU-NATAL	Charters Creek	28°12'S	32°25'E
SOUTH AFRICA	LIMPOPO	Cinergy Game Farm	24°38'S	28°45'E
SOUTH AFRICA	WESTERN CAPE	Citrusdal	32°35'S	19°01'E
SOUTH AFRICA	WESTERN CAPE	Clanwilliam	32°11'S	18°53'E
SOUTH AFRICA	FREE STATE	Clarens	28°31'S	28°25'E
SOUTH AFRICA	NORTHERN CAPE	Colesberg	30°43'S	25°06'E

SOUTH AFRICA	KWAZULU-NATAL	<b>Congella, Durban</b>	29°52'S	31°00'E
SOUTH AFRICA	EASTERN CAPE	<b>Cradock, Mountain Zebra National Park</b>	32°11'S	25°39'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Dalton</b>	29°20'S	30°37'E
SOUTH AFRICA	WESTERN CAPE	<b>Darling</b>	33°23'S	18°23'E
SOUTH AFRICA	NORTH WEST	<b>De Wildt</b>	25°38'S	27°57'E
SOUTH AFRICA	NORTHERN CAPE	<b>Debeden, Korannaberg</b>	27°18'S	22°29'E
SOUTH AFRICA	NORTHERN CAPE	<b>Dibeng</b>	27°36'S	22°53'E
SOUTH AFRICA	NORTH WEST	<b>Dinokana</b>	25°27'S	25°52'E
SOUTH AFRICA	NORTHERN CAPE	<b>Dronfield Nature Reserve</b>	28°37'S	42°48'E
SOUTH AFRICA	NORTHERN CAPE	<b>Duineveld</b>	28°26'S	21°16'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Dukuduku</b>	28°06'S	32°21'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Durban</b>	29°51'S	31°02'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Durban, Davenport</b>	29°52'S	31°00'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Durban, Glenwood</b>	29°52'S	30°59'E
SOUTH AFRICA	LIMPOPO	<b>Dwaalboom</b>	24°43'S	26°49'E
SOUTH AFRICA	EASTERN CAPE	<b>Dwesa Forest</b>	32°15'S	28°49'E
SOUTH AFRICA	EASTERN CAPE	<b>East London</b>	33°01'S	27°52'E
SOUTH AFRICA	FREE STATE	<b>Edenville</b>	27°33'S	27°40'E
SOUTH AFRICA	GAUTENG	<b>Elandsfontein</b>	26°17'S	27°52'E
SOUTH AFRICA	EASTERN CAPE	<b>Elliot</b>	33°20'S	27°51'E
SOUTH AFRICA	LIMPOPO	<b>Ellisras [=Lephalale]</b>		
SOUTH AFRICA	LIMPOPO	<b>Entabeni Forest Reserve</b>	23°00'S	30°16'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Eshowe</b>	28°54'S	31°28'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Estcourt</b>	29°01'S	29°52'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Eston</b>	29°52'S	30°30'E
SOUTH AFRICA	GAUTENG	<b>Ezenvelo Nature Reserve</b>	25°42'S	29°00'E
SOUTH AFRICA	KWAZULU-NATAL	<b>False Bay</b>	27°58'S	32°22'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Fanies Island Camp</b>	28°10'S	32°25'E
SOUTH AFRICA	MPUMALANGA	<b>Farm ALFA 417 JU</b>	25°47'S	31°03'E
SOUTH AFRICA	LIMPOPO	<b>Farm Ruimte 617</b>	24°49'S	28°46'E
SOUTH AFRICA	LIMPOPO	<b>Farm Twee Kansen 624</b>	24°49'S	28°57'E
SOUTH AFRICA	LIMPOPO	<b>Farm Zandrivier</b>	24°39'S	28°02'E
SOUTH AFRICA	FREE STATE	<b>Fauresmith</b>	29°45'S	25°19'E
SOUTH AFRICA	GAUTENG	<b>Fountains, Pretoria</b>	25°47'S	28°12'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Frere</b>	28°54'S	29°47'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Futululu</b>	28°24'S	32°14'E
SOUTH AFRICA	EASTERN CAPE	<b>Gamtoosrivier</b>	33°50'S	24°51'E
SOUTH AFRICA	MPUMALANGA	<b>Gedenkplaat, Nasionale Kruger Wildtuin</b>	25°18'S	31°31'E
SOUTH AFRICA	LIMPOPO	<b>Geelhoutbush Farm</b>	24°22'S	27°33'E
SOUTH AFRICA	WESTERN CAPE	<b>George</b>	33°58'S	22°27'E
SOUTH AFRICA	FREE STATE	<b>Gladstone</b>	29°22'S	26°50'E
SOUTH AFRICA	EASTERN CAPE	<b>Goshen</b>	32°16'S	27°03'E
SOUTH AFRICA	EASTERN CAPE	<b>Graaf-Reinet</b>	32°15'S	24°33'E
SOUTH AFRICA	EASTERN CAPE	<b>Grahamstown</b>	33°18'S	26°32'E
SOUTH AFRICA	NORTHERN CAPE	<b>Green Kalahari</b>	27°42'S	22°39'E
SOUTH AFRICA	WESTERN CAPE	<b>Greyton</b>	34°03'S	19°37'E
SOUTH AFRICA	MPUMALANGA	<b>Groblersdal, Bleauwbank</b>	25°15'S	29°35'E
SOUTH AFRICA	NORTHERN CAPE	<b>Groblershoop</b>	28°53'S	21°59'E
SOUTH AFRICA	LIMPOPO	<b>Grootpan Farm</b>	24°01'S	27°06'E
SOUTH AFRICA	LIMPOPO	<b>Hans Merensky Nature Reserve</b>	23°40'S	30°39'E

SOUTH AFRICA	WESTERN CAPE	Harkerville Reserve	34°03'S	23°14'E
SOUTH AFRICA	MPUMALANGA	Hazyview	25°03'S	31°08'E
SOUTH AFRICA	MPUMALANGA	Hectorspruit	25°30'S	31°31'E
SOUTH AFRICA	GAUTENG	Heidelberg	26°31'S	28°22'E
SOUTH AFRICA	LIMPOPO	Helena Farm	25°02'S	30°07'E
SOUTH AFRICA	KWAZULU-NATAL	Hluhluwe	28°01'S	32°16'E
SOUTH AFRICA	LIMPOPO	Hoedspruit	24°21'S	30°57'E
SOUTH AFRICA	NORTHERN CAPE	Hopetown	29°37'S	24°05'E
SOUTH AFRICA	NORTHERN CAPE	Hotazel	27°12'S	22°57'E
SOUTH AFRICA	KWAZULU-NATAL	Howick	29°29'S	30°13'E
SOUTH AFRICA	EASTERN CAPE	Humansdorp	34°00'S	24°45'E
SOUTH AFRICA	EASTERN CAPE	Igoda River Mouth	33°06'S	27°47'E
SOUTH AFRICA	NORTH WEST	Ihanti Lodge	25°28'S	27°26'E
SOUTH AFRICA	KWAZULU-NATAL	Ilovo	30°07'S	30°51'E
SOUTH AFRICA	KWAZULU-NATAL	Ingeli	30°32'S	29°41'E
SOUTH AFRICA	KWAZULU-NATAL	iSimangaliso Wetland Park, Lake Mgobelezeni	27°32'S	32°29'E
SOUTH AFRICA	KWAZULU-NATAL	Ithala Game Reserve/Itala Nature Reserve	27°30'S	31°14'E
SOUTH AFRICA	MPUMALANGA	Jericho Dam	26°40'S	30°29'E
SOUTH AFRICA	GAUTENG	Johannesburg	26°12'S	28°03'E
SOUTH AFRICA	EASTERN CAPE	Joubertina	33°49'S	23°52'E
SOUTH AFRICA	KWAZULU-NATAL	Jozini	27°26'S	32°04'E
SOUTH AFRICA	NORTHERN CAPE	Kalahari Gemsbok National Park, Grootkolk	24°53'S	20°09'E
SOUTH AFRICA	GAUTENG	Kameelfontein	25°38'S	28°25'E
SOUTH AFRICA	LIMPOPO	Kampersrus	24°31'S	30°53'E
SOUTH AFRICA	NORTHERN CAPE	Keimoes	28°33'S	20°53'E
SOUTH AFRICA	NORTHERN CAPE	Kimberley	28°44'S	24°45'E
SOUTH AFRICA	LIMPOPO	Klaserie	23°59'S	31°02'E
SOUTH AFRICA	WESTERN CAPE	Knysna	34°02'S	23°03'E
SOUTH AFRICA	EASTERN CAPE	Kobonqaba	32°34'S	28°30'E
SOUTH AFRICA	KWAZULU-NATAL	Kokstad	30°33'S	29°26'E
SOUTH AFRICA	MPUMALANGA	Komatipoort	25°52'S	31°52'E
SOUTH AFRICA	FREE STATE	Koppies	27°14'S	27°35'E
SOUTH AFRICA	FREE STATE	Koptes [=Koppies]		
SOUTH AFRICA	KWAZULU-NATAL	Kosi Bay	26°58'S	32°50'E
SOUTH AFRICA	KWAZULU-NATAL	Kosi Lake	26°59'S	32°50'E
SOUTH AFRICA	EASTERN CAPE	Kragga Kamma	33°58'S	25°27'E
SOUTH AFRICA	EASTERN CAPE	Krakakamma [=Kragga Kamma]		
SOUTH AFRICA	LIMPOPO	Kruger National Park, Nyandu Sands	22°41'S	31°22'E
SOUTH AFRICA	MPUMALANGA	Kruger National Park, Pumbe Sands	24°13'S	31°56'E
SOUTH AFRICA	LIMPOPO	Kruger National Park, Punda Maria	22°41'S	31°01'E
SOUTH AFRICA	MPUMALANGA	Kruger National Park, Skukuza Camp	25°00'S	31°36'E
SOUTH AFRICA	MPUMALANGA	Kruger National Park, Tshokwane-Nwanedzi Road	24°37'S	31°57'E
SOUTH AFRICA	KWAZULU-NATAL	Kube Yini Game Reserve	27°48'S	32°14'E
SOUTH AFRICA	NORTHERN CAPE	Kuruman	27°28'S	23°26'E
SOUTH AFRICA	FREE STATE	Ladybrand	29°12'S	27°27'E
SOUTH AFRICA	KWAZULU-NATAL	Lake Bhangazi	28°07'S	32°31'E
SOUTH AFRICA	KWAZULU-NATAL	Lake Nhalabane	28°38'S	32°16'E
SOUTH AFRICA	KWAZULU-NATAL	Lake Sibaya, Baya Camp	27°23'S	32°40'E
SOUTH AFRICA	LIMPOPO	Langjan Nature Reserve	22°52'S	29°14'E
SOUTH AFRICA	LIMPOPO	Lapalala Nature Reserve	23°53'S	28°20'E

