REVISION OF THE TAXONOMY AND DISTRIBUTION OF THE AFRICAN MILLIPEDE GENERA *Bicoxidens*, *Spirostreptus*, *Plagiotaphrus* and *Archispirostreptus* (DIPLOPODA, SPIROSTREPTIDA, SPIROSTREPTIDAE).

By

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A thesis submitted in fulfillment of the academic requirements for the degree of
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The thesis is by research papers published in internationally-recognised, peer-reviewed journals, with an overall introduction and final discussion, following the guidelines (**Format 4**) from the Faculty of Science and Agriculture.

AUTHENTICATION

As the candidate's supervisor I agree to the submission of this thesis.

……………………………………………
PROFESSOR ROBERT SLOTOW

DECLARATIONS

DECLARATION 1 - PLAGIARISM

I, TAROMBERA MWABVU (Student Number 204 509 756) declare that

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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1
Mwabvu, T., Hamer, M., & Slotow, R. (2007). A taxonomic review of the southern African millipede genus, *Bicoxidens* Attems, 1928 (Diplopoda: Spirostreptida: Spirostreptidae), with the description of three new species and a tentative phylogeny. *Zootaxa* 1452: 1–23.

TM wrote the manuscript and prepared the figures. The naming and description of new taxa were also done by TM. MH and RS were supervisors, they commented on the manuscript and approved the final version before it was submitted for publication.

Publication 2
Mwabvu, T., Hamer, M. & Slotow, R. (2009). A new species of *Bicoxidens* Attems, 1928 (Diplopoda, Spirostreptida, Spirostreptidae) species from northern Zimbabwe. *Zookeys* 7: 75–81.

TM wrote the manuscript (including naming and describing the new species) and prepared the figures. MH and RS read and commented on the manuscript before it was submitted for publication.

Publication 3
Mwabvu, T., Hamer, M., Slotow, R. & Barraclough, D. (2009). A revision of the taxonomy and distribution of *Spirostreptus* Brandt 1833 (Diplopoda, Spirostreptida, Spirostreptidae) with descriptions of a new species and a new genus of spirostreptid millipede. *Zootaxa* 2211: 36–56.

The manuscript (including naming and describing the new taxa) was written and the figures were prepared by TM. MH, RS and DB were supervisors, they reviewed the manuscript before it was submitted for publication.

Publication 4
Mwabvu, T., Hamer, M., Slotow, R. & Barraclough, D. (2009). A review of the taxonomy and distribution of *Plagiotaphrus* Attems 1914 (Diplopoda, Spirostreptida, Spirostreptidae). *Zootaxa* 2304: 51–60.

TM wrote the manuscript and prepared the figures. MH, RS and DB were supervisors, they reviewed the manuscript before it was submitted for publication.

Publication 5
Mwabvu, T., Hamer, M., Slotow, R. & Barraclough, D. (2010). A revision of the taxonomy and distribution of *Archispirostreptus* Silvestri 1895 (Diplopoda, Spirostreptida, Spirostreptidae), and description of a new spirostreptid genus with three new species. *Zootaxa* 2567: 1–49.

The manuscript (including naming and describing the new taxa) was written and the figures were prepared by TM. MH, RS and DB were supervisors, they read and commented on the manuscript before it was submitted for publication.

Publication 6
Mwabvu, T., & Van den Spiegel, D. (2009). Spirostreptid Millipedes (Myriapoda: Diplopoda) of the Taita Hills, Kenya, Including Descriptions of Three New Species. Pp. 195–207. *In*: Roble, S. M. & Mitchell, J. C. (eds.), *A Lifetime of Contributions to Myriapodology and the Natural History of Virginia: A Festschrift in Honor of Richard L. Hoffman's 80th Birthday.* Virginia Museum of Natural History Special Publication No. 16, Martinsville, VA.

TM wrote the manuscript, including naming and describing the new species. DVDS prepared all the figures. Both authors read and approved the final draft before the paper was submitted for publication.

Publication 7 (in preparation)
Mwabvu, T., Lamb, J., Slotow, R., Hamer, M., & Barraclough, D. Genetic divergence and relationships among selected African millipede genera (Diplopoda: Spirostreptida: Spirostreptidae).

The manuscript was written by TM. JL helped with the analysis of the data and, read and commented on the paper. MH, RS and DB were supervisors, they also reviewed the paper.

PREFACE

Millipedes are an ecologically important group of soil detritivores. Although abundant, millipedes are poorly known and difficult to identify. Their taxonomy is confusing, with many species in Africa as yet undiscovered and undescribed. The distributions of species are also poorly understood. Owing to poor dispersal ability, millipedes have high levels of endemism, making them vulnerable to habitat modification, and hence the urgency to describe millipede diversity and distribution patterns.

In addition, most existing classifications of arthropods are based on morphological characters. Some of these characters are not taxonomically informative, because they vary intraspecifically. Therefore, some classifications need to be re-evaluated by revising genera into monophyletic taxa, in addition, several new taxa need to be described.

The taxonomic study of African spirostreptid millipede genera presented here attempts to clarify the generic and specific limits of the taxa, improve taxonomic resolution and revise distribution data. The study should improve our fragmentary knowledge of millipede diversity, distribution patterns and processes/events that influence diversification.

This thesis is presented as a series of published papers. A general introduction forms the first chapter, followed by published papers which make up the results section. The papers are taxonomic revisions of the genera *Bicoxidens*, *Spirostreptus*, *Plagiotaphrus* and *Archispirostreptus*, as well as descriptions of new species from East Africa. The last paper assesses genetic divergence and cryptic diversity in some of the genera by comparing mitochondrial DNA gene sequences. The last chapter is a general discussion and conclusion.

The general introduction briefly introduces the terms taxonomy and systematic, and discusses species concepts. Furthermore, the introduction covers the diversity and ecological importance of millipedes. This section also discusses the threats to biodiversity caused by habitat alterations. The taxonomic problems among millipedes are identified, current trends in millipede taxonomic research are briefly described and useful taxonomic

characters are discussed. Lastly, the importance of taxonomic research is highlighted in light of the biodiversity crisis.

The taxonomic revision of *Bicoxidens* includes descriptions of three new species, an identification key to species, and a tentative phylogeny. An additional new species from northern Zimbabwe is described in a separate paper. In addition, factors that influence distribution patterns and levels of endemism are discussed.

The genus *Spirostreptus* is redefined and described in the third chapter. A new genus and a new species are described, and new distribution records are added. This revision demonstrates that diversity and distribution data of millipedes are incomplete.

Plagiotaphrus, which is probably the least known genus in the study, is revised to clarify generic boundaries and include new distribution records. The new distribution records suggest that the genus has a wider range than previously thought.

Archispirostreptus is the most widely distributed among the genera under review. Some species names are synonymised or removed from *Archispirostreptus*. The generic boundaries are re-defined resulting in splitting of the genus. A new genus, with three new species, is erected. Subtle intra-specific variations in genitalic morphology of some species suggest the existence of species complexes.

The publication on the spirostreptids of Taita Hills, Kenya, includes descriptions of new species and new distribution records of several taxa. The material was identified from unprocessed specimens in the Royal Museum of Central Africa, Belgium. This demonstrates that several taxa have not been described and that taxonomic research needs to increase.

The last manuscript looks at genetic divergence in the genera and phylogenetic relationships using mitochondrial 16S rRNA and CO1 gene sequences. Both genetic markers confirmed monophyly of the spirostreptids and the taxonomic validity of the genera, and suggest the presence of cryptic species in *Bicoxidens*.

The discussion and conclusion section explain the high levels of endemism and distribution patterns reported in this study. In addition, this section summarizes the challenges facing millipede taxonomists and conservationists, suggests areas that require urgent investigation, and recommends approaches to enhance millipede conservation.

ACKNOWLEDGEMENTS

I am indebted to my supervisors, Professor Rob Slotow, Professor Michelle Hamer and Dr David Barraclough. They are thanked for their support, guidance and encouragement, without which this work would not have been completed. Thank you

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I am also grateful to the Global Taxonomic Initiative, Belgium, for funding my research visits to the Africa Museum. The University of KwaZulu-Natal's Electron Microscope Unit (Westville Campus) and the Centre for Electron Microscopy (Pietermaritzburg Campus) are thanked for providing access to photographic equipment.

Finally, I also thank Professor H. Enghoff and Dr. D. Van den Spiegel, for their advice and guidance during my research visits to their institutions, Dr. R. Mackey for her comments on earlier drafts of two manuscripts, Alain Smith and Tarik Bodasing for assisting in mapping; Theshnie Naidoo for her patience and guidance in the molecular laboratory, Dr Sandi Willows-Munro for advice offered during the course of molecular work, and Prof. Jennifer Lamb for her assistance in analyzing molecular data and general guidance and encouragement.

ABSTRACT

Past taxonomic work on millipedes has been largely inaccurate and incomplete. It is important therefore that modern millipede systematics involves taxonomic revisions and biogeographic reviews of taxa, and phylogenetic analyses using new techniques and informative taxonomic characters (including gene sequences). The Afrotropical genera *Archispirostreptus* Silvestri 1895, *Bicoxidens* Attems 1928, *Plagiotaphrus* Attems 1914 and *Spirostreptus* Brandt 1833 belonging to the order Spirostreptida and family Spirostreptidae were identified as problematic taxa because of the ambiguity of their generic limits and their undetermined distributions and species richness. In this study, taxonomic revisions of the four genera were undertaken using morphological characters, mainly relating to the male genitalia. Furthermore, genetic divergence of *Archispirostreptus, Bicoxidens, Orthoporoides* Krabbe 1982, *Doratogonus* Attems 1914, *Plagiotaphrus, Cacuminostreptus* Mwabvu 2010 and *Spirostreptus*, and intra-specific variation in *Bicoxidens flavicollis* Attems 1928, were assessed. In addition, phylogenetic relationships among the genera were inferred by analyzing sequences of the mitochondrial 16S rRNA and cytochrome *c* oxidase 1 genes. Bayesian, maximum parsimony and neighbour-joining analyses were performed on each dataset to determine genetic distances and phylogenetic relationships among the taxa.

In addition to defining the generic boundaries of these taxa using genitalic morphology and reporting new distribution records, two new genera (*Namibostreptus* and *Cacuminostreptus*), three new species of *Cacuminostreptus*, five new species of *Bicoxidens*, a new species of *Spirostreptus*, and three new species (*Bucinogonus aviceps, Lophostreptus minimus* and *Tibiozus vulgaris*) from Taita Hills, Kenya, were described. These new taxa illustrated that in millipedes, the number of known taxa increased mostly due to discoveries in previously unsurveyed biomes. Furthermore, unlike non-genitalic characters such as body size, genitalic morphology provided characters of taxonomic value for diagnosing taxa.

Based on the gene sequences of *Archispirostreptus, Bicoxidens, Orthoporoides, Doratogonus, Plagiotaphrus, Cacuminostreptus* and *Spirostreptus*, the order Spirostreptida is monophyletic (Bayesian posterior probability 1.00). High genetic distances (> 20 %)

supported the taxonomic validity of the genera, including the recently described *Cacuminostreptus*. In addition, sequence differences between genera are congruent with classifications that are based on genitalic morphology. However, the high sequence divergence values also suggest slow genitalic evolution relative to molecular evolution. This supports the notion that millipede gonopod morphology underestimates species richness. Within the colour-polymorphic *B. flavicollis,* high sequence divergence among populations (16S rRNA = 6 %; CO1 = 19.1 %) suggests the presence of cryptic species. Although taxon sampling was limited, these results are largely concordant with morphological evidence. Because the circumscriptions are corroborated by different lines of evidence, they are considered reliable and present data of greater predictive value. Findings suggest that sequence data can be used in integrative taxonomy of spirostreptids to identify cryptic diversity and to re-assess classifications based on genitalic morphology. However, until taxon sampling improves and a large database of DNA sequences is established, comparative morphology will continue to be the dominant tool in millipede taxonomy.

The genera *Bicoxidens*, *Plagiotaphrus* and *Spirostreptus* are endemic to Southern Africa, while *Archispirostreptus* occurs throughout Africa and in the Arabian Peninsula. Although the genera are widespread, many species in woodland and montane vegetation are endemic. This suggests that vegetation types and climatic factors influence the distribution patterns of millipedes and demonstrate that most species have narrow distributions. Furthermore, distribution ranges differ among taxa, with the small-bodied species having more restricted distributions.

The taxonomic revisions of *Bicoxidens*, *Archispirostreptus*, *Plagiotaphrus* and *Spirostreptus* have illustrated that millipede diversity is underestimated, that generic boundaries need to be re-examined in other genera, and that biogeographical data on most taxa are incomplete. Therefore, future taxonomic research on millipedes should focus on sampling in unsurveyed localities, revising the taxonomy and distributions of more genera, increasing the pace of descriptions of new taxa and DNA sequencing, and producing identification keys to the species. This will assist to produce stable classifications which would provide reliable data for other disciplines, including biodiversity monitoring and conservation.

LIST OF PUBLICATIONS IN THE THESIS

Publication 1
Mwabvu, T., Hamer, M., & Slotow, R. (2007). A taxonomic review of the southern African millipede genus, *Bicoxidens* Attems, 1928 (Diplopoda: Spirostreptida: Spirostreptidae), with the description of three new species and a tentative phylogeny. *Zootaxa* 1452: 1–23.

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Publication 6
Mwabvu, T., Hamer, M., Slotow, R. & Barraclough, D. (2010). A revision of the taxonomy and distribution of *Archispirostreptus* Silvestri 1895 (Diplopoda, Spirostreptida, Spirostreptidae), and description of a new spirostreptid genus with three new species. *Zootaxa* 2567: 1–49.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

The definition of taxonomy and its position in relation to systematics is an on-going debate among biologists (see Wheeler, 2008; Enghoff, 2009). Many workers, including Wheeler, consider systematics a sub-discipline of a broader field of taxonomy; others look at taxonomy as a small part of systematics (Quicke, 1993). Many definitions of taxonomy have been proposed, in many cases the terms taxonomy and systematics have been used synonymously (Quicke, 1993; Wheeler, 2008). Enghoff (2009) listed seven activities associated with taxonomy, among these are classifying, identifying, comparing, describing and naming of taxa. In this thesis, in order to avoid ambiguity, taxonomy is defined as a science of identifying, naming and classifying organisms, and is viewed as an important part of systematics, a discipline in which the evolutionary relationships (phylogeny) among organisms are determined (Quicke, 1993; Dayrat, 2005). As such, taxonomies are based on evolutionary principles (De Queiroz & Gauthier, 1992).

Different sources of taxonomic data, including morphology, ecology and genetics, are used in taxonomy (Lee, 2004). According to Sadava *et al.* (2008), morphological data based on the shape, size and presence of body attributes have been the basis for taxonomy in most organisms. Although recent advances in DNA sequencing have resulted in increased use of molecular data in systematics, morphology is still a major source of data for describing taxa (Schlick-Steiner *et al.*, 2007; Lefébure *et al.*, 2006), particularly in poorly studied groups such as invertebrates (see Lefébure *et al.*, 2006).

The classification of organisms is based on a hierarchical system, which begins with species (the smallest and most exclusive taxonomic unit), above which there are mandatory categories (kingdom, phylum, class, order, family and genus) (De Queiroz & Gauthier, 1992). All known species have to be assigned to a taxon in each of these categories, for example related species would be placed into the same genus (De Queiroz & Gauthier, 1992). Although the term species is widely used in biology, what constitute a species is still debatable. This has been exacerbated by the drive to use DNA sequences to delimit species (see Lee, 2004; Lefébure *et al.*, 2006), despite weak correlation between genetic divergence and reproductive isolation (Lee, 2004; Adams *et al.*, 2009), and lack of consensus on the genes (Lee, 2004) and divergence thresholds to use in determining species boundaries (see Lefébure *et al.*, 2006; Wiemer & Fiedler, 2007; Meier *et al.*, 2006). Bond and Sierwald (2002) also reported that definition of species based only on gene sequences or morphology could be misleading.

Despite its importance as the currency in conservation (Agapow *et al.*, 2004) and its wide use in biological disciplines (see Agapow *et al.*, 2004; Balakrishnan, 2005; Padial & De la Riva, 2006; Pfenninger *et al.*, 2006), there is substantial contention about the definition of species (Gaston & Spicer, 1998; Barton, 2001; Wiens, 2004). As a result, more than 20 species concepts have been proposed (Hey, 2001; Agapow *et al.*, 2004), among these are the biological, morphological and phylogenetic species concepts. The biological species concept is based on reproductive isolation caused by the presence of biological barriers (Wiens, 2004; Agapow *et al.*, 2004). The phylogenetic species concept, which identifies more species than traditional concepts (Gaston & Spicer, 1998), describes a species as a group of individuals having common ancestry, and forming a single branch on a phylogenetic tree (Agapow *et al.*, 2004; Wiens, 2004). Finally, the morphological species concept describes species using heritable body and structural characteristics (Gaston & Spicer, 1998), for example, male genitalia (Funk, 1999). Descriptions of most known species are based on the morphological characters (Gaston & Spicer, 1998; Lefébure *et al.*, 2006; Padial *et al.*, 2010).

The choice of species concept in taxonomic research is critical to address the research questions adequately, because it could have implications for how organisms are assigned to taxonomic categories (Lee, 2004). Depending on the species concept applied, species may be "split", thus increasing the number of species, or "lumped" (Agapow *et al.*, 2004; De Queiroz, 2007). Generally, using the phylogenetic species concept increases the number of recognised species (Agapow *et al.*, 2004). In this study, the morphological and phylogenetic species concepts are probably the most appropriate, because the former represents the widely used traditional approach, and the latter, the new and sometimes complementary approach. It is important to note that morphology-based classifications of organisms may match their phylogeny (Padial & De la Riva, 2010), however, sometimes the two are discordant (see Pfenninger *et al.*, 2006; Vogler & Monaghan, 2007). How species are delineated based on the different species concepts has implications for the accuracy of species boundaries, which in turn is critical in addressing evolutionary, conservation and biogeographic questions (Dayrat, 2005).

The biodiversity crisis, largely due to the modification and destruction of natural habitats, has resulted in many species facing extinction, most of them before they have been classified and described (Quicke, 1993). As a result, efforts are being made to describe taxa before they become extinct. Besides the need to describe thousands of newly discovered species each year (Padial & De la Riva, 2006), taxonomic revisions are also required because many taxa are incorrectly classified or grouped with unrelated species (see Dayrat, 2005; Meier, 2008). Therefore, taxonomic research is critical in re-assessing earlier classifications, in order to ascertain the taxonomic validity of taxa, for identifying and describing new species, and for determining morphological and genetic variation, and evolutionary relationships among taxa using modern techniques (Meier, 2008). Furthermore, reliable species lists and distribution data are presented and keys to species identification produced. All these outcomes of careful taxonomic study are immediately and strongly applicable to conservation planning and management (Padial & De la Riva, 2006).

1.2 Millipedes and other invertebrates

The most numerous, diverse and specialized animals in ecological systems are invertebrates (Campbell *et al.*, 2008; Freeman, 2005; New, 1995). They make up 95 % of known animals and occupy most habitats (Campbell *et al.*, 2008). Yet, despite their high abundance and high species richness, invertebrates are under-studied. Most invertebrates remain undescribed; the ecology and distributions of described groups are incompletely known (New, 1995), and their taxonomy is confusing.

In recent years, the ecological importance of invertebrates in natural ecosystems has being increasingly recognized. Some invertebrates form an important link in ecological systems by facilitating decomposition of organic matter. In addition, the burrowing activity of some groups of invertebrates improves soil structure (New, 1995). Soil fertility and nutrient cycling, as well as the physical properties of the soil such as aeration, are also enhanced (Lee, 1991; Dangerfield & Telford, 1991).

As with other organisms, many invertebrate groups are probably facing extinction because of increasing habitat modification, anthropogenic habitat loss and habitat fragmentation (see Hamer, 2000; Hamer & Slotow, 2009). Thus far, the viability of populations of several invertebrate species (Freeman, 2005), including millipedes (Hamer & Slotow, 2009) and indigenous South African earthworm species, which have a narrow distribution and occur only in forests (Horn *et al.*, 2007), have been threatened. As such, conservation of invertebrates needs to be prioritised (Hamer & Slotow, 2002). However, the knowledge gaps that exist in taxonomy, ecology and geographical distribution of invertebrates (including millipedes), are impediments to their conservation, and to our understanding of their role in ecosystems (see Hamer & Slotow, 2009).

In some terrestrial ecosystems, millipedes are a major part of the soil macrofauna (Bueno-Villegas *et al.*, 2008; Crawford, 1992), in terms of the numbers of species and biomass (Dangerfield, 1990). In tropical environments, high densities of large-bodied millipedes emerge from the soil during the rainfall season. Dangerfield and Telford (1989) reported population densities of up to 15 individuals per square meter in Miombo woodland. As detritivores, not only do millipedes enhance organic matter breakdown (Bond & Sierwald, 2002; Sierwald & Bond, 2007), but they also mix organic matter with upper soil layers (Edwards *et al.*, 1970). Furthermore, millipedes have characteristically high ingestion rates, low assimilation efficiencies and high egestion rates, all of which positively modify soil structure and characteristics (Dangerfield & Telford, 1991). In Miombo woodland, millipedes consume an estimated 30.6 % of annual litter fall (Dangerfield & Telford, 1989) and they produce up to 21 faecal pellets per day per individual (Mwabvu, *per. obs.*). The high densities of surface active millipedes during the rainfall season, their large body size relative to other soil invertebrates and relatively high faecal pellet production, suggest a much greater importance of these detritivores in the tropics than previously thought (Dangerfield & Telford, 1989).

Although several millipede species co-occur in the savanna biome in Southern Africa (Mwabvu *et al.*, 2009), millipedes typically have low vagility, high levels of endemism (Hopkin & Read, 1992; Hamer, 2000; Hamer & Slotow, 2002; Marek & Bond, 2006; Druce *et al.*, 2007; Hamer & Slotow, 2009) and narrow geographical distributions (Sierwald & Bond, 2007). Millipedes are vulnerable to desiccation, as their spiracles cannot close completely, thus they tend to occur in patchy, moist micro-habitats, and do not disperse over long distances (Hopkin & Read, 1992). Consequently, many millipede species are geographically isolated and occur in small areas (Hopkin & Read, 1992; Druce *et al.*, 2007). Their specific habitat requirements and poor dispersal ability make millipedes particularly vulnerable to habitat disturbance and extinction (Hamer & Slotow, 2000; 2002). Thus, millipedes can be potential indicators of ecosystem functioning and environmental quality (see Hamer, 2000; Hamer & Slotow, 2002).

Despite being conspicuous, important in ecological processes, diverse, range-restricted, and habitat-specific, millipedes remain under-utilised in biodiversity and conservation studies because of the lack of data on their diversity and distribution patterns (Hamer & Slotow, 2000). In Southern Africa, the paucity of taxonomic and distribution data has also been reported in other invertebrate groups, such as earthworms (Horn *et al.*, 2007) and spiders (Foord *et al.*, 2008). Compared to other arthropods in the tropics, an understanding of millipede diversity is incomplete (Sierwald & Bond, 2007), largely because of the scarcity of millipede taxonomists (Hamer, 1997). Consequently, the number of new species described annually has decreased in recent years (Sierwald & Bond, 2007). Meanwhile, many species are probably facing extinction because of habitat destruction (Hopkin & Read, 1992).

1.3 Spirostreptid millipede taxonomy, phylogeny and distribution

Approximately 12 000 millipede species (Sierwald & Bond, 2007; Marek & Bond, 2007; Bueno-Villegas *et al.*, 2008) of an estimated 80 000 species (Sierwald & Bond, 2007) have been described. Millipedes occur on all the continents except Antarctica, and are speciose in tropical and temperate forests (Bueno-Villegas *et al.*, 2008). Currently, 2 947 genera (Sierwald & Bond, 2007) are grouped into 145 families in 16 orders (Sierwald & Bond, 2007; Bueno-Villegas *et al.*, 2008). In Southern Africa, 552 species belonging to 71 genera have been described (Hamer, 2000).

Millipede orders, including Spirostreptida, are taxonomically stable and they are considered monophyletic (Sierwald & Bond, 2007). Phylogenies of polydesmid genera using morphological and molecular characters have been studied (Bueno-Villegas *et al.*, 2008; Marek & Bond, 2006; Marek & Bond, 2007). With respect to the Spirostreptidae, Hamer and Slotow's (2000) phylogeny of *Doratogonus* Attems 1914 species, which was not resolved, and a tentative phylogeny of *Bicoxidens* Attems 1928 species (Mwabvu *et al.*, 2007), have been published. Both phylogenies were based on morphological data, mainly based on genitalic characters. Phylogenetic studies using molecular data have not been undertaken in spirostreptid genera. The reason for this, amongst many others, could be because many genera have not been revised (Hamer, 1999), and because few spirostreptids have had their DNA sequenced.

The Order Spirostreptida, which is the second largest after the Polydesmida (Hoffman *et al.*, 1996), contains four diverse families (Spirostreptidae, Harpagophoridae, Odontopygidae and Julomorphidae) of relatively large, cylindrical and worm-like millipedes that have between 40 and 70 body rings (Hamer, 1999). The family Spirostreptidae contains the largest-bodied millipedes in the order Spirostreptida, which are differentiated from the other three families by the absence of a dorsal spine on the anal valves (found in the Odontopygidae), the absence of a dorsal spine on the preanal ring (found in some Harpagophoridae), or the lack of a reduced first pair of male legs (found in the Julomorphidae) (Hamer, 1999).

The last published taxonomic account of the family Spirostreptidae by Krabbe (1982) listed 52 African genera. The family contains the understudied, large-bodied and common afrotropical spirostreptid genera, *Archispirostreptus* Silvestri 1895, *Plagiotaphrus* Attems 1914, *Spirostreptus* Brandt 1833 and *Bicoxidens*, whose taxonomy and distribution have not been reviewed since Krabbe (1982). The first three genera are morphologically similar, in terms of body colour and body size range, making it difficult to identify them without specialist knowledge (see Enghoff, 1992; Mwabvu *et al.*, 2009a; Mwabvu *et al.*, 2009b; Mwabvu *et al.*, 2010). Apart from *Archispirostreptus*, which is widely distributed in Africa (Mwabvu *et al.*, 2010), the other three genera occur in Southern Africa only (Mwabvu *et al.*, 2009a; Mwabvu *et al.*, 2009b). Krabbe (1982) listed 15 species and five subspecies of *Archispirostreptus*, six species of *Bicoxidens*, six species of *Spirostreptus* (previously *Triaenostreptus* Attems 1914) and three species of *Plagiotaphrus*. Based on my observations, the definitions of these genera are ambiguous and questionable, the validity of some species is doubtful and many species have not been described. These observations are consistent with Hamer's (2000; 2009) conclusions on *Doratogonus*, which is the most common and speciose spirostreptid millipede genus in Southern Africa.

The actual geographic distributions of many millipede species are unknown because identifications are difficult and distribution data are incomplete (Hamer, 2000). Millipedes in un-surveyed localities or in unprocessed museum collections could reveal undescribed taxa or new distribution records (Sierwald & Bond, 2007). According to Hamer and Slotow (2002) the paucity of data on the number of species and distribution patterns of millipedes hinders conservation efforts. Only after extensive sampling and after taxonomic reviews of genera are undertaken, will the distribution patterns of millipedes, and the factors that influence the patterns, be understood. Given these gaps in knowledge and that taxonomy provides data for biogeographical studies and conservation planning, taxonomic research on millipedes is critical.

1.4 History of taxonomic research in millipedes

Among the taxonomists who contributed immensely to the taxonomic knowledge of millipedes worldwide are Attems, Cook, Karsch, Silvestri, Koch, Brandt, Verhoeff, Chamberlin, Pocock, Schubart, De Saussure, Porat, Brölemann, Karsch (Sierwald & Bond, 2007), Hoffman, Lawrence, Kraus and Peters (Krabbe, 1982). According to Sierwald & Bond (2007), Attems, Chamberlin and Verhoeff each described more than 1 000 millipede species. Other notable contributions were by Silvestri who described 684 species, and Carl, Schubart, Brölemann, Loomis and Pocock who each described between 300 and 400 species (Sierwald & Bond, 2007).