SOUTH AFRICA	GAUTENG	Leeufontein Nature Reserve	25°22'S	28°37'E
SOUTH AFRICA	FREE STATE	Lemoen Farm	28°15'S	25°00'E
SOUTH AFRICA	LIMPOPO	Lephalale	23°40'S	27°45'E
SOUTH AFRICA	LIMPOPO	Letaba	23°51'S	31°34'E
SOUTH AFRICA	EASTERN CAPE	Letlapeng	30°21'S	28°22'E
SOUTH AFRICA	LIMPOPO	Letsitele	23°53'S	30°23'E
SOUTH AFRICA	NORTH WEST	Linokana [=Dinokana]		
SOUTH AFRICA	LIMPOPO	Little Muck	22°15'S	29°16'E
SOUTH AFRICA	MPUMALANGA	Lothair	26°23'S	30°26'E
SOUTH AFRICA	LIMPOPO	Louis Trichardt	23°03'S	29°54'E
SOUTH AFRICA	LIMPOPO	Luipershoek Farm	25°07'S	29°50'E
SOUTH AFRICA	MPUMALANGA	Luneberg	27°19'S	30°37'E
SOUTH AFRICA	MPUMALANGA	Lydenburg	25°05'S	30°27'E
SOUTH AFRICA	LIMPOPO	Mabalingwe Reserve	24°50'S	28°02'E
SOUTH AFRICA	GAUTENG	Mabopane	25°31'S	28°03'E
SOUTH AFRICA	LIMPOPO	Machai Pan, Kruger National Park	23°10'S	31°23'E
SOUTH AFRICA	NORTH WEST	Mafeking [=Mahikeng]		
SOUTH AFRICA	GAUTENG	Magdalisburg	25°59'S	27°32'E
SOUTH AFRICA	LIMPOPO	Magoebaskloof	23°53'S	30°01'E
SOUTH AFRICA	NORTH WEST	Mahikeng	25°51'S	25°38'E
SOUTH AFRICA	KWAZULU-NATAL	Makatini Flats	27°15'S	32°13'E
SOUTH AFRICA	NORTH WEST	Makwassie	27°19'S	26°00'E
SOUTH AFRICA	WESTERN CAPE	Malgas	34°18'S	20°35'E
SOUTH AFRICA	KWAZULU-NATAL	Malvern	29°53'S	30°55'E
SOUTH AFRICA	KWAZULU-NATAL	Manguzi	27°00'S	32°45'E
SOUTH AFRICA	KWAZULU-NATAL	Maputa [=Manguzi]		
SOUTH AFRICA	NORTH WEST	Maquassie [=Makwassie]		
SOUTH AFRICA	MPUMALANGA	Maressburg Farm	25°00'S	30°08'E
SOUTH AFRICA	NORTH WEST	Marico	25°35'S	26°46'E
SOUTH AFRICA	MPUMALANGA	Mariepskop	24°32'S	30°52'E
SOUTH AFRICA	NORTHERN CAPE	Mata Mata	25°46'S	20°00'E
SOUTH AFRICA	KWAZULU-NATAL	Mbaswane [=Mbazwana]		
SOUTH AFRICA	KWAZULU-NATAL	Mbazwana	27°30'S	32°35'E
SOUTH AFRICA	KWAZULU-NATAL	Mbibi, Lake Sibayi	27°20'S	32°45'E
SOUTH AFRICA	NORTHERN CAPE	McCarthyrust	26°12'S	22°34'E
SOUTH AFRICA	WESTERN CAPE	Melkbosstrand	33°43'S	18°27'E
SOUTH AFRICA	LIMPOPO	Melkrievier	24°06'S	28°21'E
SOUTH AFRICA	KWAZULU-NATAL	Melmoth	28°35'S	31°23'E
SOUTH AFRICA	LIMPOPO	Messina [=Musina]		
SOUTH AFRICA	LIMPOPO	Messina, Municipal Hunting Area	22°21'S	30°03'E
SOUTH AFRICA	KWAZULU-NATAL	Mfabeni Dunes	28°08'S	23°28'E
SOUTH AFRICA	MPUMALANGA	Middleburg	25°46'S	29°28'E
SOUTH AFRICA	WESTERN CAPE	Milnerton, Cape Town	33°52'S	18°30'E
SOUTH AFRICA	KWAZULU-NATAL	Mission Rocks Dune Forest	28°16'S	32°29'E
SOUTH AFRICA	KWAZULU-NATAL	Mkuze	27°37'S	32°03'E
SOUTH AFRICA	KWAZULU-NATAL	Mkuze Game Reserve, Hides	27°38'S	32°14'E
SOUTH AFRICA	KWAZULU-NATAL	Mkuze Game Reserve, Main Camp	27°36'S	32°13'E
SOUTH AFRICA	KWAZULU-NATAL	Mkuze Game Reserve, Msinga Hide	27°38'S	32°14'E
SOUTH AFRICA	KWAZULU-NATAL	Mkuze Game Reserve, Nsumu Pan	27°40'S	32°18'E
SOUTH AFRICA	KWAZULU-NATAL	Mkuze Game Reserve, Vulture Pan	27°37'S	32°13'E

SOUTH AFRICA	KWAZULU-NATAL	Mkuzi [=Mkuze]		
SOUTH AFRICA	LIMPOPO	Modimolle	24°42'S	28°24'E
SOUTH AFRICA	LIMPOPO	Mokopane	24°11'S	29°01'E
SOUTH AFRICA	LIMPOPO	Mokopane, Shikwaru Lodge	24°14'S	28°54'E
SOUTH AFRICA	KWAZULU-NATAL	Monzi	28°24'S	32°21'E
SOUTH AFRICA	GAUTENG	Mooiplaats	25°48'S	28°24'E
SOUTH AFRICA	LIMPOPO	Mookgopong	24°28'S	28°40'E
SOUTH AFRICA	LIMPOPO	Moorddrift	24°14'S	28°58'E
SOUTH AFRICA	LIMPOPO	Mopane	23°18'S	30°43'E
SOUTH AFRICA	NORTH WEST	Morokweng	26°08'S	23°47'E
SOUTH AFRICA	EASTERN CAPE	Mount Frere	30°54'S	28°59'E
SOUTH AFRICA	MPUMALANGA	Mount Sheba	24°56'S	30°43'E
SOUTH AFRICA	LIMPOPO	Mphome	23°50'S	29°53'E
SOUTH AFRICA	EASTERN CAPE	Mthatha	31°36'S	28°47'E
SOUTH AFRICA	KWAZULU-NATAL	Mtubatuba	28°25'S	32°11'E
SOUTH AFRICA	KWAZULU-NATAL	Mtunzini	28°57'S	31°46'E
SOUTH AFRICA	LIMPOPO	Musina	22°21'S	30°02'E
SOUTH AFRICA	KWAZULU-NATAL	Muzi	26°52'S	32°41'E
SOUTH AFRICA	LIMPOPO	Naboomspruit [=Mookgopong]		
SOUTH AFRICA	KWAZULU-NATAL	Ndalen	29°53'S	30°15'E
SOUTH AFRICA	KWAZULU-NATAL	Ndumo Game Reserve	26°53'S	32°16'E
SOUTH AFRICA	KWAZULU-NATAL	Ndumu	26°56'S	32°17'E
SOUTH AFRICA	MPUMALANGA	Nelshoogte, Knuckles	25°47'S	30°49'E
SOUTH AFRICA	KWAZULU-NATAL	Ngome State Forest	27°48'S	31°25'E
SOUTH AFRICA	LIMPOPO	Northam	24°58'S	27°16'E
SOUTH AFRICA	KWAZULU-NATAL	Ntinini Nature Reserve	29°56'S	30°37'E
SOUTH AFRICA	EASTERN CAPE	Ntsubane Forest	31°27'S	29°44'E
SOUTH AFRICA	MPUMALANGA	Numbi Cave	25°07'S	31°11'E
SOUTH AFRICA	LIMPOPO	Nylstrom [=Modimolle]		
SOUTH AFRICA	LIMPOPO	Nylsvley	24°39'S	28°42'E
SOUTH AFRICA	LIMPOPO	Nylsvley Nature Reserve	24°39'S	28°42'E
SOUTH AFRICA	LIMPOPO	Nylsvley, Smith Farm	24°40'S	28°42'E
SOUTH AFRICA	LIMPOPO	Olifants, Kruger National Park	24°00'S	31°44'E
SOUTH AFRICA	NORTHERN CAPE	Olifantshoek	27°56'S	22°44'E
SOUTH AFRICA	KWAZULU-NATAL	Oribi Gorge	30°43'S	30°15'E
SOUTH AFRICA	KWAZULU-NATAL	Paddock	30°43'S	30°17'E
SOUTH AFRICA	LIMPOPO	Pafuri	22°27'S	31°19'E
SOUTH AFRICA	GAUTENG	Petronella	25°30'S	28°15'E
SOUTH AFRICA	LIMPOPO	Pienaars River	25°13'S	28°18'E
SOUTH AFRICA	MPUMALANGA	Piet Retief	27°00'S	30°48'E
SOUTH AFRICA	KWAZULU-NATAL	Pietermaritzburg	29°36'S	30°23'E
SOUTH AFRICA	LIMPOPO	Pietersburg [=Polokwane]		
SOUTH AFRICA	KWAZULU-NATAL	Pinetown	29°49'S	30°51'E
SOUTH AFRICA	LIMPOPO	Polokwane	23°54'S	29°27'E
SOUTH AFRICA	KWAZULU-NATAL	Pongola River Bridge	27°24'S	31°50'E
SOUTH AFRICA	EASTERN CAPE	Port Elizabeth	33°57'S	25°36'E
SOUTH AFRICA	KWAZULU-NATAL	Port Shepstone	30°45'S	30°27'E
SOUTH AFRICA	EASTERN CAPE	Port St Johns	31°38'S	29°32'E
SOUTH AFRICA	WESTERN CAPE	Porterville	33°01'S	19°00'E
SOUTH AFRICA	NORTH WEST	Potchefstroom Cantonments	26°43'S	27°06'E