The spirostreptid fauna of Southern Africa was extensively studied pre-1970 by Attems, Lawrence and Schubart. More recently, Dangerfield and Telford (1989; 1991) studied millipede ecology. Hamer (2000) revised the taxonomy of *Doratogonus* and described 15 new species, presented a checklist of Southern African millipedes (Hamer, 1998) and a key to the identification of Southern Africa genera (Hamer, 1999). Despite these contributions, millipede taxonomy remains problematic and is a huge challenge to the small group of taxonomists (Sierwald & Bond, 2007) working on African millipedes.

1.5 Taxonomic problems in millipedes

Only 12 % of existing millipede diversity has so far been described (Hoffman, 1993; Sierwald & Bond, 2007) and several taxonomic problems have been identified. Hence, taxonomic research on millipedes needs to increase and should focus on taxonomic descriptions of taxa, specifically genus and species diagnoses, inferring phylogenetic relationships and determining distribution patterns of the taxa.

The classification of millipedes in general has many nomenclatorial problems at different taxonomic levels (Hoffman, 1991). Some genera are poorly defined and not monophyletic (Hamer, 1999), and very little is known about millipede phylogeny (Sierwald & Bond, 2007). Hamer (2000) reported that problems in millipede taxonomy are a result of the choice of morphological characters used. Good taxonomic characters should diagnose taxa consistently and the characters should not be influenced by environmental conditions (Krabbe, 1979). Traits that are plastic, such as body size for example, which varies intra-specifically in the spirostreptids, are taxonomically uninformative (Enghoff, 1992). Furthermore, descriptions of some species were based on few specimens or female specimens only, and other descriptions did not compare male genitalia among described taxa, which resulted in isolated descriptions and erection of invalid taxa (Hamer, 2000). As a consequence, many taxa have been misidentified (Hamer, 2000) and many of the taxonomic and biogeographic data are incomplete (Redman & Hamer, 2003). The lack of expertise in collecting, identifying and publishing results (Hamer, 1997; Bond & Sierwald, 2002) compound these problems. Based on this evidence, taxonomic revisions, which are a major part of modern millipede taxonomy (Sierwald & Bond, 2007) and which lead to identification of monophyletic taxa (Smith, 1994), should be the focus of taxonomic research.

Taxonomic revisions of genera should also be undertaken using informative characters. These taxonomic reviews, such as that of *Doratogonus* (Hamer, 2000), not only identify taxonomically useful characters and define taxa boundaries, but also update data on species composition and distribution patterns, provide keys to species identification and accumulate data that can be used in conservation planning. The importance of taxonomic and distribution data to conservation was highlighted in the assessment of *Doratogonus* which lead to 14 species being identified as facing extinction (Hamer, 2009).

For African millipedes specifically, the problems in taxonomy were illustrated in Hamer's (2000) review of the diverse genus *Doratogonus*. In brief, Hamer (2000) indicated that accurate distribution data are scarce and that many species were synonyms or undescribed. These problems are compounded by post-colonial name changes to several regions and towns in Africa, that make the actual identification of localities from literature or specimen labels problematic. In addition, some type specimens on which species descriptions are based, are missing from museum collections. Furthermore, political strife in many countries has rendered several regions inaccessible to taxonomists.

1.6 Taxonomic characters

According to Winston (1999) taxonomic characters can be morphological, genetic, chemical, physiological, behavioural, reproductive or ecological. However, Quicke (1993) cautioned against assuming that all such characters are of taxonomic value, because their expression may be influenced by age, nutritional status or diet and the organism's health or stage in its breeding cycle. In millipedes, morphological features are the primary sources of taxonomic characters and species descriptions are based on morphology of body characters and male genitalia (Hamer, 2000). Recent advances in molecular techniques have made DNA sequences an additional source of taxonomic characters. For example, DNA sequences have been used to reassess morphology-based classifications in other non-volant invertebrate taxa, such as annelids (Kupriyanova *et al.*, 2006), polydesmid millipedes (Marek & Bond, 2007) and spirobolid millipedes (Bond & Sierwald, 2002).

Taxonomic characters need to be defined unequivocally and should be homologous (Pfenninger *et al.*, 2006; see Lee, 2004; Dayrat, 2005; Meier, 2008). This is of particular importance in millipedes because external attributes appear to be of limited taxonomic value because they are often correlated with the habitats of the animal, thus making them unreliable indices of taxon validity (Krabbe, 1979). Although some external characters are plastic and taxonomically uninformative, in the spirostreptid millipedes the homology of male gonopod features is not contentious and, therefore, gonopods are comparable between species (Hoffman, 1971).

External body features have also been employed as secondary taxonomic characters in millipedes (Hamer, 2000). These characters include the shapes of prefemoral processes of the first pair of legs of males, the shape of the collum, the body colour, number of body rings and the size of the body (Hamer, 2000). Although body size can be used to distinguish taxa at higher taxon level, its usefulness appears to vary among taxa (Enghoff, 1992). Generally, size is not a reliable taxonomic character in spirostreptid millipedes because it is influenced by ancestry, age, sex, food quality and quantity, altitude, latitude, habitat and coexisting competitors (Enghoff, 1992). Habitat type influences body size in millipedes because of the size-desiccation resistance correlation; for example, specimens of *Archispirostreptus tumuliporus judaicus* (Attems 1926) from arid areas have larger and a greater number of body rings than those of the same stadia from different habitats (Enghoff, 1992). Enghoff (1992) also reported that two coexisting species are likely to differ in size and exploit different micro-habitats to reduce direct competition. Thus, size can distinguish sympatric species, as in *Anadenobolus* spp. (Bond & Sierwald, 2002). Although closely related species may have similar body size ranges, Enghoff (1992) cautioned against using body size as a taxonomic character because of size polymorphism and convergence in most invertebrates. However, because the addition of new body rings is terminated after reaching maturity, the number and diameter of body rings are potentially useful taxonomic characters in spirostreptid millipedes (Enghoff, 1992).

1.6.1 Genitalic morphology

Male genitalia/gonopods of arthropods are assumed to be fast evolving and diverging (Svensson *et al.*, 2004; Jacob *et al.*, 2004; Taylor & Knouft, 2006; Soto *et al.*, 2007). Thus, these structures have been used extensively in taxonomy as the main source of diagnostic characters (Bond *et al.*, 2003; Jacob *et al.*, 2004; Marek & Bond, 2006; Sierwald & Bond, 2007; Soto *et al.*, 2007) and form the basis of hypothesized phylogenetic relationships. Because they do not vary widely within species (Huber *et al.*, 2005), male gonopods are considered reliable indices of taxon validity (Hamer, 2000). Although several hypotheses have been reported to explain the evolution of genital morphology, two have considerable support. The lock and key hypothesis states that the evolution of male genitalia is driven by selection to fit into female genitalia (Huber *et al.*, 2005; Soto *et al.*, 2007), while the sexual selection hypothesis explains the rapid evolution of male genitalia compared to other traits is driven by selection for increased reproductive success (Soto *et al.*, 2007).

Male gonopods have been used in millipede taxonomy for more than 100 years (Krabbe, 1979). They are derived from the anterior pair of legs of the 7th body ring, the posterior pair being lost in the adult stage (Hamer, 1999). The gonopod has two main parts, the telocoxite and the telopodite, which are useful in distinguishing taxa (Hamer, 1999). While the proximal half of the telopodite is enclosed by the enlarged and variously modified coxite, the distal part is free and emerges from the coxite anteriorly (Hamer, 1999). Hoffman (1971; 1991) considered male genitalia to be consistent indicators of millipede identity because they are homologous and, therefore, comparable between species. However, because of morphological stasis, when morphological change does not occur because of stabilizing selection (Bickford *et al.*, 2006, Adams *et al.*, 2009), speciation may occur in the absence of morphological divergence in male genitalia (Bond *et al.*, 2003), especially in sibling species (Winston, 1999). Hence, using only gonopod morphological characters to diagnose or distinguish millipedes could result in fewer taxa being recognized (Bond & Sierwald, 2002).

Bond and Sierwald (2002) observed that genitalic morphology was too inclusive and failed to separate genetically distinct millipede species in the *Anadenobolus excisus* complex. Bond *et al.* (2003) also reported speciation in the absence of clear morphological divergence in male genitalia. That being the case, groups that were differentiated using gonopod morphology need to be re-evaluated against other character suites, particularly molecular characters, because genitalic morphology alone could underestimate diversity (Sierwald & Bond, 2007; Padial *et al.*, 2010).

Although recent advances in molecular techniques have resulted in increased use of DNA sequences in species identification and estimating phylogenies (Meier, 2008), morphology-based taxonomy is still extensively used in delimiting taxa (Schlick-Steiner *et al.*, 2007). However, as molecular sequencing techniques become increasingly available, more taxonomists are advocating exclusive use of DNA in alpha taxonomy (Tautz *et al.*, 2003; Hebert *et al.*, 2003; Hebert *et al.*, 2004).

1.6.2 DNA in taxonomy

In the past, the requirement of fresh biological material limited the use of DNA in taxonomy (Quicke, 1993). However, advances in polymerase chain reaction and gene cloning technologies allow extraction of usable DNA from old specimens (Quicke, 1993). As a result, using DNA in species identification has increased in recent years (see Bond & Sierwald, 2002;

Tautz *et al.*, 2003; Hebert *et al.*, 2004; Brower, 2006; Bickford *et al.*, 2006; Vogler & Monaghan, 2006; Hickerson *et al.*, 2006; Hajibabaei *et al.*, 2007; Wiemers & Fiedler, 2007; Van Velzen *et al.*, 2007; Burns *et al.*, 2008), and has helped to identify cryptic species and improve taxonomic resolution (Will *et al.*, 2005).

DNA sequence data can be used in taxonomy in two different but not exclusive ways; DNA barcoding and DNA taxonomy. DNA barcoding uses a short section of DNA to identify species (Dasmahapatra & Mallet, 2006; Vogler & Monaghan, 2006; Winston, 1999; Will & Rubinoff, 2004) by sequencing a gene from an unknown specimen (Tautz *et al.*, 2003; Hebert *et al.*, 2003; Moritz & Cicero, 2004; Winker, 2009; Van Velzen *et al.*, 2007), after which the sequence is compared to reference sequences in the database (Wiemers & Fiedler, 2007). The mitochondrial *cytochrome c oxidase* Subunit 1 (CO1) gene is widely considered a suitable marker (Hebert *et al.*, 2003; Hajibabaei *et al.*, 2007). This system was proposed as a rapid method for identifying and discovering species (Hebert *et al.*, 2003; Blaxter, 2004; Hebert *et al.*, 2004; Gregory, 2005; DeSalle *et al.*, 2005; Rubinoff *et al.*, 2006; Vogler & Monaghan, 2006; Wiemers & Fiedler, 2007). Currently, DNA barcoding is considered better suited for distinguishing taxa than determining species boundaries (Will & Rubinoff, 2004). In DNA taxonomy, sequences that are not in databases are highlighted for taxonomic study, leading to definition of taxon boundaries (see Vogler & Monaghan, 2006). Thus, DNA barcoding would identify unknown groups prior to taxonomic descriptions (see Moritz & Cicero, 2004; DeSalle *et al.*, 2005).

Potentially, DNA sequences complement other sources of data in identifying cryptic diversity (Rubinoff *et al.*, 2006; Gregory, 2005; Pfenninger *et al.*, 2007) and resolving taxonomic problems that other approaches fail to solve (Pfenninger *et al.*, 2007), particularly in groups such as spirostreptid millipedes that are considered taxonomically difficult (Sierwald & Bond, 2007). Therefore, several authors advocate using DNA characters (Tautz *et al.*, 2003; Bond *et al.*, 2003), more so because sequencing techniques are becoming available to more taxonomists, and because there are numerous DNA characters that can be used in phylogenetic analysis and delimiting taxa (Hillis, 1987).

The use of mitochondrial DNA sequences to complement morphology-based taxonomy (see Wahlberg & Nylin, 2003; Schlick-Steiner *et al.*, 2006) is likely to reduce misidentification of species, increase identification of cryptic taxa, and result in faster and reliable identification (Dayrat, 2005; Dasmahapatra & Mallet, 2006). Using mitochondrial DNA also allows for the testing of interesting and better phylogenetic hypotheses, and provides data of greater predictive value (Marek & Bond, 2007; Hajibabaei *et al.*, 2007). Although they have not been used in taxonomic studies of spirostreptid millipedes, mitochondrial gene sequences have been employed in taxonomic research of other invertebrates. For example, the mitochondrial CO1 gene sequences revealed cryptic species in a butterfly genus *Cymothoe* (van Velzen *et al.*, 2007) and was used to infer phylogeny in mites and ticks (Cruickshank, 2002), and the spider genus *Apomastus* (Bond, 2004). In addition, the mitochondrial 16S rRNA gene sequences also identified cryptic species in a spirobolid millipede *Anadenobolus excisus* (Bond & Sierwald, 2002). At present, only Edgecombe and Giribet (2004) are known to have used both COI and 16S rRNA genes to assess the phylogeny of centipedes, which are a sister taxon of millipedes.

The use of DNA sequences in taxonomy is an area of intense debate (Tauz *et al.*, 2003; Will & Rubinoff, 2004; DeSalle *et al.*, 2005; Hickerson *et al.*, 2006; Wiemers & Fiedler, 2007). Critics of DNA in taxonomy have identified several disadvantages of using only DNA sequences. Among the disadvantages are the lack of standardised sequencing (Moritz & Cicero, 2004), the use of small and potentially insufficient sections of a gene sequence, the lack of broader sampling which underestimates intra-specific variation (Dasmahapatra & Mallet, 2006; Rubinoff *et al.*, 2006; Brower, 2006) and the limited understanding of biodiversity (Will & Rubinoff, 2004). In addition, Van Velzen *et al.* (2007) questioned the accuracy of taxon diagnosis when the separation of intra-specific and interspecific divergence is not consistent. Will and Rubinoff (2004) consider the determination of the levels of sequence differences that define taxa as arbitrary. Additionally, because of the limited number of nucleotides, there is greater likelihood of homoplasy (mainly reversals) occurring in nucleotide sequences than in morphological characters (Fitch, 1997; Simmons, 2000). Furthermore, DNA sequences may fail to distinguish morphologically distinct species which have recently diverged (Pfenninger *et al.*, 2007), as in the cichlid fish in Lake Victoria (Tautz *et al.*, 2003). Despite these shortcomings, it is likely that using multiple gene sequences rather than single gene sequences to separate closely related taxa and morphologically indistinct species (Mallet & Willmott, 2003; Vogler & Monaghan, 2006) would increase taxonomic stability and resolution.

1.6.3 Assessment of taxonomic characters

Although morphological data collection is time consuming and requires expertise (see Bond, 2004), these data give more information about the organism than the limited set of sequenced genes (Wahlberg & Nylin, 2003). However, morphology, such as the shapes of structures, is associated with intra-specific variation if the shapes of the structures are correlated to their function. As a result, such structures could be taxonomically unreliable. Apart from the additional complication of phenotypic plasticity, morphology-based taxonomy is limited by failure to detect cryptic diversity (see Pfenninger *et al.*, 2006) and reliance on one life stage of an organism to diagnose taxa (Bond, 2004). In addition, besides the low character/taxon ratio in morphology-based taxonomy, some morphological characters are ambiguous and not independent (Scotland *et al.*, 2003) to estimate phylogenies reliably. More importantly, the definition and coding of non-discrete morphological characters by taxonomists are often unclear or subjective (Scotland *et al.*, 2003), leading to biased comparisons and resulting in inaccurate phylogenies. According to Scotland *et al.* (2003), such ambiguities are not found in nucleotides because the unit of comparison occurs in all taxa. However, because morphological characters can have potentially many character states, homoplasy is not a serious problem as in molecular characters, which have a limited number of character states (Smith, 1994).

Among the problems of using only DNA sequences in taxonomy, are the facts that sequenced genes constitute a small fraction of an organism's genome, that sequences which diverge by less than 5 % are considered conspecific in some groups and that sequences do not provide additional biological information (Lipscomb *et al.*, 2003) compared to when species are described using morphological, ecological and behavioural characters (Hillis, 1987). In addition, DNA may fail to diagnose recently diverged taxa (Pfenninger *et al.*, 2006) because morphologically distinct species could have similar CO1 sequences (Wiemer & Fiedler, 2007).

Although DNA sequences complement morphological data (Mallet & Willmott, 2003) by identifying cryptic diversity (see Bond, 2004), sequencing technology may be unavailable in developing countries (which coincidentally have the most biodiversity), because of the prohibitive costs of setting up laboratories and the shortage of expertise (Seberg *et al.*, 2003). However, it takes a relatively shorter time to master molecular techniques than morphology-based methods (Bond, 2004).

With increasing use of DNA taxonomy as an identification tool, many biologists advocate an integrative approach using all the available evidence in species discovery and distinguishing species (Will & Rubinoff, 2004; Gregory, 2005; Dayrat, 2005; Brower, 2006; Schlick-Steiner *et al.*, 2006; Dasmahapatra & Mallet, 2006; Bickford *et al.*, 2006; Wiemers & Fiedler, 2007; Winker, 2009; Padial *et al.*, 2010). Phylogenetic analyses which combine morphological and molecular (mitochondrial and nuclear gene sequences) datasets produce comparatively more stable and resolved phylogenies, than those that are analysed separately

(Wahlberg & Nylin, 2003). Given the disadvantages of using one character source in millipede taxonomy, the integrative approach should produce reliable circumscriptions, reduce misdiagnosis or misidentification of taxa, and provide reliable data for use in conservation planning and other fields. Thus using all the available data is not only going to improve taxonomic resolution but also make taxonomic conclusions and conservation decisions non-arbitrary.

1.7 Conclusion

The increasing human population and associated demand for land have increased pressure on natural environments and threatened survival of many species, particularly endemics, which may be on the brink of extinction (Hamer, 2009). Because of the threats to biodiversity due to habitat loss (Hamer & Slotow, 2009), it is essential that surveys and taxonomic research are conducted to establish species diversity and distribution patterns. The number of millipede species recorded in Southern Africa is expected to increase substantially once more localities are sampled, existing and new material studied, and the genera are revised (Hamer, 1997).

Using genital morphology and DNA sequence data in taxonomy should reduce misdiagnoses and misidentifications of taxa, and provide reliable circumscriptions (see Dayrat, 2005; Padial *et al.*, 2010)). Furthermore, revising genera and describing new species should be prioritised because the results of this are of more than academic interest. Accurate definitions of taxa have far reaching implications for biogeographic interpretations, phylogenetic conclusions and biodiversity conservation (see Hamer & Slotow, 2002). The role of phylogenies in conservation is critical because they show relationships between taxa/populations, thus if lineages that are threatened with extinction are identified they could be targeted for conservation. In addition, events or processes that drive diversification could be identified and studied, and the localities that have high levels of unique taxa should be protected.

After Hamer's (2000) taxonomic revision of *Doratogonus*, the other common Southern African spirostreptid genera *Bicoxidens*, *Spirostreptus, Plagiotaphrus* and *Archispirostreptus,* were identified as requiring revision because they have nomenclatural problems. Furthermore, not only are *Bicoxidens*, *Spirostreptus* and *Plagiotaphrus* endemic to Southern Africa, several species within these genera have not been described and their distribution patterns and phylogenetic relationships are poorly understood. Additionally, more reliable taxonomic and distribution data that can be used in biodiversity conservation planning for millipedes are needed. As such, taxonomic revisions of the genera using informative morphological characters to define generic limits and to describe new species are undertaken. In addition, new species of East African spirostreptid genera that were collected from previously unsurveyed localities are described. Finally, mitochondrial 16S rRNA and CO1 gene sequences are employed for the first time in the Spirostreptidae to assess the reliability of morphology-based taxon boundaries. This is in order to estimate the phylogeny of the taxa, and to investigate intra-specific variation, inter-specific and inter-generic divergence, and cryptic diversity in the selected taxa.

1.8 Aim of the study

To revise the taxonomy and investigate the biogeographical distribution of selected African spirostreptid millipede genera, to describe new taxa and to determine the phylogenetic relationships of the genera. This will contribute to broader understanding of species diversity, relationships among taxa, their geographical distribution patterns and the factors that determine these patterns. This information will be important in conservation planning in which millipedes can be used as surrogate taxa for other soil invertebrates that also have low vagility and narrow distributions.

Objectives of the study

1. Title of Section: A taxonomic review, phylogeny and biogeography of *Bicoxidens*.

Objectives:

a) to revise the genus and describe new taxa;
b) to construct a key to species identification; and
c) to establish phylogenetic relationships and biogeographic patterns of *Bicoxidens* species.

2. Title of Section: A taxonomic revision and distribution of *Spirostreptus*.

Objectives:

a) to revise *Spirostreptus* and describe new taxa;
b) to construct a key to species identification; and
c) to establish biogeographic patterns.

3. Title of Section: A review of the taxonomy and distribution of *Plagiotaphrus*.

Objectives:

a) to ascertain the taxonomic validity of *Plagiotaphrus*;
b) to construct a key to species identification; and
c) to establish biogeographic patterns.

4. Title of Section: A review of the taxonomy and distribution of *Archispirostreptus*.

Objectives:

a) to revise *Archispirostreptus* and describe new taxa;
b) to construct keys to the identification of the selected genera;
c) to construct keys to the identification of *Archispirostreptus* species; and
d) to establish biogeographic patterns of *Archispirostreptus* spp.

5. Title of Section: Spirostreptid millipedes of Taita Hills, Kenya.

Objectives:

a) to present a checklist of species and
b) to describe new taxa and present a key to identification of species.

6. Title of Section: Genetic divergence and phylogenetic relationships of selected African genera.

Objectives:

a) to determine genetic divergence among the genera using mitochondrial 16S rRNA and CO1 genes and to establish whether there is concordance with morphologic divergence;
b) to investigate intraspecific variation in *B. flavicollis*; and
c) to determine phylogenetic relationships among selected taxa.

1.9 References

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CHAPTER 2

A TAXONOMIC REVIEW OF THE SOUTHERN AFRICAN MILLIPEDE GENUS, *Bicoxidens* Attems, 1928 (DIPLOPODA: SPIROSTREPTIDA: SPIROSTREPTIDAE) WITH THE DESCRIPTION OF THREE NEW SPECIES AND A TENTATIVE PHYLOGENY.

A NEW SPECIES OF *Bicoxidens* ATTEMS, 1928 (DIPLOPODA, SPIROSTREPTIDA, SPIROSTREPTIDAE) SPECIES FROM NORTHERN ZIMBABWE.

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A taxonomic review of the southern African millipede genus, *Bicoxidens* Attems, 1928 (Diplopoda: Spirostreptida: Spirostreptidae), with the description of three new species and a tentative phylogeny

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Abstract

The eight species of *Bicoxidens* were studied in order to verify their taxonomic validity and determine the status of new material. Two new synonymies are established: *B. grandis* Lawrence, 1965 = *B. matabele* (Schubart, 1966) and *B. flavicollis* Attems, 1928 = *B. nasti* Mwabvu, 2000. *B. polyptychus*, incorrectly placed in *Bicoxidens*, on the basis of morphological characters, including gonopods, is moved to *Brevitibius* Attems, 1950. Three new species, *B. matopoensis* Mwabvu, *B. nyathi* Mwabvu and *B. gokwensis* Mwabvu are described. An identification key to the species, a phylogenetic analysis based on gonopod morphology and distribution data for each species are also presented.

Key words: gonopod, telocoxite, telopodite, lateral leaf, median leaf

Introduction

According to Hamer (2000) southern Africa has a rich millipede fauna with 71 genera and 552 species recorded. However, many species from inaccessible or unsurveyed areas remain unknown to science. Some described species are invalid or poorly defined and need revision. Thus our knowledge of diversity and distribution of many millipede taxa in southern Africa is poor. Although representatives of the Spirostreptida are familiar and conspicuous in southern Africa, only one genus, *Doratogonus* Attems, 1914 has recently been revised (Hamer, 2000), and information on the other genera including *Bicoxidens* Attems, 1928 is incomplete.

Members of the genus *Bicoxidens* occur in southern Africa. They have been collected in savanna woodland, *Brachystegia* sp. or *Acacia* sp. dominated habitats, riverine vegetation and mountain forests. The present known distribution suggests a species hotspot south of the Zambezi River (assuming unbiased sampling). Only one species, *B. polyptychus* Kraus, 1958 has been recorded north of Zambezi River but it probably belongs to another genus (see below). However, the probability of finding un-described species in regions and habitats that have not been surveyed is high especially in remote areas such as the eastern highlands along the Mozambique-Zimbabwe border.

Bicoxidens is defined by a characteristic gonopod telopodite which has no femoral process or torsion of the femur but has one or two lobes just before the bend after the femur (Figs. 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a). The genus includes medium to large species that exhibit intra-specific differences (possibly a result of adaptations to different habitats) in body colour and number of body rings. Shades of black or brown are the common body colours although orange-yellow specimens have been collected in the eastern highlands of Zimbabwe.

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The genus and two species, *B. nigerrimus* and *flavicollis*, were described by Attems (1928) based on specimens collected in Harare, Zimbabwe. Since then six more species have been described: *polyptychus* Kraus, 1958, *grandis* Lawrence, 1965, *matabele* (Schubart, 1966), *brincki* Schubart, 1966, *nasti* Mwabvu, 2000 and *friendi* Mwabvu, 2000. Male gonopod morphology and external body characteristics were described for each species. In recent species descriptions, characters that were previously used to define species were discarded because they are of no taxonomic value, or otherwise relegated to generic definition. The challenge, therefore, is to find and use characters that do not vary intraspecifically, one of which is the shape of prefemoral process of the first leg pair of males.

The species composition of *Bicoxidens* and the taxonomic validity and distribution of some species are uncertain. Some species were described based on material from localities less than 300 km apart. These may be synonymous, for example, *nasti* and *flavicollis*; and *grandis* and *matabele*. *Bicoxidens? polyptychus* also requires further investigation especially because it appears to fall far outside the generic distribution range of the genus.

The objectives of this study are to revise the genus and existing species, to describe new taxa, to develop a key to species identification (based mainly on gonopod morphology); present a phylogeny; and to identify biogeographic patterns and possible barriers which may have influenced distribution and speciation of *Bicoxidens.*

Materials and Methods

This study relied on material from various museums and recent field surveys. Museum abbreviations used in this presentation are as follows:

NMZ	Natural History Museum, Bulawayo, Zimbabwe
NMSA	Natal Museum, Pietermaritzburg, South Africa
MRAC	Royal Museum of Central Africa, Tervuren, Belgium
SAMC	South Africa Museum, Cape Town, South Africa
MZLU	Lund Universitets Zoologiska Museum, Sweden

Body, leg and antenna colour were recorded and the number of body rings (all except head and anal valve) counted. Body length was measured using a soft wire placed against the line of ozopores. Where the body rings were separated (as was the case for old preserved specimens) the body was reconstructed and length measured as before. Vernier calipers were used to measure the minimum and maximum body width. All the measurements are in millimeters and based on male specimens, unless otherwise stated.

First leg pair of the male, collum and gonopods were studied using a Carl Zeiss Stereo Microscope and photographed using an auto montage software (Leica Microscope MZ12s with 3 CCD Toshiba Camera). Final images were manipulated and the plates prepared using Adobe Photoshop CS (version 8).

Telocoxite and telopodite are the two parts of male gonopods (Figs. 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a). They can be separated to allow examination of each component. Size, position and number of processes or lobes and spines, the degree of overlap of processes, branching pattern, width, degree of looping and twisting of the telopodite, length of sternite, setosity and relative length of various gonopod structures were examined. Descriptions are based on male specimens including holotypes.

Character and data matrices were constructed based mainly on gonopod characters. A phylogenetic analysis was performed using PARS 3.6 and CONSENSE 3.6 (both in the PHYLIP package of phylogeny inference program) to produce an extended majority rule consensus tree. A bootstrap analysis with 1000 replicates was used to test the reliability of the tree. For comparative purposes *Spirostreptus sebae* Brandt, 1833 was selected as outgroup because the structure of the telocoxite and external body features are comparable to those in the ingroup.