SOUTH AFRICA	LIMPOPO	Potgietersrus [=Mokopane]		
SOUTH AFRICA	GAUTENG	Premier Mine Game Reserve	25°40'S	28°29'E
SOUTH AFRICA	GAUTENG	Pretoria	25°45'S	28°14'E
SOUTH AFRICA	GAUTENG	Pretoria North	25°41'S	28°11'E
SOUTH AFRICA	LIMPOPO	Punda Milia, Kruger National Park	22°42'S	31°01'E
SOUTH AFRICA	EASTERN CAPE	Queenstown	31°54'S	26°53'E
SOUTH AFRICA	EASTERN CAPE	Qumbu	31°10'S	28°52'E
SOUTH AFRICA	KWAZULU-NATAL	Richard's Bay	28°17'S	32°17'E
SOUTH AFRICA	KWAZULU-NATAL	Richards Bay Arboretum	28°45'S	32°04'E
SOUTH AFRICA	KWAZULU-NATAL	Richmond	29°52'S	30°16'E
SOUTH AFRICA	LIMPOPO	Richmond Farm	24°59'S	30°05'E
SOUTH AFRICA	NORTHERN CAPE	Riemvasmaak	28°27'S	20°19'E
SOUTH AFRICA	GAUTENG	Rietondale, Pretoria	25°44'S	28°13'E
SOUTH AFRICA	WESTERN CAPE	Riviersonderend Mountains	34°04'S	19°55'E
SOUTH AFRICA	WESTERN CAPE	Rondebosch, Cape Town	33°58'S	18°29'E
SOUTH AFRICA	LIMPOPO	Rooiberg	24°46'S	27°44'E
SOUTH AFRICA	LIMPOPO	Rooibokraal	24°32'S	26°50'E
SOUTH AFRICA	NORTHERN CAPE	Rooipoort Nature Reserve	23°38'S	24°16'E
SOUTH AFRICA	WESTERN CAPE	Rosebank	33°57'S	18°28'E
SOUTH AFRICA	LIMPOPO	Rust de Winter	25°12'S	28°37'E
SOUTH AFRICA	NORTH WEST	Rustenburg	25°40'S	27°15'E
SOUTH AFRICA	MPUMALANGA	Sabie	25°06'S	30°47'E
SOUTH AFRICA	NORTH WEST	Sandfontein	25°11'S	27°16'E
SOUTH AFRICA	GAUTENG	Sandringham, Johannesburg	26°09'S	28°07'E
SOUTH AFRICA	NORTHERN CAPE	Schmidtsdrift	28°42'S	24°03'E
SOUTH AFRICA	LIMPOPO	Shiluvane	24°02'S	30°17'E
SOUTH AFRICA	KWAZULU-NATAL	Sihangwane	27°02'S	32°25'E
SOUTH AFRICA	KWAZULU-NATAL	Sileza Nature Reserve	27°06'S	32°26'E
SOUTH AFRICA	NORTHERN CAPE	Sishen	27°47'S	22°59'E
SOUTH AFRICA	FREE STATE	Smithfield	30°12'S	26°32'E
SOUTH AFRICA	NORTHERN CAPE	Smythe Farm	27°53'S	22°55'E
SOUTH AFRICA	KWAZULU-NATAL	Sodwana Bay	27°33'S	32°40'E
SOUTH AFRICA	NORTHERN CAPE	Soetvlakte Flat	26°45'S	22°50'E
SOUTH AFRICA	KWAZULU-NATAL	Sokhulu Forest Reserve	28°37'S	32°17'E
SOUTH AFRICA	NORTHERN CAPE	Sonstraal	27°02'S	22°21'E
SOUTH AFRICA	KWAZULU-NATAL	Southbroom	30°56'S	30°18'E
SOUTH AFRICA	MPUMALANGA	Southern African Wildlife College	24°30'S	31°19'E
SOUTH AFRICA	GAUTENG	Soutpan, Pretoria	25°25'S	28°05'E
SOUTH AFRICA	LIMPOPO	Soutpansberg	22°54'S	29°41'E
SOUTH AFRICA	KWAZULU-NATAL	St Lucia	28°22'S	32°25'E
SOUTH AFRICA	NORTH WEST	Stella	26°33'S	24°52'E
SOUTH AFRICA	WESTERN CAPE	Suurbraak	34°00'S	20°39'E
SOUTH AFRICA	LIMPOPO	Swartwater	22°51'S	28°12'E
SOUTH AFRICA	WESTERN CAPE	Swellendam	34°02'S	20°26'E
SOUTH AFRICA	KWAZULU-NATAL	Tembe Elephant Park	27°03'S	32°25'E
SOUTH AFRICA	EASTERN CAPE	The Haven	32°15'S	28°55'E
SOUTH AFRICA	FREE STATE	Theunissen	28°24'S	26°42'E
SOUTH AFRICA	LIMPOPO	Tom Burke	23°04'S	28°00'E
SOUTH AFRICA	LIMPOPO	Torino Ranch	24°37'S	28°38'E
SOUTH AFRICA	LIMPOPO	Tshakuma	23°03'S	30°18'E

SOUTH AFRICA	LIMPOPO	<b>Tshange Viewpoint, Kruger National Park</b>	23°14'S	31°14'E
SOUTH AFRICA	NORTHERN CAPE	<b>Tswalu Nature Reserve</b>	27°15'S	22°30'E
SOUTH AFRICA	NORTHERN CAPE	<b>Twee Rivieren</b>	26°28'S	20°37'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Tygerkloof</b>	27°51'S	31°19'E
SOUTH AFRICA	LIMPOPO	<b>Tzaneen</b>	24°16'S	30°36'E
SOUTH AFRICA	LIMPOPO	<b>Ubundu Lodge</b>	25°05'S	28°17'E
SOUTH AFRICA	LIMPOPO	<b>Uitzicht, Zoutpansberg</b>	23°30'S	28°40'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Umbilo</b>	29°53'S	30°59'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Umlalazi Game Reserve, Mtunzini Forest</b>	28°58'S	31°45'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Umtamvuna</b>	31°00'S	30°09'E
SOUTH AFRICA	EASTERN CAPE	<b>Umtata [=Mthatha]</b>		
SOUTH AFRICA	NORTHERN CAPE	<b>Upington</b>	28°27'S	21°15'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Utrecht</b>	27°40'S	30°19'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Van Reenen</b>	28°22'S	29°23'E
SOUTH AFRICA	EASTERN CAPE	<b>Van Stades River [=Van Stadensrivier]</b>		
SOUTH AFRICA	EASTERN CAPE	<b>Van Stadensrivier</b>	33°54'S	25°12'E
SOUTH AFRICA	NORTHERN CAPE	<b>Van Zylsrus</b>	26°53'S	22°03'E
SOUTH AFRICA	NORTH WEST	<b>Vierboslaagte</b>	25°20'S	28°01'E
SOUTH AFRICA	LIMPOPO	<b>Vivo, Soutpansberg</b>	23°04'S	29°38'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Volksrust</b>	27°22'S	29°53'E
SOUTH AFRICA	FREE STATE	<b>Vredefort</b>	27°00'S	27°22'E
SOUTH AFRICA	FREE STATE	<b>Vredefort Dom</b>	26°50'S	28°38'E
SOUTH AFRICA	NORTH WEST	<b>Vryburg</b>	26°57'S	24°44'E
SOUTH AFRICA	KWAZULU-NATAL	<b>Vryheid</b>	27°46'S	30°48'E
SOUTH AFRICA	LIMPOPO	<b>Warmbaths [=Bela-Bela]</b>		
SOUTH AFRICA	NORTHERN CAPE	<b>Warrenton</b>	28°08'S	24°51'E
SOUTH AFRICA	LIMPOPO	<b>Waterberg Game Reserve</b>	24°11'S	28°20'E
SOUTH AFRICA	LIMPOPO	<b>Waterberg, Farm 223</b>	24°11'S	27°50'E
SOUTH AFRICA	MPUMALANGA	<b>Waterval Onder</b>	25°38'S	30°20'E
SOUTH AFRICA	MPUMALANGA	<b>White River</b>	25°20'S	31°01'E
SOUTH AFRICA	GAUTENG	<b>Windy Brow</b>	25°41'S	28°30'E
SOUTH AFRICA	NORTHERN CAPE	<b>Witsand Nature Reserve</b>	28°33'S	22°29'E
SOUTH AFRICA	NORTH WEST	<b>Wondergat</b>	25°52'S	25°53'E
SOUTH AFRICA	LIMPOPO	<b>Woodbush Forest Reserve</b>	23°50'S	29°59'E
SOUTH AFRICA	WESTERN CAPE	<b>Worcester</b>	33°39'S	19°27'E
SOUTH AFRICA	WESTERN CAPE	<b>Wynberg, Cape Town</b>	34°01'S	18°28'E
SOUTH AFRICA	FREE STATE	<b>Zastron</b>	30°18'S	27°05'E
SOUTH AFRICA	LIMPOPO	<b>Zebediela</b>	24°18'S	29°16'E
SOUTH AFRICA	GAUTENG	<b>Zwavelpoort</b>	25°50'S	28°22'E
SOUTH SUDAN	IMATONG	<b>Assua River</b>	03°43'N	31°55'E
SOUTH SUDAN	JUBEK	<b>Gondokoro</b>	04°54'N	31°40'E
SOUTH SUDAN	IMATONG	<b>Nimule</b>	03°35'N	32°04'E
SOUTH SUDAN	EASTERN NILE	<b>Renk</b>	11°50'N	32°48'E
SOUTH SUDAN	EASTERN LAKES	<b>Shambe</b>	07°06'N	30°46'E
SOUTH SUDAN	NORTHERN LIECH	<b>UNMISS Bentiu</b>	09°20'N	29°47'E
SOUTH SUDAN	WAU	<b>Wau</b>	07°42'N	28°00'E
SUDAN	NORTH DARFUR	<b>Al Fashir</b>	13°37'N	25°21'E
SUDAN	NORTH DARFUR	<b>El Fashir [=Al Fashir]</b>		

SUDAN	EAST DARFUR	El Lait	11°57'N	27°03'E
SUDAN	EAST DARFUR	Futaha	11°47'N	26°52'E
SUDAN	SOUTH DARFUR	Kashalongo	11°56'N	24°56'E
SUDAN	KHARTOUM	Khartoum	15°33'N	32°33'E
SUDAN	KHARTOUM	Omdurman	15°38'N	32°29'E
SUDAN	SOUTH KORDOFAN	Talodi	10°38'N	30°23'E
SWAZILAND	MANZINI	Luyengo	26°35'S	31°10'E
SWAZILAND	HHOHHO	Malolotja Nature Reserve	26°06'S	31°05'E
SWAZILAND	HHOHHO	Mbabane	26°19'S	31°08'E
TANZANIA	ARUSHA	Arusha National Park, Momella Lodge	03°14'S	36°52'E
TANZANIA	MANYARA	Babati	04°13'S	35°45'E
TANZANIA	PWANI	Bagamojo [=Bagamoyo]		
TANZANIA	PWANI	Bagamoyo	06°26'S	38°54'E
TANZANIA	RUKWA	Bismarckburg [=Kasanga]		
TANZANIA	KAGERA	Bukoba	01°20'S	31°49'E
TANZANIA	RUKWA	Chala	07°36'S	31°16'E
TANZANIA	MBEYA	Conde [=Konde]		
TANZANIA	DAR ES SALAAM	Dar es Salaam	06°49'S	39°17'E
TANZANIA	DODOMA	Dodoma	06°10'S	35°45'E
TANZANIA	KILIMANJARO	Engare Nairobi	03°02'S	37°03'E
TANZANIA	MWANZA	Geita Forest Reserve	02°54'S	32°08'E
TANZANIA	MANYARA	Giting, Mount Hanang	04°24'S	35°25'E
TANZANIA	KILIMANJARO	Gonja, Chome Nature Reserve	04°15'S	37°58'E
TANZANIA	TANGA	Handeni, Makinda	05°23'S	38°10'E
TANZANIA	MOROGORO	Hondo Hondo, Udzungwa Mountains	07°50'S	36°54'E
TANZANIA	KILIMANJARO	Ibaya Camp	03°58'S	37°48'E
TANZANIA	IRINGA	Idetero	08°32'S	35°01'E
TANZANIA	TABORA	Igunga	04°17'S	33°53'E
TANZANIA	RUVUMA	Ilebula Hospital	08°54'S	34°34'E
TANZANIA	IRINGA	Iringa	07°46'S	35°41'E
TANZANIA	MOROGORO	Itumba	06°20'S	37°00'E
TANZANIA	IRINGA	Iyayi savanna	08°51'S	34°31'E
TANZANIA	KAGERA	Kafuro	01°44'S	31°00'E
TANZANIA	RUKWA	Kalambo Forest Reserve	08°22'S	31°15'E
TANZANIA	TANGA	Kange Estate	05°06'S	39°02'E
TANZANIA	ARUSHA	Karatu	03°20'S	35°40'E
TANZANIA	RUKWA	Kasanga	08°28'S	31°08'E
TANZANIA	MANYARA	Katesh	04°30'S	35°23'E
TANZANIA	RUKWA	Katisunga	06°51'S	31°06'E
TANZANIA	ARUSHA	Kibaone	03°20'S	35°47'E
TANZANIA	PWANI	Kibiti	07°43'S	38°56'E
TANZANIA	KIGOMA	Kibondo	03°31'S	30°43'E
TANZANIA	KILIMANJARO	Kibongoto	03°11'S	37°06'E
TANZANIA	KILIMANJARO	Kibonoto [=Kibongoto]		
TANZANIA	IRINGA	Kidugala	09°08'S	34°32'E
TANZANIA	MOROGORO	Kidugallo	06°48'S	38°12'E
TANZANIA	RUVUMA	Kigonsera	10°48'S	35°04'E
TANZANIA	MOROGORO	Kihonda	06°46'S	37°39'E

TANZANIA	MARA	<b>Kilimafeza</b>	02°16'S	34°55'E
TANZANIA	ARUSHA	<b>Kilimamoga [=Kilimamoja]</b>		
TANZANIA	ARUSHA	<b>Kilimamoja</b>	03°21'S	35°50'E
TANZANIA	MOROGORO	<b>Kilosa</b>	06°50'S	36°59'E
TANZANIA	KILIMANJARO	<b>Kisangiro</b>	03°38'S	37°33'E
TANZANIA	KAGERA	<b>Kiyamyulwa</b>	02°09'S	31°37'E
TANZANIA	MARA	<b>Klein's Camp</b>	01°42'S	35°11'E
TANZANIA	DODOMA	<b>Kolo</b>	04°44'S	35°50'E
TANZANIA	MBEYA	<b>Konde</b>	09°29'S	33°53'E
TANZANIA	TANGA	<b>Kwediboma</b>	05°26'S	37°35'E
TANZANIA	RUKWA	<b>Lac Rukwa</b>	08°20'S	32°15'E
TANZANIA	MANYARA	<b>Lake Manyara</b>	03°37'S	35°50'E
TANZANIA	ARUSHA	<b>Lake Ndutu, Serengeti National Park</b>	02°59'S	35°01'E
TANZANIA	MBEYA	<b>Langenburg [=Lumbira]</b>		
TANZANIA	LINDI	<b>Lindi</b>	10°00'S	39°42'E
TANZANIA	IRINGA	<b>Little Ruaha Campsite</b>	07°48'S	35°48'E
TANZANIA	RUVUMA	<b>Liuli</b>	11°06'S	34°39'E
TANZANIA	MARA	<b>Lobo</b>	02°00'S	35°10'E
TANZANIA	ARUSHA	<b>Lolkisale</b>	03°46'S	36°26'E
TANZANIA	MTWARA	<b>Lukuledi</b>	10°34'S	38°48'E
TANZANIA	MBEYA	<b>Lumbira</b>	09°35'S	34°09'E
TANZANIA	KILIMANJARO	<b>Machame</b>	03°12'S	37°13'E
TANZANIA	MBEYA	<b>Madibira</b>	08°13'S	34°48'E
TANZANIA	PWANI	<b>Madimola</b>	06°43'S	38°44'E
TANZANIA	PWANI	<b>Madinula [=Madimola]</b>		
TANZANIA	KILIMANJARO	<b>Madschame [=Machame]</b>		
TANZANIA	MANYARA	<b>Magugu</b>	04°05'S	35°45'E
TANZANIA	MOROGORO	<b>Mahenge Mountains</b>	08°41'S	36°43'E
TANZANIA	MBEYA	<b>Manow</b>	09°16'S	33°47'E
TANZANIA	MANYARA	<b>Manyara-See [=Lake Manyara]</b>		
TANZANIA	DODOMA	<b>Mapinduzi</b>	06°14'S	35°56'E
TANZANIA	KILIMANJARO	<b>Marangu, Kilimanjaro</b>	03°11'S	37°31'E
TANZANIA	MOROGORO	<b>Maskati, Nguru Mountains</b>	06°03'S	37°29'E
TANZANIA	MBEYA	<b>Massewe</b>	09°23'S	33°37'E
TANZANIA	PWANI	<b>Matumbi Highlands</b>	08°21'S	38°58'E
TANZANIA	RUKWA	<b>Mbizi Forest, Sumbawanga</b>	07°54'S	31°41'E
TANZANIA	MANYARA	<b>Mbulu</b>	03°51'S	35°33'E
TANZANIA	IRINGA	<b>Mdonya Sand River, Ruaha National Park</b>	07°40'S	34°48'E
TANZANIA	IRINGA	<b>Mgololo</b>	08°43'S	35°19'E
TANZANIA	MOROGORO	<b>Mhonda</b>	06°07'S	37°35'E
TANZANIA	MOROGORO	<b>Mikese Hills</b>	06°14'S	37°58'E
TANZANIA	MTWARA	<b>Mikindani</b>	10°17'S	40°07'E
TANZANIA	MOROGORO	<b>Mikumi</b>	07°24'S	36°59'E
TANZANIA	MOROGORO	<b>Mizimu, Udzungwa Mountains National Park</b>	07°48'S	36°51'E
TANZANIA	KILIMANJARO	<b>Mkongga Forest Reserve, South Pare Mountains</b>	04°08'S	37°46'E
TANZANIA	KIGOMA	<b>Mkuyu</b>	05°30'S	29°51'E
TANZANIA	IRINGA	<b>Mlangali, Livingstone Mountains</b>	09°47'S	34°31'E
TANZANIA	TANGA	<b>Mlingano Sisal Research Station</b>	05°08'S	38°52'E
TANZANIA	MOROGORO	<b>Morogoro</b>	06°50'S	37°40'E
TANZANIA	KILIMANJARO	<b>Moshi</b>	03°21'S	37°20'E

TANZANIA	KILIMANJARO	Mount Kilimanjaro	03°06'S	37°20'E
TANZANIA	ARUSHA	Mount Meru	03°16'S	36°45'E
TANZANIA	ARUSHA	Mount Meru, Momella	03°15'S	36°50'E
TANZANIA	MOROGORO	Mpapua [=Mpwapwa]		
TANZANIA	MOROGORO	Mpwapwa	06°21'S	36°29'E
TANZANIA	RUKWA	Msambia	08°24'S	31°52'E
TANZANIA	RUKWA	Msamwia [=Msambia]		
TANZANIA	SINGIDA	Mshughaa	04°49'S	35°11'E
TANZANIA	ARUSHA	Mto wa Mbu	03°23'S	35°53'E
TANZANIA	TANGA	Mwanga	04°48'S	38°12'E
TANZANIA	MOROGORO	Mwanihana, Udzungwa Mountains National Park	07°49'S	36°50'E
TANZANIA	MANYARA	Naberera	04°12'S	36°56'E
TANZANIA	ARUSHA	Namanga	02°33'S	36°47'E
TANZANIA	LINDI	Namkongo Forest	09°47'S	39°27'E
TANZANIA	KILIMANJARO	Ndarakwai	03°01'S	36°59'E
TANZANIA	RUVUMA	Ndongosi	10°25'S	34°50'E
TANZANIA	ARUSHA	Ndutu Safari Lodge	03°01'S	35°00'E
TANZANIA	RUVUMA	Neu-Heligoland [=Liuli]		
TANZANIA	MOROGORO	Ngerengere	06°45'S	38°07'E
TANZANIA	ARUSHA	Ngorongoro Crater	03°10'S	35°34'E
TANZANIA	MOROGORO	Nguru Mountains	06°06'S	37°30'E
TANZANIA	TANGA	Nguu Mountains, Makuyu	06°16'S	37°21'E
TANZANIA	TANGA	Nguu Mountains, Tamota Forest	05°36'S	37°34'E
TANZANIA	MOROGORO	Njia Panda, Udzungwa Mountains National Park	07°47'S	36°50'E
TANZANIA	NJOMBE	Njombe	09°20'S	34°46'E
TANZANIA	MOROGORO	Nongwe, Ukaguru Mountains	06°28'S	36°54'E
TANZANIA	MWANZA	Nyegezi	02°36'S	32°54'E
TANZANIA	ARUSHA	Olchoromyokie, Mount Kitumbeine	02°55'S	36°15'E
TANZANIA	ARUSHA	Orekeryan, Mount Longido	02°44'S	36°43'E
TANZANIA	TANGA	Pangani	05°25'S	38°58'E
TANZANIA	RUVUMA	Peramiho	10°38'S	35°28'E
TANZANIA	PWANI	Pugu	06°52'S	39°10'E
TANZANIA	KILIMANJARO	Riviere Himo, Kilimanjaro	03°20'S	37°31'E
TANZANIA	LINDI	Rondo Plateau	10°07'S	39°14'E
TANZANIA	IRINGA	Ruaha National Park	07°47'S	35°00'E
TANZANIA	RUVUMA	Ruanda	10°33'S	34°57'E
TANZANIA	PWANI	Rufiji	07°47'S	38°15'E
TANZANIA	MBEYA	Rungwe	09°10'S	33°33'E
TANZANIA	MBEYA	Rutenganio	09°21'S	33°37'E
TANZANIA	MOROGORO	Sali Forest, Mahenge Mountains	08°56'S	36°40'E
TANZANIA	KILIMANJARO	Same	04°04'S	37°45'E
TANZANIA	MOROGORO	Sanje Falls, Udzungwa Mountains National Park	07°46'S	36°54'E
TANZANIA	SINGIDA	Saranda	05°43'S	34°59'E
TANZANIA	TANGA	Savane de Mwenga [=Mwanga]		
TANZANIA	PWANI	Selous Game Reserve	07°48'S	38°15'E
TANZANIA	MWANZA	Sengerema	02°39'S	32°39'E
TANZANIA	ARUSHA	Serena Lodge	03°22'S	35°50'E
TANZANIA	SHINYANGA	Serengeti National Park, Naabi Gate	02°50'S	35°00'E
TANZANIA	ARUSHA	Seronera, Serengeti National Park	02°25'S	34°48'E
TANZANIA	SHINYANGA	Shinyanga	03°40'S	33°26'E