Specimen data are presented as stated on the labels, beginning with country followed by locality, grid reference or co-ordinates, year of collection, collector and catalogue number.

Terminology and classification used in this revision follow Hamer (1999).

Taxonomy

Genus *Bicoxidens* Attems, 1928

Bicoxidens Attems, 1926, 1928; Schubart, 1966; Demange 1971; Hoffman, 1971, 1979; Krabbe, 1982; Hamer, 1998; Mwabvu, 2000, 2005
Rhodesiostreptus Schubart, 1966

Type Species: *Bicoxidens nigerrimus* Attems, 1928

Diagnosis: (after Attems, 1928, with modifications) Anal valves with two furrows on either side of opening, innermost pair deeper and flanking opening, outer pair shallow. Width and depth of furrows varies.

Apical part of the telocoxite enlarged with processes of various shapes and sizes. Apically (at point of telopodite exit from gonocoel) median leaf densely setose. Sternite conical; paracoxite basally rounded and tightly joined to lateral leaf (Figs. 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a). Telopodite slender and cylindrical without large lateral spines, apex with roundish lobe and an adjacent pointed side branch. Telopodite acutely bent at exit from gonocoel; post knee telopodite typically L-shaped with two distinct bends along its length (Figs. 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a). Telopodite abruptly narrowed at approximately mid-length and deflected medially at the level of paracoxites.

Femur without femoral process and torsion. Femur, just before the curve of the canal, with one or two lobes. Distal regions of opposite telopodites overlap medially.

Distribution: Africa south of the Zambezi River.

Remarks: *Bicoxidens* is characterised by the form of the telopodite. Unlike other spirostreptid genera the telopodite is L-shaped (post knee), lacks a femoral process and spines, and the distal regions of opposite telopodites overlap medially.

B. brincki Schubart, 1966
Fig. 1

Bicoxidens brincki Schubart, 1966; Lawrence, 1966; Krabbe, 1982; Hamer, 1998; Mwabvu, 2000, 2005

Type material (examined): Holotype: SOUTH AFRICA: 1 ♂, Kruger National Park [22° 08'S, 31°03'E], Transvaal, 6.v.1951 (MZLU/L951/3645).

Additional material examined: ZIMBABWE: 1 ♂, Beitbridge [22°02'S, 30°00'E], x.1985, F. Nyathi (NMZ/D835); 1♂, Crooks Corner [2231A4], 18.xii.1996, (NMZ/D841); 1 ♂, Pande Mine [2230A4], 9.ii.1994, F. Nyathi (NMZ/D756); 1 ♂, Lundi River [2131B4], 20.vi.1984, (NMZ/D196); 1 ♂, Malipati [2231A2], (NMZ/D842); 1 ♂, Matopo National Park, [2028D1], 6.xi.1987, J. Minshull (NMZ/D480); 1 ♂, Dwala Ranch [2129B2], 18.iv.1987, (NMZ/D486); 1 ♂, Doddieburn Ranch [2129A4], 15.iv.1986, F. Nyathi (NMZ/D382); 1 ♂, Shashi Wilderness Camp [2129C3], 18.iv.1990, (NMZ/D670).

Diagnosis: Distal telocoxite with a large rounded lateral process, a distal median process, a slender beak-like process medially overlapping that from opposite gonopod, and a small bulbous lobe below it (Fig. 1a).

Description:

Size: Body length 84–155 mm; minimum and maximum body width 2–5 mm and 4–11 mm; antenna length 5–9 mm.

Number of body rings: 51–62.

Colour: Body brown or black; antennae and legs brown.

Collum: Rounded, two complete folds (Fig. 1d).

Pre-femoral process of 1st pair of male legs: Broad, rounded with a short pointed apex (Fig.1c).

Sigilla on body ring: Three rows present (the third one poorly developed), becoming 2 or reduced to 1 laterally.

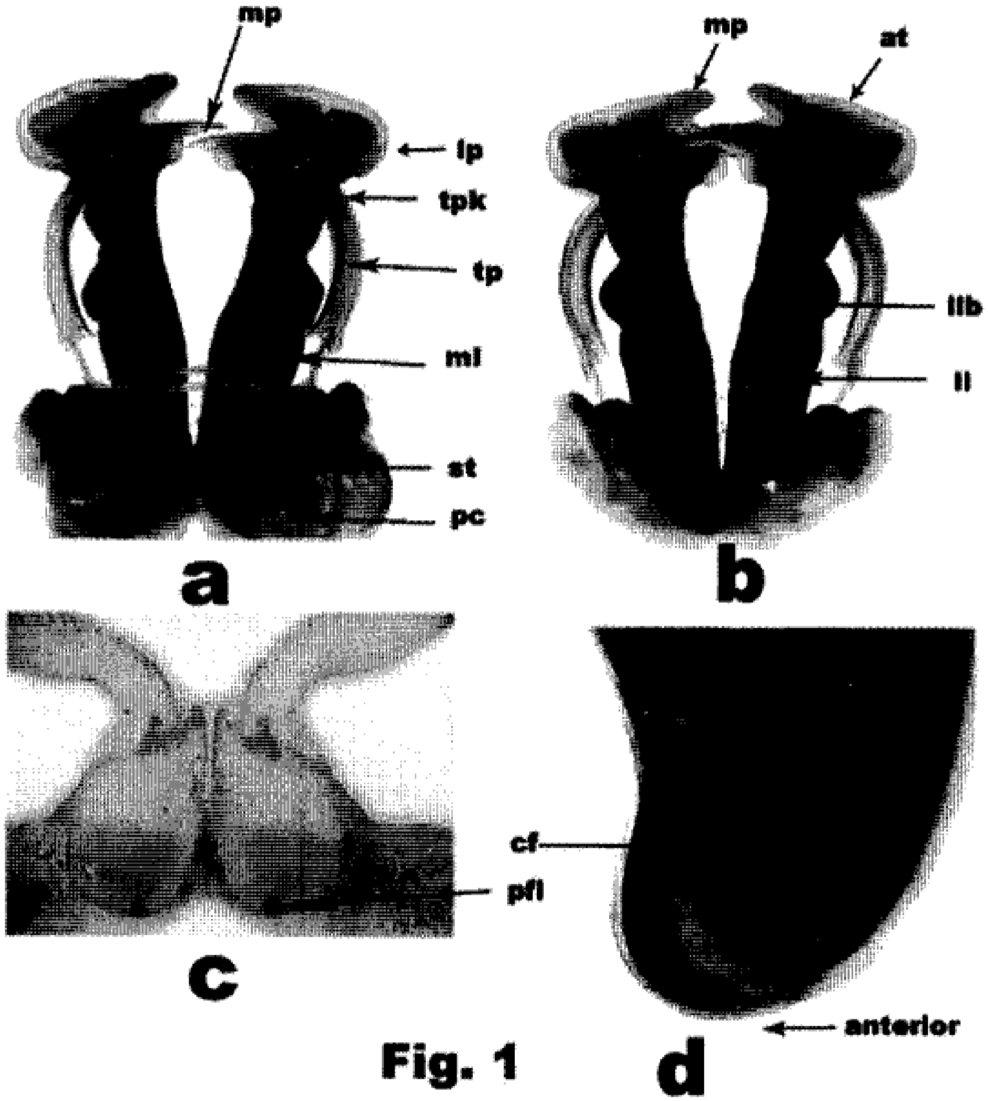

FIGURE 1. *B. brincki* (MZLU/L951/3645). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.
Abbreviations: at, apical telocoxite; cf, collum fold; llb, lateral leaf lobe; ll, lateral leaf; lp, lateral process; ml, median leaf; mp, median process; pc, paracoxite; pfl, prefemoral lobe; st, sternite; tp, telopodite; tpk, telopodite knee.

Gonopod: 5–6 mm long. Apical telocoxite with three median processes, the middle beak-shaped and overlapping opposite median process, below it a rounded lobe; rounded lateral process folded and partly overhanging knee of telopodite (Fig. 1a). Median leaf with a small sub-apical lateral lobe facing telopodite (Fig.1a).

Aborally, a raised bulb-shaped, basally rounded lobe present on lateral leaf below the level of median leaf tip (Fig. 1b). Postfemur of telopodite overlap over sternite and terminates in an incomplete loop.

Distribution: Kruger National Park, South Africa and southern part of Zimbabwe (Fig. 10).

Remarks: Other than in colour there appears to be no variation between populations, especially in the form of the gonopods. This species is one of the largest species in *Bicoxidens*, it falls in the same size range as *grandis*. It differs from *grandis* by having three median processes and an aboral bulbous lobe (Fig. 1b), and a rounded lateral leaf lobe as in *matopoensis*, *gokwensis*, *friendi* and *nigerrimus* (Figs. 1b, 3b, 4b, 6b, 7b). The apex of the inner margin of the median leaf lacks the axe-shaped median processes that are only found in *flavicollis* and *grandis* (Figs. 2a, 5a).

B. flavicollis **Attems, 1928**
Fig. 2

Bicoxidens flavicollis Attems, 1928; Lawrence, 1965; Schubart, 1966; Krabbe, 1982; Hamer, 1998; Mwabvu, 2005
Bicoxidens nasti Mwabvu, 2000, 2005 **Syn. n.**

Type material (examined): Holotype: ZIMBABWE: 1 ♂, Umtali [18°50'S, 32°35'E], 1926 (SAMC13743).

Additional material examined: ZIMBABWE: 1 ♂, Chivi Police Station [2030B3], 5.ii.1994. F. Nyathi (NMZ/D750); 1 ♂, Matopos [20°04'S, 28°06'E], (NMZ/D691); 1 ♂, Lumene [2028B2], 1.xii.1992, M. Fitzpatrick (NMZ/D698); 1 ♂, Bubiana Conservancy [2129B2], 26.xi.1993, (NMZ/D710); 1 ♂, Kungwe Farm [1829B3], 4.v.1984, R. Jooste (NMZ/D143); 1 ♂, Vumba [19° 05'S, 32°40'E], 20.ii.1985, C. T. Masango (NMZ/D232); 1 ♂, Dwala Ranch [2129B2], 18.iv.1987, (NMZ/D485); 1 ♂, Maleme (NMZ/D655); 1 ♂, Murewa, Maramba [17°10'S, 31°50'E], 15.xii.1997, T. Mwabvu (NMSA20521); 1 ♂, Mutasa, Sahumani [18°30'S, 32°30'E], xi.1997, T. Mwabvu (NMSA20526); 1 ♂, Chiredzi [2131B1], 26.iii.1985, M. Davy (NMZ/D236); 1 ♂, Vumba [19° 05'S, 32°40'E], i.1955, Stuckernberg (NMSA6261); 1 ♂, Old Mutare [18°45'S, 32°30'E], xi.1997, T. Mwabvu (NMSA20527); 3 ♂, Salisbury [17°30' S, 31°05' E], xii.1967, P. Hulley (NMSA18955); MOZAMBIQUE: 1 ♂, Maguge [2032D1], 8.xii.1991, D. G. Broadley (NMZ/D648).

Diagnosis: Lateral edge of apical telocoxite folds and extends medially into a long weakly curved, flattened and tapering median process that completely overlaps the opposite one, aborally (Figs. 2a, 2b). Apical region of telocoxites also with a prominent rounded median lobe distal to the axe-shaped process. Aborally, a small lobe extends downwards from the apical telocoxite (Fig. 2b).

Description:

Size: Body length 82–110 mm; minimum and maximum body width 3–8 mm and 6–9 mm; antenna length 4–6 mm.

Number of body rings: 49–59.

Colour: Body yellow or brown or black; antennae and legs brown.

Collum: Square, with two complete folds (Fig. 2d).

Pre-femoral process of 1st pair of male legs: Long and narrow distally, tips weakly directed away from each other (Fig. 2c).

Sigilla on body ring: Two to three rows present, become one ventrally.

Gonopod: 4–5 mm long. Apical telocoxite with a flattened median process which completely overlaps the opposite one (Fig. 2b). Median leaf apically with median axe-shaped process (Fig. 2a). Apically lateral leaf with a small, rounded nipple below level of axe-shaped processes, aborally (Fig. 2b). Telopodite forming a complete loop apically.