TANZANIA	SINGIDA	Singida	04°49'S	34°45'E
TANZANIA	ARUSHA	Sinya Mine	02°43'S	37°03'E
TANZANIA	RUVUMA	Songea	10°40'S	35°39'E
TANZANIA	TANGA	Soni, Usambara Mountains	04°51'S	38°22'E
TANZANIA	TABORA	Tabora	05°02'S	32°49'E
TANZANIA	IRINGA	Tandala Camp, Ruaha National Park	07°46'S	35°00'E
TANZANIA	TANGA	Tanga	05°05'S	39°06'E
TANZANIA	MANYARA	Tarangire National Park Camp	03°46'S	36°01'E
TANZANIA	MANYARA	Tarangire National Park Lodge	03°46'S	36°01'E
TANZANIA	MARA	Togoro Grassland, East Serengeti	02°10'S	34°58'E
TANZANIA	TABORA	Tschaja	05°34'S	34°04'E
TANZANIA	RUKWA	Tumba	07°30'S	31°32'E
TANZANIA	TABORA	Tura	05°30'S	33°51'E
TANZANIA	PWANI	Ubenzomozi	06°38'S	38°10'E
TANZANIA	MANYARA	Ufiome	04°14'S	35°48'E
TANZANIA	KIGOMA	Uha [=Kibondo]		
TANZANIA	MWANZA	Ukerewe Island	02°06'S	33°05'E
TANZANIA	MOROGORO	Uluguru Mountains	07°01'S	37°44'E
TANZANIA	MANYARA	Umbugwe [=Magugu]		
TANZANIA	DAR ES SALAAM	University of Dar es Salaam Campus	06°46'S	39°12'E
TANZANIA	SHINYANGA	Unyanembe	03°37'S	33°49'E
TANZANIA	ARUSHA	Usa River	03°22'S	36°51'E
TANZANIA	TANGA	Usambara	05°07'S	38°32'E
TANZANIA	MBEYA	Usangu [=Usungu]		
TANZANIA	MBEYA	Usungu	07°52'S	33°53'E
TANZANIA	NJOMBE	Uttelewe	09°16'S	34°34'E
TANZANIA	PWANI	Zaraninge Forest, Saadani National Park	06°09'S	38°36'E
TANZANIA	RUKWA	Zimba	07°51'S	31°49'E
TOGO	MARITIME	Aneho	06°14'N	01°35'E
TOGO	KARA	Dapaong	10°52'N	00°12'E
TOGO	PLATEAUX	Forêt de Missahohé	6°56'N	00°34'E
TOGO	MARITIME	Klein-Popo [=Aneho]		
TOGO	PLATEAUX	Kloto	06°59'N	00°44'E
TOGO	PLATEAUX	Kpalimé	06°54'N	00°38'E
TOGO	MARITIME	Lome	06°10'N	01°14'E
TOGO	KARA	Tapung [=Dapaong]		
TOGO	CENTRALE	Tchamba	09°02'N	01°25'E
UGANDA	NORTHERN	Alero	02°42'N	33°02'E
UGANDA	CENTRAL	Buddu	00°25'N	31°40'E
UGANDA	WESTERN	Budongo Forest	01°46'N	31°33'E
UGANDA	WESTERN	Bujumbura Escarpment	00°44'S	29°54'E
UGANDA	CENTRAL	Bukalasa	00°14'S	31°44'E
UGANDA	CENTRAL	Bunjako	00°00'N	32°08'E
UGANDA	EASTERN	Busia	00°28'N	34°07'E
UGANDA	EASTERN	Bussu	00°34'N	33°27'E
UGANDA	WESTERN	Butiaba	01°48'N	31°20'E
UGANDA	EASTERN	Buvuma Island, Magyo	00°11'N	33°17'E
UGANDA	NORTHERN	Chobe Lodge	02°15'N	32°08'E

UGANDA	WESTERN	Daro Forest	00°26'N	30°23'E
UGANDA	NORTHERN	Elero [=Alero]		
UGANDA	CENTRAL	Entebbe	00°05'N	32°29'E
UGANDA	WESTERN	Fort Portal	00°39'N	30°17'E
UGANDA	NORTHERN	Gulu	02°46'N	32°18'E
UGANDA	WESTERN	Hoima	01°26'N	31°21'E
UGANDA	EASTERN	Iganga Forest	00°36'N	33°28'E
UGANDA	CENTRAL	Ile Bugala, Bulolombe	00°03'N	33°16'E
UGANDA	EASTERN	Jinja	00°26'N	33°12'E
UGANDA	CENTRAL	Kampala	00°20'N	32°34'E
UGANDA	NORTHERN	Karamoja	02°31'N	34°38'E
UGANDA	CENTRAL	Katigondo	00°14'S	31°44'E
UGANDA	EASTERN	Kigulu	00°37'N	32°50'E
UGANDA	CENTRAL	Kitabi Hill, Entebbe	00°04'N	32°28'E
UGANDA	NORTHERN	Kotido	03°00'N	34°07'E
UGANDA	EASTERN	Luuka	00°46'N	33°20'E
UGANDA	EASTERN	Magunga	00°31'N	33°27'E
UGANDA	CENTRAL	Masaka	00°20'S	31°45'E
UGANDA	CENTRAL	Mawakota	00°01'N	32°01'E
UGANDA	EASTERN	Mbale	01°05'N	34°10'E
UGANDA	NORTHERN	Metu	03°40'N	31°47'E
UGANDA	CENTRAL	Mitiyana	00°24'N	32°02'E
UGANDA	NORTHERN	Moroto	02°32'N	34°40'E
UGANDA	EASTERN	Mount Elgon	01°07'N	34°19'E
UGANDA	WESTERN	Mubuki River, SE Ruwenzori	00°16'N	30°07'E
UGANDA	NORTHERN	Murchison Falls National Park, Chobe	02°14'N	32°08'E
UGANDA	NORTHERN	Murchison Falls National Park, Paraa	02°17'N	31°34'E
UGANDA	CENTRAL	Musenyi Bay	00°28'N	32°29'E
UGANDA	CENTRAL	Mwera	00°19'N	32°09'E
UGANDA	EASTERN	Nakagyo	00°39'N	33°15'E
UGANDA	EASTERN	Nakajo [=Nakagyo]		
UGANDA	CENTRAL	Nakajongola [=Nakasongola]		
UGANDA	CENTRAL	Nakasongola	01°19'N	32°28'E
UGANDA	WESTERN	Namwamba Valley [=Nyamwamba Valley]		
UGANDA	CENTRAL	Nkose Island	00°44'S	32°18'E
UGANDA	CENTRAL	Nkosi Island [=Nkose Island]		
UGANDA	EASTERN	Northern shore of Lake Salisbury	01°41'N	33°57'E
UGANDA	WESTERN	Nyakasura	00°40'N	30°13'E
UGANDA	WESTERN	Nyamwamba Valley	00°14'N	29°58'E
UGANDA	NORTHERN	Ochodri [=Ocodri]		
UGANDA	NORTHERN	Ocodri	03°04'N	31°05'E
UGANDA	NORTHERN	Patiko	03°01'N	32°19'E
UGANDA	NORTHERN	Rhino Camp	02°58'N	31°24'E
UGANDA	WESTERN	Ruzumburu Escarpment [=Bujumbura Escarpment]		
UGANDA	EASTERN	Serere	01°30'N	33°34'E
UGANDA	CENTRAL	Sesse Islands	00°25'S	32°14'E
UGANDA	CENTRAL	Singo	00°41'N	32°11'E
UGANDA	CENTRAL	Tero Forest	00°50'S	31°39'E
UGANDA	EASTERN	Tororo	00°41'N	34°11'E
UGANDA	WESTERN	Valley of the Kafu River	01°38'N	32°05'E

ZAMBIA	NORTHERN	Abercorn [=Mbala]		
ZAMBIA	CENTRAL	Broken Hill [=Kabwe]		
ZAMBIA	SOUTHERN	Bruce-Miller Game Farm	16°38'S	27°01'E
ZAMBIA	NORTH-WESTERN	Chavuma Forest Reserve	13°04'S	92°56'E
ZAMBIA	SOUTHERN	Chiliabufu's	15°38'S	26°35'E
ZAMBIA	CENTRAL	Chingombe	14°25'S	29°58'E
ZAMBIA	MUCHINGA	Chinsali	10°33'S	32°04'E
ZAMBIA	CENTRAL	Chisanga	13°50'S	27°50'E
ZAMBIA	NORTHERN	Chisimbe Falls	10°06'S	30°55'E
ZAMBIA	CENTRAL	Chunga Camp, Kafue National Park	14°57'S	25°49'E
ZAMBIA	MUCHINGA	Danger Hill	11°36'S	31°24'E
ZAMBIA	CENTRAL	Fibwe Mushitu, Kasanka National Park	12°35'S	30°15'E
ZAMBIA	CENTRAL	Forest Inn	13°43'S	29°09'E
ZAMBIA	COPPERBELT	Greystone, Kitwe	12°56'S	28°14'E
ZAMBIA	SOUTHERN	Highlands, Livingstone	17°49'S	25°52'E
ZAMBIA	NORTH-WESTERN	Hillwood, Ikelenge	11°16'S	24°19'E
ZAMBIA	CENTRAL	Huntley Farm, Chisamba	15°02'S	28°09'E
ZAMBIA	WESTERN	Ijobwe, Sioma Ngwezi National Park	16°54'S	23°36'E
ZAMBIA	NORTH-WESTERN	Jiwundu Swamp	11°52'S	25°33'E
ZAMBIA	NORTHERN	Kabwe	08°34'S	29°33'E
ZAMBIA	CENTRAL	Kabwe	14°26'S	28°27'E
ZAMBIA	CENTRAL	Kabwe, Kasanka National Park	12°32'S	30°13'E
ZAMBIA	CENTRAL	Kacheleko Wildlife Outpost, Kafue National Park	15°01'S	26°25'E
ZAMBIA	NORTHERN	Kalaba & Seranani	?	
ZAMBIA	LUAPULA	Kalundu	10°18'S	29°23'E
ZAMBIA	MUCHINGA	Kalungu	09°41'S	32°43'E
ZAMBIA	NORTHERN	Kambole	08°47'S	30°46'E
ZAMBIA	WESTERN	Kaoma	14°49'S	24°48'E
ZAMBIA	MUCHINGA	Kapishya Hot Springs	11°10'S	31°36'E
ZAMBIA	COPPERBELT	Kashitu	13°44'S	28°39'E
ZAMBIA	LUAPULA	Kawambwa	09°48'S	29°05'E
ZAMBIA	SOUTHERN	Kazangula	17°47'S	25°17'E
ZAMBIA	LUAPULA	lac Bangwelo [=Lake Bangweulu]		
ZAMBIA	LUAPULA	lac Moero [=Lake Mweru]		
ZAMBIA	LUAPULA	Lake Bangweulu	11°12'S	29°45'E
ZAMBIA	LUAPULA	Lake Mweru	08°56'S	28°46'E
ZAMBIA	MUCHINGA	Lavushi Hills, Lavushi Manda National Park	12°23'S	30°52'E
ZAMBIA	WESTERN	Lealui	15°13'S	23°01'E
ZAMBIA	CENTRAL	Lilemone	15°26'S	26°09'E
ZAMBIA	SOUTHERN	Livingstone	17°51'S	25°50'E
ZAMBIA	LUSAKA	Lower Zambezi National Park	15°22'S	29°18'E
ZAMBIA	CENTRAL	Lubungu	14°34'S	26°27'E
ZAMBIA	NORTH-WESTERN	Lukwakwa, West Lunga National Park	12°40'S	24°26'E
ZAMBIA	NORTHERN	Lumangwe Falls	09°33'S	29°23'E
ZAMBIA	EASTERN	Lundazi	12°17'S	33°10'E
ZAMBIA	NORTHERN	Lupele	09°07'S	29°37'E
ZAMBIA	LUSAKA	Lusaka	15°23'S	28°19'E
ZAMBIA	WESTERN	Lusu	17°12'S	24°06'E
ZAMBIA	WESTERN	Lyangu, Liuwa Plain National Park	14°47'S	22°35'E