Distribution: Widely distributed in east, north, south west and central Zimbabwe (Fig. 10)

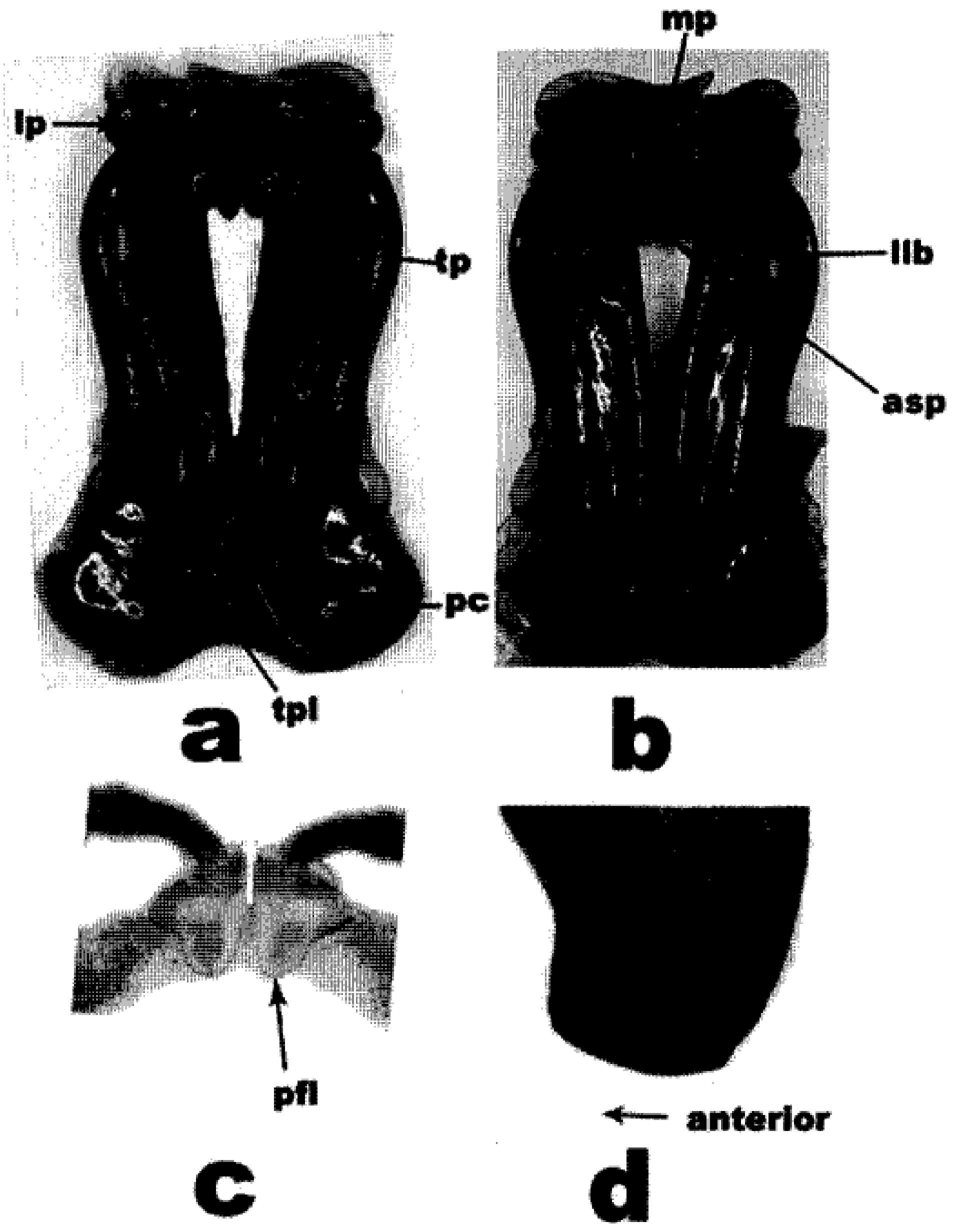

Fig. 2

FIGURE 2. *B. flavicollis* (NMZ/D232). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.
Abbreviations: asp, axe-shaped process; llb, lateral leaf lobe; lp, lateral process; mp, median process; pc, paracoxite; pfl, prefemoral lobe; tp, telopodite; tpl, telopodite loop.

Remarks: There are variations in colour and size (including gonopod) between populations. Many colour morphs (some yellow) with similar gonopods and external morphological characters have been collected in the eastern region of Zimbabwe. This species is part of the group of relatively small-bodied *Bicoxidens* species that includes *nyathi*, *matopoensis*, *friendi*, *gokwensis* and *nigerrimus*. Like *grandis*, the gonopods of *flavicollis* have long overlapping median processes on apical telocoxites, median axe-shaped processes on the median leaf and lack an aboral lobe on the lateral leaf. This species also resembles *grandis* by having a relatively long and curved femoral lobe (Figs. 2a, 3a).

B. friendi Mwabvu, 2000

Fig. 3

Bicoxidens friendi Mwabvu, 2000, 2005

Type material (examined): Holotype: ZIMBABWE: 1 ♂, Murewa, Maramba [17°10'S, 31°55'E], on granite rock outcrop, 21.xii.1996, T. Mwabvu ((MRAC 20557)

Additional material examined: ZIMBABWE: 1 ♂, Showe River (NMZ/D628); 1 ♂, Limestone Ridge [1630A1], 11.xii.1984 (NMZ/D262); 1 ♂, Murewa, Maramba [17°10'S, 31°55'E], 21.xii.1996, T. Mwabvu (NMSA20545); 1 ♂, Limestone Ridge [1630A1], 11.xii.1984 (NMZ/D262); 2 ♂, Makoni [18°30'S, 32°10'E], xi.1962, D. G. Broadley (NMSA8883).

Diagnosis: Apical region of telocoxite T-shaped, folded downwards with the rim just above knee bend, with one tapering lateral process and three median processes (Figs. 3a, 3b). The middle and longer median process overlaps the process from the opposite gonopod, the shorter process is peg-like.

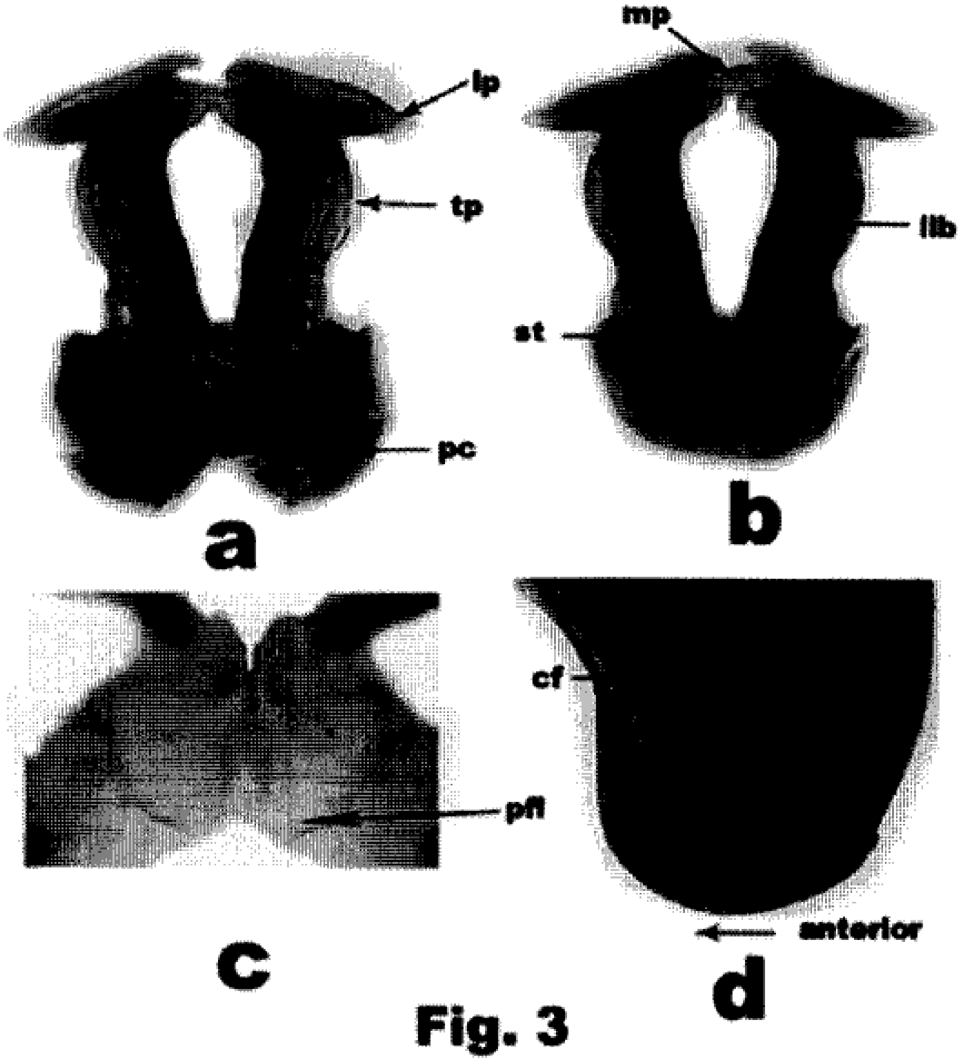

FIGURE 3. *B. friendi* (MRAC 20557). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.
Abbreviations: cf, collum fold; llb, lateral leaf lobe; lp, lateral process; mp, median process; pc, paracoxite; pfl, prefemoral lobe; st, sternite; tp, telopodite.

Description:

Size: Body length 90–113 mm; minimum and maximum body width 3–7 mm and 6–8 mm; antenna length 5–6 mm.

Number of body rings: 48–61.

Colour: Body brown to greenish-black; antennae and legs dark brown.

Collum: Rounded, with two complete and one to three incomplete folds (Fig. 3d).

Pre-femoral process of 1st pair of male legs: Relatively long, rounded and furthest apart distally (Fig. 3c).

Sigilla on body ring: One row present, flanked by two discontinuous rows.

Gonopod: 4–5 mm long. Apical telocoxite T-shaped, with three median processes and a distally tapering and curved lateral process. Apically, telocoxite folded over self with rim just above knee (Fig. 3a). The longest median process overlaps with the process from the opposite gonopod, the shorter peg-like. Aborally, a bulb-shaped basally rounded lobe present on lateral leaf. Distal part of telopodites tips forming an incomplete loop (Fig. 3a)

Distribution: Known only from north-eastern Zimbabwe

Remarks: This species has a large bulbous lobe that extends downwards from the apical telocoxite (aborally) this is similar to *gokwensis*, *nigerrimus*, *matopoensis,* and *brincki*. The overlapping median processes of the apical telocoxite are straight, rather than curved as found in *flavicollis* and *grandis*. The femoral lobe is reduced unlike in *grandis* and *flavicollis*.

B. gokwensis sp. n. Mwabvu

Fig. 4

Type material (examined): Holotype: ZIMBABWE: 1 ♂, Gokwe, Kuwirirana Centre [18°02'S, 28°08'E], 18.ii.1998, T. Mwabvu (MRAC 20556).

Etymology: So named to highlight type locality, Gokwe, Zimbabwe.

Additional material examined: 1 ♂, Gokwe, Kuwirirana Centre [18°02'S, 28°08'E], 18.ii.1998, T. Mwabvu (NMZ uncatalogued).

Diagnosis: Antennae yellow. Laterally, apical telocoxite folded inwards into an ear-shaped lobe just above the knee. Inner margin of apical telocoxite with a short median process and a rounded proximal median lobe that are separated by a U-shaped groove (Figs. 4a, 4b).

Description:

Size: Body length 95–132 mm, minimum and maximum body width 5–7 mm and 8–9 mm; antenna length 6–7 mm.

Number of body rings: 54–55.

Colour: Body black, legs reddish-brown; antennae yellow.

Collum: Rounded, with two complete folds (Fig. 4d).

Pre-femoral process of 1st pair of male legs: Spade-shaped distally (Fig. 4c).

Sigilla on body ring: Three rows present, merging to a single ventral row.

Gonopod: 4–6 mm long. Apical telocoxite with two median processes separated by a deep U-shaped groove. Orally, lateral leaf folded just above the knee bend and extending distally to the apex of telocoxite (Fig. 4a).

Aborally an extension from the proximal lobe forms a median process, which may touch but not overlap the opposite process (Figs. 4a, 4b).

Aborally, a large basally rounded-bulb shaped lobe on lateral leaf extends below level of median leaf apex. Distally telopodite forms a complete loop (Fig. 4a).

Distribution: Known only from type locality, Gokwe, Zimbabwe (Fig. 10).

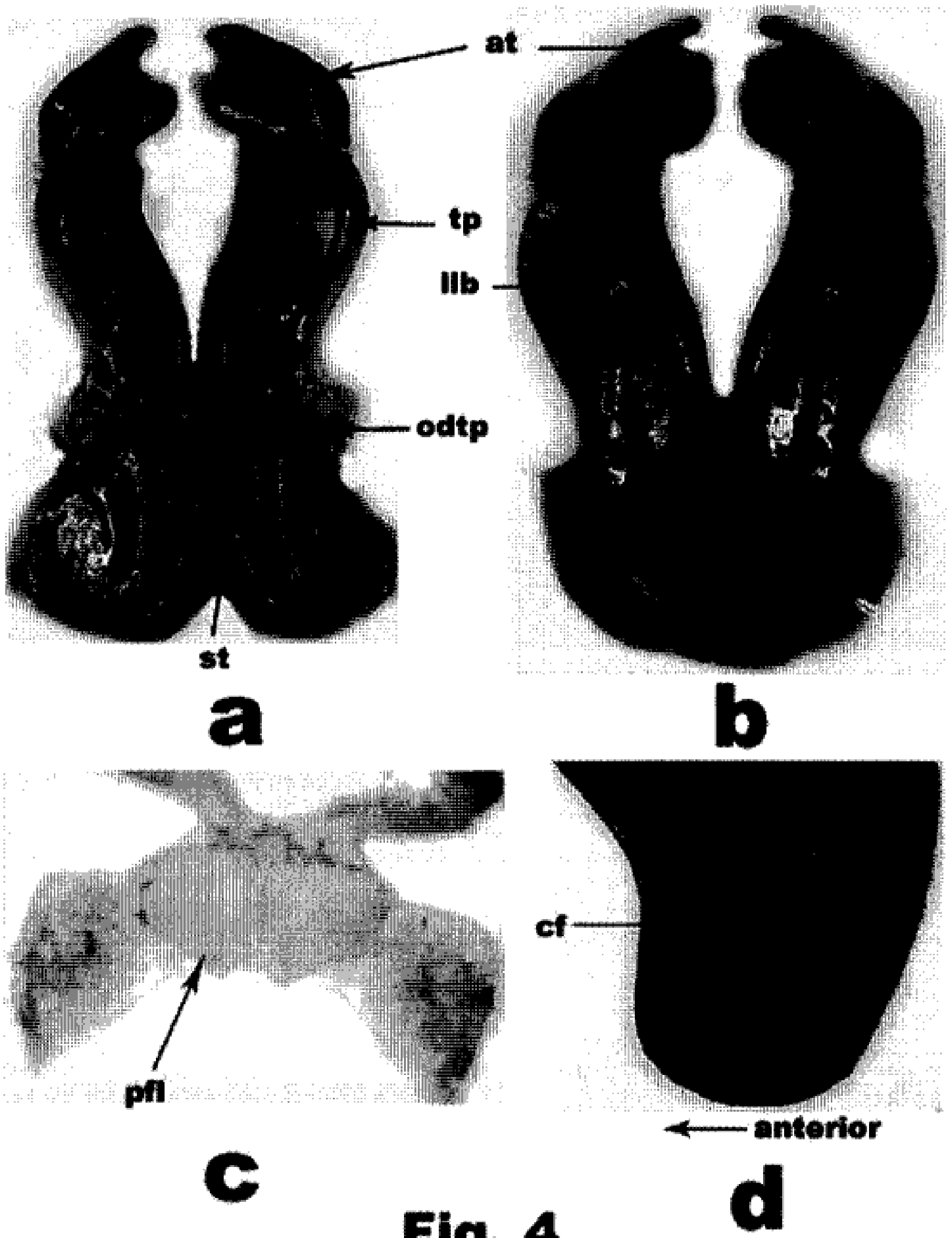

Fig. 4

FIGURE 4. *Bicoxidens gokwensis* sp. nov. (MRAC 20556). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.
Abbreviations: at, apical telocoxite; cf, collum fold; llb, lateral leaf lobe mp, median process; odtp, overlapping distal telopodite; pfl, prefemoral lobe; st, sternite; tp, telopodite.