ZAMBIA	LUAPULA	<b>Madona</b>	11°08'S	28°33'E
ZAMBIA	CENTRAL	<b>Mayukuyuku, Kafue National Park</b>	14°55'S	26°04'E
ZAMBIA	NORTHERN	<b>Mbala</b>	08°51'S	31°22'E
ZAMBIA	LUAPULA	<b>Medona [=Madona]</b>		
ZAMBIA	NORTH-WESTERN	<b>Mfumbwe</b>	13°09'S	25°01'E
ZAMBIA	EASTERN	<b>Mfuwe, South Luangwa National Park</b>	13°05'S	31°47'E
ZAMBIA	CENTRAL	<b>Mfwanta</b>	13°07'S	30°20'E
ZAMBIA	CENTRAL	<b>Mkushi</b>	13°37'S	29°23'E
ZAMBIA	MUCHINGA	<b>Mpika</b>	11°50'S	31°27'E
ZAMBIA	NORTHERN	<b>Mporokoso</b>	09°23'S	30°08'E
ZAMBIA	LUSAKA	<b>Mukamba Gate, Lower Zambezi National Park</b>	15°16'S	29°13'E
ZAMBIA	WESTERN	<b>Mutata wa Siyenge, Liuwa National Park</b>	14°36'S	22°35'E
ZAMBIA	MUCHINGA	<b>Mutinondo Wilderness Area</b>	12°27'S	31°17'E
ZAMBIA	MUCHINGA	<b>Muyombe</b>	10°35'S	33°27'E
ZAMBIA	COPPERBELT	<b>Mwengwa</b>	13°00'S	27°40'E
ZAMBIA	NORTHERN	<b>Mweru-Wantipa</b>	08°46'S	29°32'E
ZAMBIA	NORTH-WESTERN	<b>Mwinilunga</b>	11°44'S	24°25'E
ZAMBIA	SOUTHERN	<b>Nanzhila Plains, Kafue National Park</b>	16°17'S	25°54'E
ZAMBIA	COPPERBELT	<b>N'Changa</b>	12°31'S	27°51'E
ZAMBIA	NORTH-WESTERN	<b>Nchila Wildlife Reserve</b>	11°16'S	24°19'E
ZAMBIA	WESTERN	<b>Ndanda</b>	15°05'S	23°46'E
ZAMBIA	NORTHERN	<b>Nkamba Bay, Sumbu National Park</b>	08°36'S	30°33'E
ZAMBIA	NORTHERN	<b>Nkole</b>	10°35'S	31°11'E
ZAMBIA	NORTHERN	<b>N'Koli [=Nkole]</b>		
ZAMBIA	NORTH-WESTERN	<b>Nkwaji, Mwinilunga</b>	11°31'S	24°33'E
ZAMBIA	EASTERN	<b>Nkwali, South Luangwa GMA</b>	13°23'S	29°33'E
ZAMBIA	LUAPULA	<b>Ntumbachushi Falls</b>	09°51'S	28°57'E
ZAMBIA	WESTERN	<b>Sefula</b>	15°26'S	23°15'E
ZAMBIA	CENTRAL	<b>Serenje</b>	13°14'S	30°14'E
ZAMBIA	MUCHINGA	<b>Shiwa Ngandu</b>	11°12'S	31°44'E
ZAMBIA	SOUTHERN	<b>Simonga</b>	17°48'S	25°43'E
ZAMBIA	NORTH-WESTERN	<b>Solwezi</b>	12°10'S	26°23'E
ZAMBIA	NORTH-WESTERN	<b>Source of the Zambezi River</b>	11°22'S	24°19'E
ZAMBIA	EASTERN	<b>South Luangwa National Park</b>	13°05'S	31°47'E
ZAMBIA	NORTHERN	<b>Tupele [=Lupele]</b>		
ZAMBIA	SOUTHERN	<b>Victoria Falls</b>	17°55'S	25°52'E
ZIMBABWE	MASHONALAND EAST	<b>Arcturus</b>	17°47'S	31°19'E
ZIMBABWE	MATABELELAND SOUTH	<b>Balla Balla [=Mbalabala]</b>		
ZIMBABWE	MASHONALAND EAST	<b>Beatrice</b>	18°15'S	30°51'E
ZIMBABWE	MATABELELAND SOUTH	<b>Beitbridge</b>	22°12'S	30°00'E
ZIMBABWE	MASHONALAND CENTRAL	<b>Bindura</b>	17°18'S	31°19'E
ZIMBABWE	MASVINGO	<b>Birchenough Bridge</b>	17°58'S	32°20'E
ZIMBABWE	MASVINGO	<b>Bubye River</b>	21°43'S	30°30'E
ZIMBABWE	BULAWAYO	<b>Bulawayo</b>	20°09'S	28°35'E
ZIMBABWE	MANICALAND	<b>Chipinga [=Chipinge]</b>		
ZIMBABWE	MANICALAND	<b>Chipinge</b>	20°12'S	32°38'E
ZIMBABWE	MASHONALAND EAST	<b>Chivhu</b>	19°00'S	30°54'E
ZIMBABWE	MANICALAND	<b>Christmas Pass</b>	18°57'S	32°38'E
ZIMBABWE	MASHONALAND CENTRAL	<b>Christon Bank</b>	17°36'S	31°00'E

ZIMBABWE	MASHONALAND WEST	Darwendale	17°43'S	30°33'E
ZIMBABWE	MATABELELAND SOUTH	Empandeni	20°42'S	27°54'E
ZIMBABWE	MASHONALAND EAST	Enkeldoorn [=Chivhu]		
ZIMBABWE	HARARE	Epworth	17°53'S	31°09'E
ZIMBABWE	MASHONALAND EAST	Featherstone	18°43'S	30°50'E
ZIMBABWE	MASVINGO	Fort Victoria [=Masvingo]		
ZIMBABWE	MASHONALAND WEST	Gadzema	18°02'S	30°09'E
ZIMBABWE	MASHONALAND WEST	Glen Clova	17°24'S	30°07'E
ZIMBABWE	MASVINGO	Great Zimbabwe	20°16'S	30°56'E
ZIMBABWE	MATABELELAND NORTH	Gwai River [=Gwayi]		
ZIMBABWE	MATABELELAND NORTH	Gwayi	19°17'S	27°41'E
ZIMBABWE	MIDLANDS	Gwelo [=Gweru]		
ZIMBABWE	MIDLANDS	Gweru	19°28'S	29°49'E
ZIMBABWE	HARARE	Harare	17°50'S	31°02'E
ZIMBABWE	MATABELELAND NORTH	Hwange National Park	18°43'S	26°57'E
ZIMBABWE	MATABELELAND SOUTH	Insiza	20°32'S	29°17'E
ZIMBABWE	MASHONALAND WEST	Kariba	16°31'S	28°51'E
ZIMBABWE	MATABELELAND NORTH	Kenmaur	19°07'S	27°58'E
ZIMBABWE	MASVINGO	Kyle Game Reserve	20°11'S	31°00'E
ZIMBABWE	MASVINGO	Kyle Recreational Park, Lake Mutirikwi	20°10'S	31°01'E
ZIMBABWE	MANICALAND	Laurenceville	19°04'S	32°44'E
ZIMBABWE	MASVINGO	Lundi [=Runde]		
ZIMBABWE	MASHONALAND EAST	Macheke	18°09'S	31°51'E
ZIMBABWE	MASVINGO	Makuti	16°19'S	29°15'E
ZIMBABWE	MANICALAND	Marandellas [=Marondera]	18°10'S	31°36'E
ZIMBABWE	MASHONALAND WEST	Marongora	16°13'S	29°10'E
ZIMBABWE	MASVINGO	Masvingo	20°05'S	30°50'E
ZIMBABWE	MATABELELAND SOUTH	Matobo Game Reserve	20°35'S	28°27'E
ZIMBABWE	MATABELELAND SOUTH	Matopos Game Reserve [=Matobo Game Reserve]		
ZIMBABWE	MATABELELAND SOUTH	Matopos siding	20°25'S	28°28'E
ZIMBABWE	MASHONALAND CENTRAL	Mazoe	17°30'S	30°59'E
ZIMBABWE	MATABELELAND SOUTH	Mbalabala	20°27'S	29°02'E
ZIMBABWE	MANICALAND	Mount Chirinda/Chirinda Forest	20°25'S	32°42'E
ZIMBABWE	MANICALAND	Mpudzi Ricer	19°23'S	32°34'E
ZIMBABWE	MANICALAND	Mutare	18°59'S	32°39'E
ZIMBABWE	MATABELELAND SOUTH	Nuantesi River Bridge	21°42'S	30°30'E
ZIMBABWE	MANICALAND	Penhalonga	18°53'S	32°40'E
ZIMBABWE	MATABELELAND SOUTH	Plumtree	20°29'S	27°48'E
ZIMBABWE	MASVINGO	Providential Pass	20°11'S	30°47'E
ZIMBABWE	MASHONALAND WEST	Rekometjie	16°08'S	29°24'E
ZIMBABWE	MASVINGO	Runde	20°54'S	30°47'E
ZIMBABWE	MANICALAND	Rusape	18°32'S	32°08'E
ZIMBABWE	MANICALAND	Rusape River	18°32'S	32°07'E
ZIMBABWE	HARARE	Salisbury [=Harare]		
ZIMBABWE	MIDLANDS	Sebakwe	19°02'S	30°13'E
ZIMBABWE	MANICALAND	Silverstreams River Bridge	20°00'S	32°42'E
ZIMBABWE	MATABELELAND SOUTH	Solusi	20°12'S	28°09'E
ZIMBABWE	MANICALAND	Umtali [=Mutare]		
ZIMBABWE	MATABELELAND NORTH	Victoria Falls	17°56'S	25°51'E
ZIMBABWE	MATABELELAND NORTH	Victoria Falls National Park, Chamabondo	17°56'S	25°49'E

ZIMBABWE	MANICALAND	<b>Vumba Road</b>	19°01'S	32°36'E
ZIMBABWE	MANICALAND	<b>Vumba, "Loop"</b>	19°05'S	32°45'E
ZIMBABWE	MASVINGO	<b>Wadonda River Bridge</b>	20°18'S	30°41'E
ZIMBABWE	MATABELELAND NORTH	<b>Wankie National Park [=Hwange National Park]</b>		
ZIMBABWE	MATABELELAND NORTH	<b>Zambezi National Park Camp, Victoria Falls</b>	17°54'S	25°48'E
ZIMBABWE	MASVINGO	<b>Zimbabwe Ruins [=Great Zimbabwe]</b>		



## Taxonomic notes concerning the genus *Catharsius* Hope, 1837 (Scarabaeidae, Scarabaeinae)

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### Abstract

The taxonomic status of *Catharsius harpagus* Harold, 1877 is discussed and synonymised with the Asian species *Catharsius birmanensis* Lansberge, 1874. *Catharsius parafastidiosus* Ferreira, 1971 is also synonymised with *C. birmanensis*. These are the first cases of purported African species of this genus being synonymised with an Asian species. This leaves the *C. harpagus* sensu Ferreira, 1960 (nec Harold) without a name and *Catharsius haroldi* sp. nov. is here described. *Catharsius convexiusculus* (Shipp, 1897) is transferred to the genus *Metacatharsius* and *Metacatharsius omoensis* (Müller, 1941) is restored to its original combination in the genus *Catharsius*.

Key Words: taxonomy, synonymy, Africa, Asia, Harold, Shipp, Péringuey, Ferreira.

### Introduction

The mega-diverse genus *Catharsius* Hope 1837 currently contains 89 taxa (87 species) in sub-Saharan Africa. These beetles are primarily coprophagous in habit although some species have developed necrophagic tastes. The most recent comprehensive review of the genus was undertaken by Ferreira (1960) and it has since been the go to reference for identification of this genus. Although a number of new species have been described in isolation, the genus is in need of a holistic taxonomic revision implementing modern systematic tools and in advance of its publication by the author, a few nomenclatural issues are here corrected.

The following abbreviations are used in the text:

BMNH	The Natural History Museum, London, United Kingdom
MCST	Museo Civico di Storia Naturale, Trieste, Italy
MNHN	Muséum national d'Histoire Naturelle, Paris, France
MTD	Museum für Tierkunde, Dresden, Germany
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom
SANC	South African National Collection of Insects, Pretoria, South Arica
ZMHB	Museum für Naturkunde, Berlin, Germany

Primary label data has been transcribed verbatim with “//” denoting a different label and ‘/’ denoting a line break followed by a description of the media for each label in square brackets. If no indication is given, the label is printed on white card. Body measurements are from the apex of the pronotum to the apex of the elytra. Specimens were photographed using a Canon EOS 5D SR with Macro 100mm or MP-E 65mm lenses. The aedeagus was photographed through a Leica MS5 stereo microscope. Images were stacked using Helicon Focus 6.0.

### *Catharsius harpagus* Harold, 1877

Edgar von Harold (1877) described this species from a vague locality of “*Afric. austral.*” with at least a male and female in the syntypic series, giving a range in size of 22–30mm. Although Harold states

in his original description that the type specimens of *C. harpagus* were housed in the ZMHB, the type series was found in the MNHN collections. This series consists of two males and one female, the largest male with a typical Harold type label (Figs. 1–2). Rather surprisingly, the two males pertain to the Asian species *Catharsius birmanensis* Lansberge, 1874 while the female specimen is a West African *Catharsius phidias* (Olivier, 1789). In order to stabilise the taxonomy of this species by fixing the published name to a single specimen, the largest male with the following label data is here **designated as the lectotype**:

“// Afr. austr. / C. / Harpagus / Typ. Harold [cream card with red border; handwritten] // Ex. Musaeo / E. Harold [cream card with black border] // MUSEUM PARIS / ex coll. / OBERTHÜR / 1953 // LECTOTYPE / CATHARSIUS / harpagus / Harold / det. H Takano 2017 [white card with red border; partially handwritten] //”

Louis Péringuey (1901) synonymised *C. harpagus* under *Catharsius laticeps* Boheman, 1857 without giving any justification. *C. laticeps* was described from a female specimen by Boheman and Péringuey incorrectly associated a male which belonged to a different species. The male specimen he described and figured as *C. laticeps* (Fig. 3) is unmistakably a male of *C. harpagus* Harold and so, despite the incorrect assumption of this being the male of *C. laticeps*, he correctly synonymised *C. harpagus* under *C. laticeps* sensu Péringuey (nec Boheman).

Maria Corinta Ferreira (1971) re-examined this very male specimen upon which Péringuey based his description and correctly stated that this is not a male of *C. laticeps* nor is *C. harpagus* sensu Ferreira (nec Harold) a synonym of *C. laticeps*. She proceeded to describe this specimen as *Catharsius parafastidiosus*. The holotype in the SANC (Figs. 4–5) with the following label data was examined:

“// no 3 / Copris laticeps / m# [cream paper; handwritten in Péringuey’s hand] // HOLOTIPO m# / Catharsius parafas- / tidiosus n.sp. / M.C. Ferreira det., 1971 [partially handwritten in Ferreira’s hand] // HOLOTYPUS / m# [red card] // NATIONAL COLL. / OF INSECTS (SANC) / Pretoria, South Africa [black border] // TYPH00479 [red card] //”

Both *C. harpagus* and *C. parafastidiosus* are here synonymised with *C. birmanensis* thus:

***Catharsius birmanensis* Lansberge 1874**

*Catharsius birmanensis* Lansberge, 1874: 11.

*Catharsius harpagus* Harold, 1877: 97. (**syn. nov.**)

*Catharsius laticeps* sensu Péringuey, 1901 (nec Boheman): 335, Plate XXXIII, Fig. 23 & 23a.

*Catharsius parafastidiosus* Ferreira, 1971: 5. (**syn. nov.**)

In the late 19<sup>th</sup> Century, European ships travelling to and from Asia would likely stop at Cape Town or Durban to resupply and it is possible that unlabelled specimens from the Orient were exchanged or sold by naturalists ending up in the collections of individuals such as Péringuey or the South African museums causing the confusions over its true provenance.

***Catharsius harpagus* sensu Ferreira, 1960 (nec Harold)**

On studying the ZMHB collections leading up to her review on the genus *Catharsius*, Ferreira (1960) studied a male in the collections standing under *C. harpagus* and re-described the species based on that specimen. In later publications, she described the female (1964a) and included the description of both sexes in a work on the dung beetle fauna of Mozambique (1967).

In their work on the *Catharsius* species described by Harold, Génier & Josso (2016) studied three specimens standing under *C. harpagus* in the ZMHB of which two had been collected after the date of description and designated the remaining male as a lectotype. This specimen was collected in Delagoa Bay and had likely belonged in the collection of Carl Felsche. One of the labels ([D.O. Africa / 36] refer to Fig. 10 in Génier & Josso, 2016) is a handwritten label in Felsche’s very distinctive hand. It

may be possible that this was the specimen studied by Ferreira in her 1960 publication, but nevertheless it cannot be a syntype and hence their designation of a lectotype is invalid.

The above synonymy leaves this taxon undescribed and the description of a new species follows:

***Catharsius haroldi* sp. nov.** (Figs. 6–9)

*Catharsius harpagus* sensu Ferreira, 1960 (nec Harold): 225; 1964: 7; 1967: 234; 1972: 270; Génier & Josso, 2016: 335.

**HOLOTYPE** m# (BMNH):

“// MOZAMBIQUE, 2m, Transect 4, / Maputo Special Reserve, / (Hygrophilous Grassland, 100m / from Sand Forest Ecotone) / 26°29'8.3"S, 32°45'8.9"E / 5.XII.2016. Human Dung Pitfall / Aristophanous, M., Cristóvão, J., / Laszlo, G., Miles, W. leg. / BMNH(E) 2016–262 / Trip Ref: MZ–001 (ANHRT 22) // NHMUK010367768 [QR code] //”

**PARATYPES** (16m#m# 20f##f#):

**MOZAMBIQUE:** **MAPUTO:** Maputo Special Reserve, 2m (26°29'S, 32°45'E), 4–5.vi.2017, M. Aristophanous, G. László, W. Miles & A. Vetina (1m# 3f## BMNH); Maputo Special Reserve, Transect 4, 2m (26°29'S, 32°45'E), 5.xii.2016, M. Aristophanous, J. Cristóvão, G. László & W. Miles (5m#m# 6f## BMNH); Maputo Special Reserve, Transect 5, 2m (26°29'S, 32°45'E), 5.xii.2016, M. Aristophanous, J. Cristóvão, G. László & W. Miles (2m#m# 5f## BMNH); Maputo Special Reserve, Transect 6, 2m (26°29'S, 32°45'E), 5.xii.2016, M. Aristophanous, J. Cristóvão, G. László & W. Miles (6m#m# 4f## BMNH); Maputo Special Reserve, West Gate, 22m (26°30'S, 32°43'E), 21–30.xi.2016, M. Aristophanous, J. Cristóvão, G. László & W. Miles (2m#m# 2f## BMNH);

**Description: Male:** Holotype (Figs. 6–7). **Size:** Length: 25 mm, width, 17 mm. **Colour:** Black with a reddish undertone; pubescence light brown. **Head:** anterior clypeal edge evenly arcuate with continuous clypeal margin. Clypeal surface rugose anteriorly becoming more granulose posteriorly; genal edge rounded and acutely angled, surface with granules disappearing and becoming smooth internally. Clypeogenal suture well defined to base of cephalic horn. Cephalic horn, long and straight, wide on basal third, edges of basal portion converging slightly; apicolateral angles rounded and obtuse. Cephalic suture laterally well-defined from base to apex. **Pronotum:** Anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateral edges broadly arcuate. Pronotal disc with short but sharply pointed horns anteriorly, gently diverging and curved upwards, placed evenly between the midline and lateral margin; the apex of the horns in line with the edge of the clypeogenal suture. Pronotal disc with continuous margin posteriorly; surface of disc covered in fine granules except for a smooth ovaline region each side of the midline; lateral declivity with fovea; surface completely granulate. Surface of anterior declivity smooth; in frontal view, the smooth area extends from the horns to the anterior margin. **Elytra:** carinate basally; elytral striae well defined, with weak punctures encroaching slightly on intervals; surface of interstriae smooth except for 2mm portion basally of fine alutaceous microsculpture; carina on ninth interval very short. **Pygidium:** transverse, fully margined, smooth centrally becoming more alutaceous towards edges; fine ovaline punctures throughout. **Legs:** Protibia tridentate; spur curved gently apically; three longitudinal striae ventrally. Metatibial spur long, square ended. **Male genitalia:** parameres almost as long as phallobase; laterally arcuate with shallow concavity anteriorly (Fig. 9).

**Female** (Fig. 8): **Head:** anterior clypeal edge evenly arcuate with continuous clypeal margin. Clypeal surface transversally rugose anteriorly becoming more granulose posteriorly; genal edge rounded and acutely angled, surface with granules disappearing and becoming smooth internally. Clypeogenal suture well defined to base of clypeal carina. Clypeal carina raised, broadly triangular in frontal view and weakly tridentate, the central point slightly bifurcate. **Pronotum:** Anterior margin continuous, obliquely orientated anteriorly on each side of eyes. Lateral edges broadly arcuate. Pronotal disc with short carina anteriorly, arcuate and medially emarginate; length of carina no longer than distance between eyes. Surface of disc completely granulose except for a small smooth region either side of the mid line; smooth area rounded internally, tapering to a point laterally. Lateral declivity with fovea; surface completely granulate. Surface of anterior declivity completely granulate. **Elytra:** carinate basally; elytral striae well defined, with weak punctures encroaching slightly on intervals; surface of interstriae smooth except for 2mm portion anteriorly of fine alutaceous microsculpture; carina on ninth interval very short. **Pygidium:** transverse, fully margined, smooth centrally becoming more

alutaceous towards edges; fine ovaline punctures throughout. **Legs:** Protibia tridentate; spur curved gently apically; three longitudinal striae ventrally. Metatibial spur long, square ended.