Remarks: This is the only species of *Bicoxidens* with yellow antennae. Other species have antennae and legs of the same colour. As in *brincki, matopoensis, nyathi, nigerrimus* and *friendi* the gonopod lacks median axe-shaped processes on median leaf, but it has a raised basally rounded or bulb or flask-shaped lobe on the lateral leaf as in *brincki, friendi, gokwensis, matopoensis, nigerrimus* and *nyathi* (Figs. 1b, 3b, 5b, 6b, 7b, 8b).

B. grandis Lawrence, 1965

Fig. 5

Bicoxidens grandis Lawrence, 1965; Krabbe, 1982; Hamer, 1998; Mwabvu, 2000, 2005
Rhodesiostreptus matabele Schubart, 1966 **syn. n.**
Bicoxidens matabele Krabbe, 1982; Hamer, 1998; Mwabvu, 2000

Type material *B. grandis* (examined): Holotype: ZIMBABWE: 1 ♂, 15 km West of Birchenough Bridge [19°50'S, 32°30'E], 20.ii.1962, D. G. Broadley (NMSA8884)

Type material *B. matabele* (examined): Holotype: ZIMBABWE: 1 ♂, WN West Nicholson, 6.v.1951 (MZLU/L951/3730)

Additional material examined: ZIMBABWE: 1 ♂, Silobela [19°20' S, 29°35'E], xi.1997, T. Mwabvu (NMZ uncatalogued); 1 ♂ 2♀, Birchenough Bridge [19°55'S, 32°35'E], 1998, T. Mwabvu (NMSA20528); 1 ♂ 3♀, Zvomukonde [20°50'S, 30°30'E], xii.1998, T. Mwabvu (NMZ uncatalogued); 2 ♂ 4♀, Silobela [19°20' S, 29°30'E], xii.1998, T. Mwabvu (NMSA20546).

Diagnosis: Apical telocoxite with a horizontal apically acute lateral process and a curved median process that overlaps with median process from opposite gonopod (Figs. 5a, 5b). Aborally, an apical ear-shaped lobe present on lateral leaf at same level as axe-shaped median process.

Description:

Size: Body length 135 mm; minimum and maximum body width 7–8 mm and 8–11 mm; antenna length 7–9 mm

Number of body rings: 52–62.

Colour: Body black; antennae and legs brown.

Collum: With three complete folds (Fig. 5d).

Pre-femoral process of 1st pair of male legs: Proximal halves parallel, almost touching; rounded distally, with apical nipples deflected to face the other (Fig. 5c).

Sigilla on body ring: Three rows, becoming one ventrally.

Gonopod: 6–7 mm long. Orally, apical telocoxite with a lateral and median process (Fig. 5a). Median process crescent-shaped and overlapping the opposite process. Lateral process horizontal, long and apically acute. Distally, median leaf with median axe-shaped process not touching the opposite one (Fig.5a).Femoral lobe typically long, (Fig. 5a).

Aborally, a small almost ear- shaped transverse projection is present on the lateral leaf (Fig. 5b) at same level as the axe-shaped process (Fig. 5b).

Distribution: Current records are from southern Zimbabwe (Fig.10)

Remarks: The gonopod of *Rhodesiostreptus matabele* Schubart, 1966 is identical to that of *B. grandis*, and the taxa also have overlapping distributions. Additionally, they both have an ear-shaped projection on the lateral leaf behind the median leaf apex, as well as identical telocoxites and median leaves and a telopodite with a much longer femoral lobe unlike the other species of *Bicoxidens*. *B. matabele* is therefore a junior synonym of *B. grandis.*

Although *grandis* is larger than *flavicollis*, their gonopods are similar in that they have overlapping, flattened median processes on the distal telocoxites and axe-shaped processes on the median leaf unlike the other species. The two species are, however, quite distinct; *flavicollis* does not have a lateral process on the apical telocoxite or an aboral ear-shaped projection on the lateral leaf. Unlike *flavicollis*, the paracoxite of *grandis* is not tightly attached to the lateral leaf as in *friendi* and *gokwensis*. *B. grandis* has only been recorded in hot and dry areas.

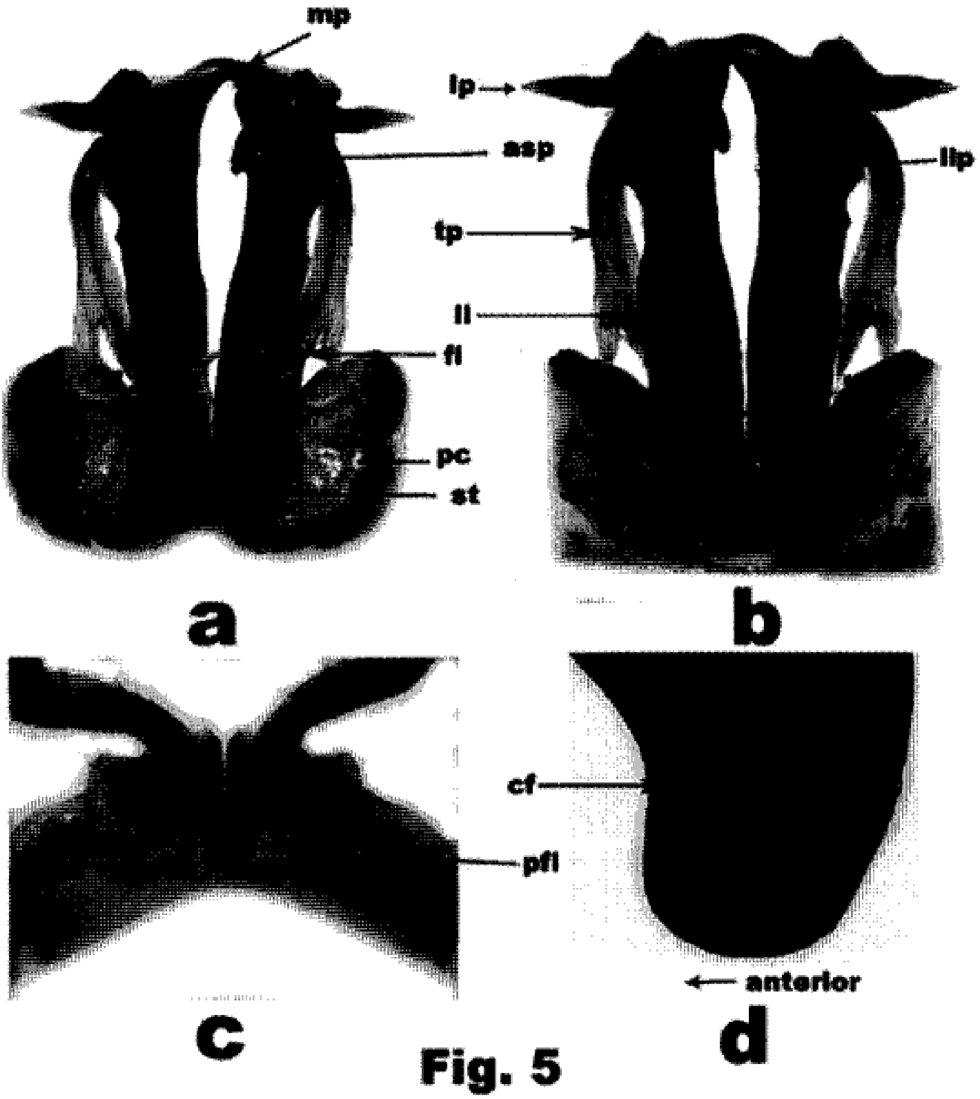

FIGURE 5. *B. grandis* (NMSA 8884). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.
Abbreviations: asp, axe-shaped process; at, apical telocoxite; cf, collum fold; fl, femoral lobe; llp, lateral leaf projection; ll, lateral leaf; lp, lateral process; mp, median process; pc, paracoxite; pfl, prefemoral lobe; st, sternite; tp, telopodite

B. matopoensis sp. n. Mwabvu
Fig. 6

Type material (examined): Holotype: ZIMBABWE: 1 ♂, Matopo National Park, Maleme Rest Camp [2028D1], 6.iii.1989, J. Minshull (NMZ/D562)

Additional material examined: ZIMBABWE: 1 ♂, Doddieburn Ranch [2129A4], 10.xii.1985, J. Minshull (NMZ/D356).

Etymology: So named to highlight the type locality in Zimbabwe.

Diagnosis: Apical telocoxite with broadly rounded lateral process and two median processes that form a V-shape; the rounded lateral process folded downwards with the rim or edge just above the telopodite knee and extending into a distal median process (Fig. 6a). Proximal median process tilted away from the distal median process; the opposite median processes are in touch, leaving a median window between the opposite telocoxites (Figs. 6a, 6b).

A sub-apical constriction of median leaf produces a lateral lobe below the setose region (Fig. 6a).

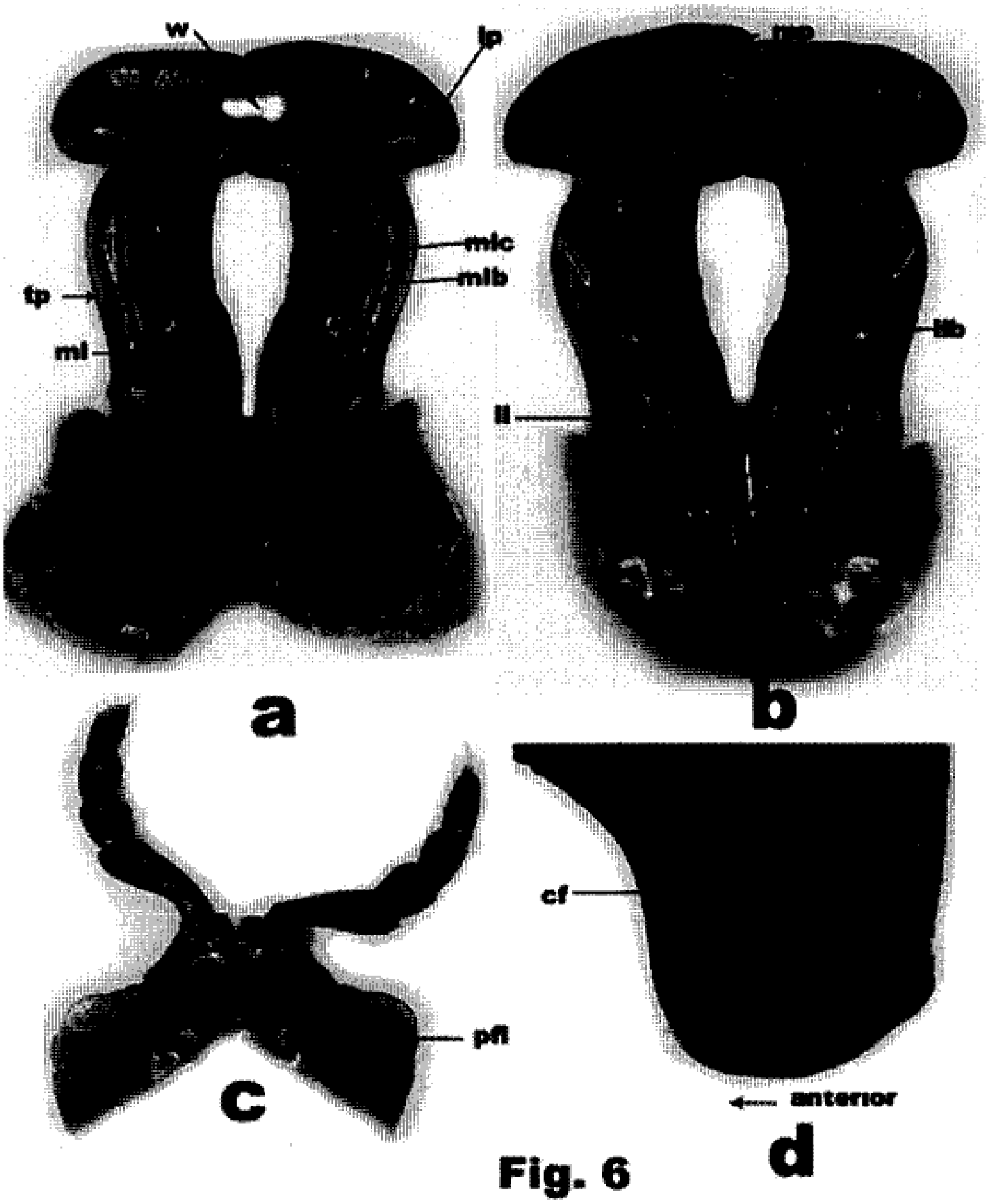

Fig. 6

FIGURE 6. *B. matopoensis* sp. nov. (NMZ/D562). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.
Abbreviations: cf, collum fold; llb, lateral leaf lobe; ll, lateral leaf; lp, lateral process; ml, median leaf; mlb, median leaf lobe; mlc, median leaf constriction; mp, median process; pfl, prefemoral lobe; tp, telopodite; w, window.

Description:

Size: Body length 110–104 mm; minimum and maximum body width 3–5 mm and 6–8 mm; antenna length 5–6 mm.

Number of body rings: 56–61.

Colour: Body black; head brown; leg and antennae brown to dark brown.

Collum: With three complete folds (Fig. 6d) and one to three incomplete folds.

Pre-femoral process of 1st pair of male legs: Trowel-shaped (Fig. 6c).

Sigilla on body ring: Three rows present, becoming one ventrally.

Gonopod: 4–5 mm long. Orally, apical telocoxite with a median process gently tilted away from main apical process, thus forming a V-shaped incision, and touching the opposite one as does the distal median process (Figs. 6a, 6b). Lateral process of distal telocoxite broadly rounded and folded over itself, ending in a thick rim just above the telopodite knee. Rim extending to the midpoint of distal telocoxite. Below the setose apex of median leaf a deep constriction forms a neck and a lateral lobe.