**Variation:** Measurements. Length: male 20–25 mm, female 21–26 mm. In smaller males the anterior declivity is completely granulose; the pronotal horns are reduced to tubercles and the cephalic horn is reduced to a broad equilateral triangle in frontal view.

**Derivatio nominis:** this species is named after the Coleopterist Edgar von Harold (1830–1886), who described *Catharsius harpagus*, the species with which subsequent authors have confused this new species.

**Distribution:** Mozambique & South Africa.

### ***Copris convexiusculus* Shipp, 1897**

This species was described by John William Shipp [note his initials in the original description of I.W. Shipp is an error] from a single specimen collected by Arthur Donaldson Smith on his expedition through Somalia and Ethiopia. The specimen was captured on 19<sup>th</sup> March 1895 between “Aimola and Himo” but as Donaldson Smith kept exceptionally accurate records of each specimen he collected (Jordan, 1897), it is possible to pinpoint the type locality to 4°01’N, 40°09’E, an area in modern day Ethiopia very near the Kenya border, by cross-referencing the label data with the maps detailing the route of his expedition (Donaldson Smith, 1897).

This taxon was placed in the genus *Catharsius* by Gillet (1911) and listed in Ferreira’s works on the genus (1960; 1972) but on studying the holotype (by original monotypy) housed in MTD (and not the BMNH as stated by Ferreira), it has become apparent that this species belongs in the genus *Metacatharsius*. Based on the above, the following new combination is established:

#### ***Metacatharsius convexiusculus* (Shipp, 1897) comb. nov.**

*Copris convexiusculus* Shipp, 1897: 450.

*Catharsius convexiusculus* (Shipp, 1897): Gillet, 1911: 68; Ferreira, 1960: 248; 1972: 264.

There have been a number of recent revisional works in which Shipp’s types could not be located (Forgie et al., 2002; Silva & Vaz-de-Mello, 2015) and although only the *Catharsius* specimens were studied by the author in the MTD, it is likely that the majority of Shipp’s types stated as being in the Tring Museum are found in the Felsche collection housed in the MTD. This, however, does not include any species described by Shipp from collections other than Tring; types of *Irrorhotides fryi* Shipp, 1895 stated in the original description as belonging in the Fry Collection (housed in the BMNH) and *Spodochalmys poultoni* Shipp, 1895 in the Hope Museum (OUMNH) are still preserved in these respective collections.

The reference to the whereabouts of Shipp’s collection in Horn et al. (1990) is likely to refer specifically to his personal collection which was sold at Steven’s Auctioneers to Percy May Bright and henceforth sold to Tring. It is well known that the majority of the Tring Lepidoptera collection was bequeathed by Lord Walter Rothschild to the BMNH but large parts of the Coleoptera collection were sold off and the Coprophaga was purchased by Felsche (see under *Tring Museum* in Horn et al., 1990: 397). This is supported by a number of letters from the turn of the 20<sup>th</sup> Century in the archives of the BMNH from Felsche to Karl Jordan, a curator at Tring, discussing prices of beetles such as *Heliocopris*, *Catharsius* and *Phanaeus*. It is through these sales that Shipp’s types have ended up in Felsche’s collection and not in the BMNH. Subsequent and recent references to Shipp’s types being deposited in the BMNH (such as the unverified reference to the presence of Shipp’s types of *Heliocopris donaldsoni* and *Heliocopris coriaceus* in the BMNH by Pokorny et al., 2009) are likely as a result of an assumption made through the Horn et al. reference.

### ***Catharsius omoensis* Müller, 1941**

This species was described by Giuseppe Müller from specimens collected by Edoardo Zavattari in Murle (5°09'N, 36°13'E) on the left bank of the Omo River, about 50km from Lake Turkana in southern Ethiopia. A male syntype was studied by Ferreira and she transferred this taxon into the subgenus *Metacatharsius* based purely on body size (1964b), despite having been omitted from Balthasar's comprehensive work on the subgenus (1965). Subsequently, *Metacatharsius* has been raised to genus level (e.g. Montreuil, 1998) and having re-examined a male syntype housed in the MCST, it has become evident that the original placement of this taxon in the genus *Catharsius* was correct.

***Catharsius omoensis* Müller, 1941 stat. res.**

*Catharsius omoensis* Müller, 1941: 340.

*Catharsius (Metacatharsius) omoensis* Müller, 1941; Ferreira, 1964: 382, 415; 1972: 308.

*Metacatharsius omoensis* (Müller, 1941): Montreuil, 1998: 137.

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## References

- Balthasar, V. (1965) Monographie der Untergattung *Metacatharsius* Paul. (Gattung *Catharsius* Hope) (Coleoptera). *Entomologische Abhandlungen Museum für Tierkunde Dresden*, 31 (1), 1–48.
- Boheman, C.H. (1857) *Insecta Caffraria annis 1838–1845 a J.A.Wahlberg collecta amici auxilios sultus descripsit. Coleoptera*. Officina Norstedtiana, Holmiae, 2: 395 pp.
- Donaldson Smith, A. (1897) *Through Unknown African Countries*. Edward Arnold, London, 471 pp.
- Ferreira, M.C. (1960) Revisão das espécies Etiópicas do subgenera *Catharsius* s.str.. *Revista Entomologia Moçambique*, 3 (2), 155–270.
- Ferreira, M.C. (1964a) Contribuição para o estudo dos Escarabídeos Africanos. *Novos Taxa Entomológicos*, 35, 3–9.
- Ferreira, M.C. (1964b) Contribuição para o estudo das espécies Africanas do subgénero *Metacatharsius* Paulian (Coleoptera Scarabaeidae, Género *Catharsius* Hope). *Revista de Entomologia de Moçambique*, 7 (2), 381–450.
- Ferreira, M.C. (1967) Os Escarabídeos de Moçambique. I.. *Revista de Entomologia de Moçambique*, 10(1-2), 5–778.
- Ferreira, M.C. (1971) Contribuição para o estudo dos Escarabídeos Africanos. Descrição de uma espécie nova de *Catharsius* s. str.. *Novos Taxa Entomológicos*, 96, 5–6.
- Ferreira, M.C. (1972) Os Escarabídeos de Africa (sul do Saara). I. *Revista de Entomologia de Moçambique*, 11, 5–1088.
- Forge, S.A., Grebennikov, V.V. & Scholtz, C.H. (2002) Revision of *Sceliages* Westwood, a millipede-eating genus of southern African dung beetles (Coleoptera: Scarabaeidae). *Invertebrate Systematics*, 16, 931–955.

- Génier, F. & Josso, J.-F. (2016) Notes on Afrotropical *Catharsius* species described by Edgar von Harold (Coleoptera: Scarabaeidae, Scarabaeinae). *Zootaxa*, 4072 (3), 333–342.
- Gillet, J.J. (1911) Pars 38. Scarabaeidae: Coprinae. I. in S. Schenkling (ed.), *Coleopterorum Catalogus*, W. Junk, Berlin.
- Harold, E. von (1877) Coleopterorum species novae. *Mittheilungen der Münchner entomologischen Verein*, 1, 97–111.
- Horn, W., Kahle, I., Friese, G. & Gaedike, R. (1990) *Collectiones Entomologicae*. Akademie der Landwirtschaftswissenschaften der Deutschen Demokratischen Republik, 2 parts, 573 pp.
- Jordan, K. (1897) in Appendix I of Donaldson Smith, A., *Through Unknown African Countries*. Edward Arnold, London.
- Lansberge, G.W. van. (1874) Description de quelque Lamellicornes Coprophages. *Coleopterologische Hefte*, 12 (2), 4–12.
- Montreuil, O. (1998) Analyse phylogénétique et paraphylie des Coprini et Dichotomiini (Coleoptera: Scarabaeidae). Scénario biogéographique. *Annales de la Société Entomologique de France (Nouvelle Série)*, 34, 135–148.
- Müller, G. (1941) Nuovi Coleotteri dell’Africa orientale. *Atti del Museo Civico di Storia Naturale di Trieste*, 14 (23), 319–352.
- Péringuey, L. (1901) Descriptive catalogue of the Coleoptera of South Africa (Lucanidae & Scarabaeidae). *Transactions of the South African Philosophical Society*, 12 (1), 1–563.
- Pokorný, S., Zídek, J. & Werner, K. (2009) *The Giant Dung Beetles of the Genus Heliocopris*. Taita, Czech Republic, 136 pp.
- Shipp, W.J. (1897) in Appendix I of Donaldson Smith, A., *Through Unknown African Countries*. Edward Arnold, London.
- Silva, F.A.B. & Vaz-de-Mello, F. (2015) A revision of the genus *Aphengium* Harold, 1868 (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini). *Zootaxa*, 3955 (4), 505–520.

**FIGURES 1–9.** *Catharsius* spp. *C. harpagus* Harold (lectotype m#). 1. habitus, dorsal view; 2. labels; *C. laticeps* sensu Péringuey (nec Boheman). 3. reproduction of figures 23 and 23a from plate XXXIII in Péringuey, 1901; *C. parafastidiosus* Ferreira (holotype m#). 4. habitus, dorsal view; 4. labels; *C. haroldi* sp. nov. (holotype m#). 6. habitus, dorsal view 7. lateral view; 9. aedeagus, lateral view; *C. haroldi* sp. nov. (paratype f#) 8. habitus, dorsal view. Scale 5 mm unless otherwise specified.

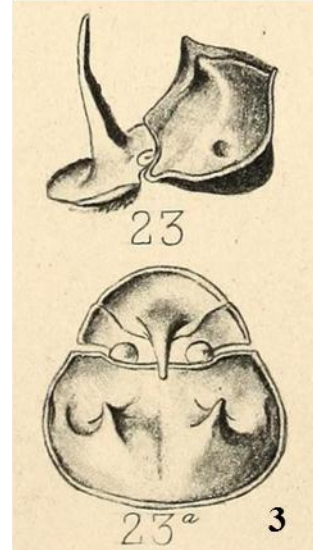


Afr. austr.  
C.  
Harpagus  
Typ. Haroid

Ex Musæo  
E. Haroid

MUSEUM PARIS  
ex coll.  
OBERTHÜR  
1953

**LECTOTYPE**  
CATHARSUS  
harpagus Haroid  
det. H Takano 20 17



no 3  
Cath. laticeps ♂

HOLOTIPO ♂  
Catharsius parafas-  
tidiosus n. sp.  
M.C. Ferreira det., 1971

**HOLOTYPE**  
♂

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