Aborally, apical telocoxite raised with a short median process and a wider proximal rounded median process. A broadly rounded lateral process overhangs the telopodite knee (Fig. 6a, 6b). Lateral leaf with a bulb-shaped, basally rounded lobe (Fig. 6b). Apical telopodite with incomplete looping.

Distribution: South west of Bulawayo, Zimbabwe (Fig. 10).

Remarks: The folding of the apical telocoxite in *matopoensis* is similar to that in *brincki* and, to a lesser extent, *gokwensis*. However, the extent and relative position of folding differs. Unlike *brincki*, it has two median processes. Like *friendi*, *nigerrimus*, *flavicollis*, *brincki* and *gokwensis*, it also has a large bulb- or flask-shaped lobe on the lateral leaf. Both *matopoensis* and *gokwensis* have a constricted median leaf sub-apically, just below the setose area, but *gokwensis* lacks an obvious proximal lateral lobe.

B. nigerrimus **Attems, 1928**

Fig. 7

Bicoxidens nigerimus Attems, 1928; Lawrence, 1965; Schubart, 1966; Krabbe, 1982; Hamer, 1998; Mwabvu, 2000, 2005

Type material (examined): Holotype: ZIMBABWE: 1 ♂, Salisbury [17°35'S, 31°05'E], 1926 (SAMB3361); Paratype: 1 ♂, Salisbury [17°35'S, 31°05'E], 1926 (SAMB3351)

Additional material examined: ZIMBABWE: 1 ♂, Taru Dam [2030A4], 7.ii.1994, F. Nyathi (NMZ/D753)

Diagnosis: Apical telocoxite slightly tilted upwards, with a rounded lateral process which extends into a distal median process (Fig. 7a); two short rounded median processes present (Fig. 7b).

Description:

Size: Body length 110–135 mm; minimum and maximum body width 4 mm and 7 mm; antenna length 5–6 mm.

Number of body rings: 55–61.

Colour: Body black; antennae and legs brown.

Collum: With two complete folds and an incomplete fold.

Pre-femoral process of 1st pair of male legs: Rounded tips weakly turned medially.

Sigilla on body ring: Three rows, becoming one ventrally.

Gonopod: 4–5 mm long. Apical telocoxite wide, with a rounded lateral process and three median processes (Fig. 7a). Smaller median process proximal to middle one. Upper and longer process separated from middle one by a U-shaped invagination (Fig. 7a). Aborally, bulb shaped basally rounded lobe present on lateral leaf. The postfemur forms an incomplete loop near the extremity.

Distribution: Harare and Bulawayo, Zimbabwe (Fig. 10)

Remarks: This small-bodied species is not widely distributed as *flavicollis*. The gonopod has a bulb- or flask-shaped lobe on the lateral leaf as in *friendi*, *matopoensis*, *brincki*, and *gokwensis*; the apical folding of the telocoxite resembles that in *matopoensis* and *brincki*, but differs from them by being smaller and tilted upwards.

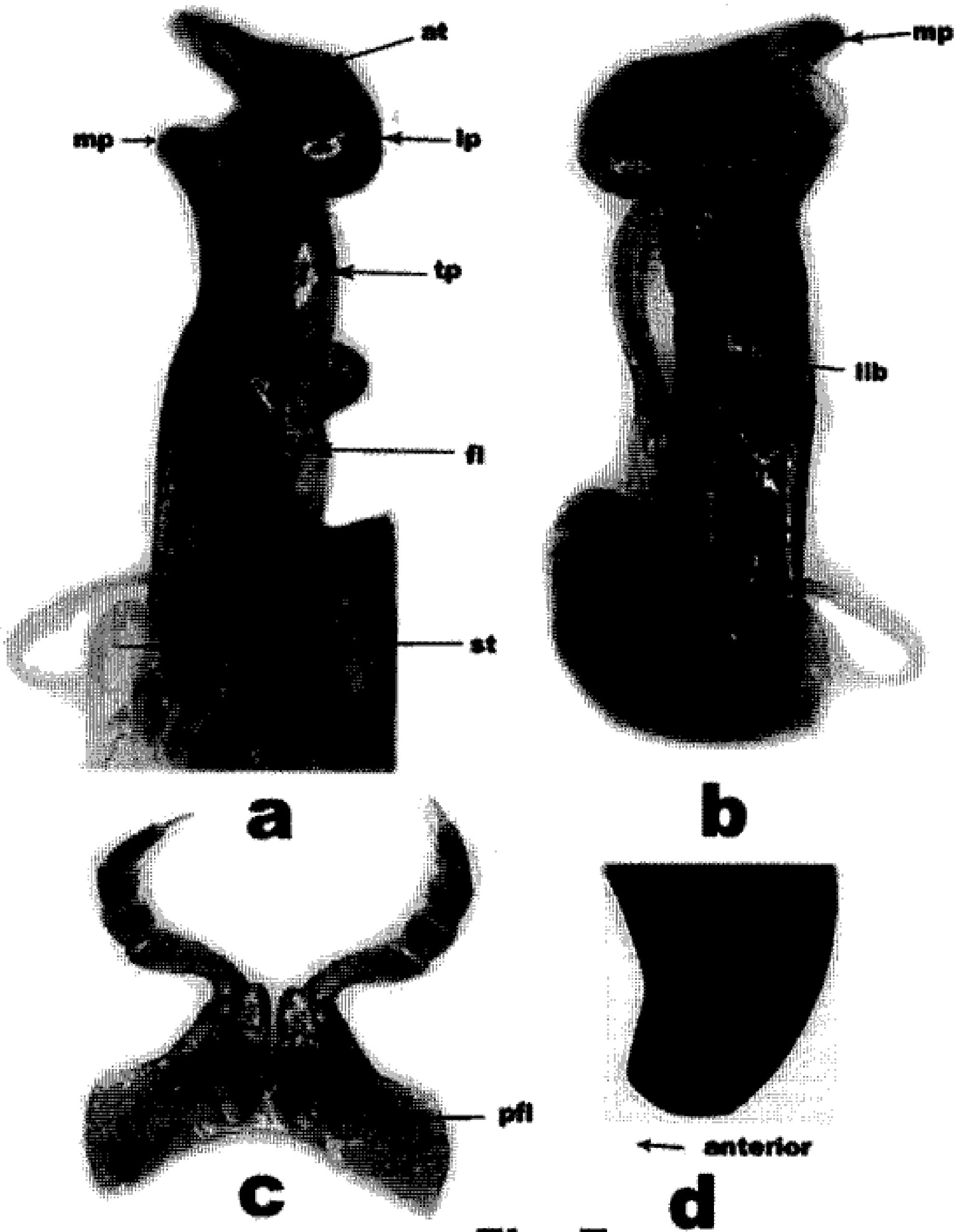

Fig. 7

FIGURE 7. *B. nigerrimus* (SAM B3361). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.
Abbreviations: at, apical telocoxite; cf, collum fold; llb, lateral leaf lobe; lp, lateral process; mp, median process; pfl, prefemoral lobe; st, sternite; tp, telopodite

B. nyathi **sp. n. Mwabvu**
Fig. 8

Type material (examined): Holotype: ZIMBABWE: 1 ♂, Mudzwiru River [2030B4], 4.ii.1994, F. Nyathi (NMZ/D747)

Etymology: Named after Mr Francis Nyathi (Natural History Museum, Bulawayo, Zimbabwe) in recognition of his contribution to the collection and study of invertebrates in Zimbabwe.

Diagnosis: Apical telocoxite with a lateral and median process resulting in an oval shape (Fig. 8a); subapically, the median leaf has a raised subapical process (Fig. 8b). A laterally deflected aboral lateral leaf lobe, more tapered than rounded, is present (Fig. 8b).

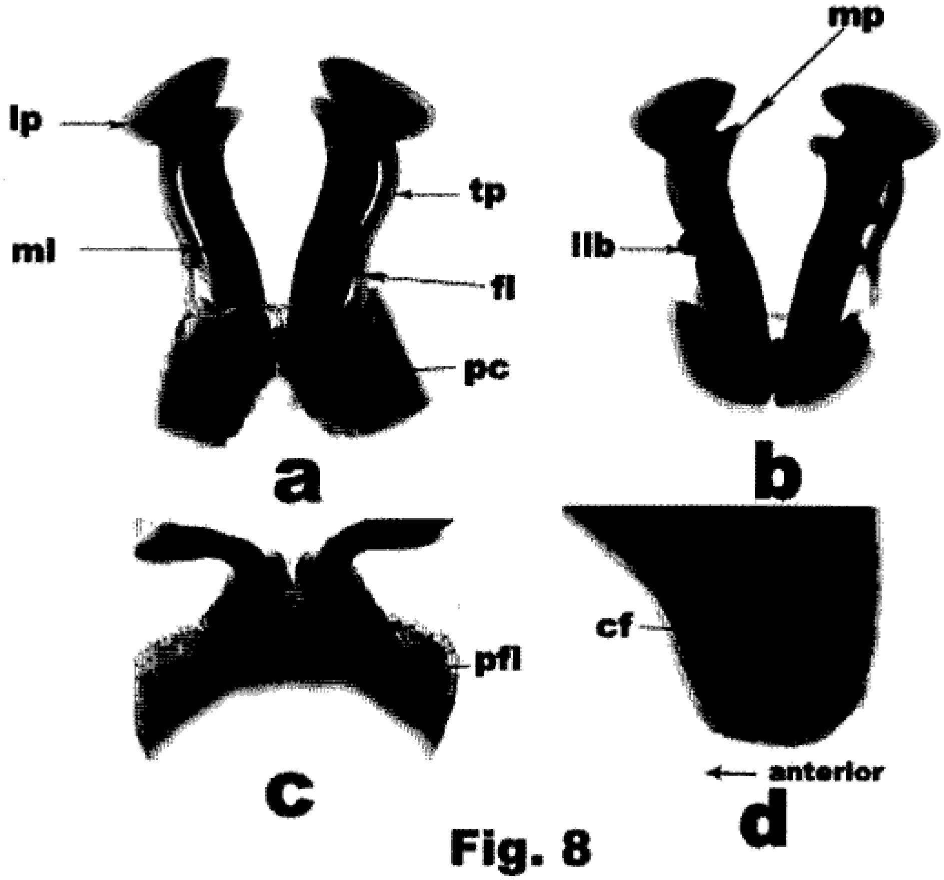

FIGURE 8. *B. nyathi* sp. nov. (NMZ/D747). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.
Abbreviations: cf, collum fold; fl, femoral lobe; llb, lateral leaf lobe; lp, lateral process; ml, median leaf; mp, median process; pc, paracoxite; pfl, prefemoral lobe; tp, telopodite.

Description:

Size: Body length 115 mm; minimum and maximum body width 4–5 and 6–7 mm; antenna length 5–6 mm.

Number of body rings: 52

Colour: Body black; legs and antennae brown.

Collum: With three complete folds and an incomplete fold (Fig. 8d).

Pre-femoral process of 1st pair of male legs: Subtriangular, proximally parallel, with a rounded tip (Fig. 8c).

Sigilla on body ring: Three irregular rows, reduced to one ventrally.

Gonopod: Orally, apical telocoxite oval. A median process is present, directed distally, not overlapping the opposite one. Aborally, apex of median leaf slightly raised (Fig.8b). An aboral, lateral leaf lobe extending from apical telocoxite (below the level of the apex of the median leaf) deflected laterally, more tapered than rounded. The telopodite forms an incomplete loop distally (Fig. 8a)

Distribution: Known from Mudzwiru River, south of Gweru, Zimbabwe (Fig. 10). Specimen found under a granite rock.

Remarks: The apical telocoxite is oval and simple, unlike other species. However, it resembles *matopoensis, nigerrimus, friendi, gokwensis* and *brincki* by having an aboral lobe on the lateral leaf. However, in *nyathi* the lobe is smaller, deflected laterally and is more tapered than rounded.

Species removed from *Bicoxidens* Attems, 1928

Brevitibius polyptychus (Kraus, 1958) comb. n.

Fig. 9

Bicoxidens? polyptychus Kraus, 1958
Bicoxidens polyptychus: Krabbe, 1982; Mwabvu, 2000

Type material (examined): Holotype: DEMOCRATIC REPUBLIC OF CONGO: 1 ♂, Parc Natinal. de L'Upemba, Katanga Province [8°30'S, 26°20'E], 2.iv.1948, G.F. de Witte (HT018.229); Paratype: 3 ♂, Parc National. de L'Upemba, Katanga Province [8°30'S, 26°20'E], 2.iv.1948, G.F. de Witte (018.130)

Diagnosis: Apical telocoxite with a long diagonal lateral process and a short median process (Figs. 9a, 9b). Post knee telopodite with torsion and a femoral spine (Fig. 9c).

Description:

Size: Body length 155–168 mm; minimum and maximum body width 8–10 mm and 10–12 mm; antenna length 8–10 mm.

Number of body rings: 70–72.

Colour: Body, legs and antennae brown.

Collum: With anterior lobe, with 7–9 complete folds (Fig. 9e).

Pre-femoral process of 1st pair of male legs: Bean-shaped (Fig. 9d).

Sigilla on body ring: One row.

Gonopod: 8–9 mm long. Orally, apical telocoxite with a long diagonal lateral and a short median process (Fig. 9a). Aborally, lateral leaf without lobes or processes. Paracoxite arrow-head shaped (Fig. 9a); sternite reduced. Telopodite with femoral torsion and a black femoral spine distal to it (Fig. 9c).

Distribution: Katanga Province, Democratic Republic of Congo

Remarks: Unlike *Bicoxidens* species, this species is large-bodied, the anal valve has one furrow on each side and the collum has an anterior lobe with seven folds. The telopodite is not L-shaped but has torsion; the paracoxite is arrowhead-shaped (not rounded as in *Bicoxidens* species).

It appears to be closely related to central African species most of which were previously assigned to *Spirostreptus* in Krabbe (1982). A revision of these taxa needs to be undertaken in order to clarify the position of *polyptychus* in Spirostreptida.

However, we have tentatively assigned it to *Brevitibius* Attems, 1950, based on the form of the telopodite. The femoral process is distal to the knee after which there is an abrupt narrowing and twisting of the telopodite around the femoral region, this is consistent with *Brevitibius*.

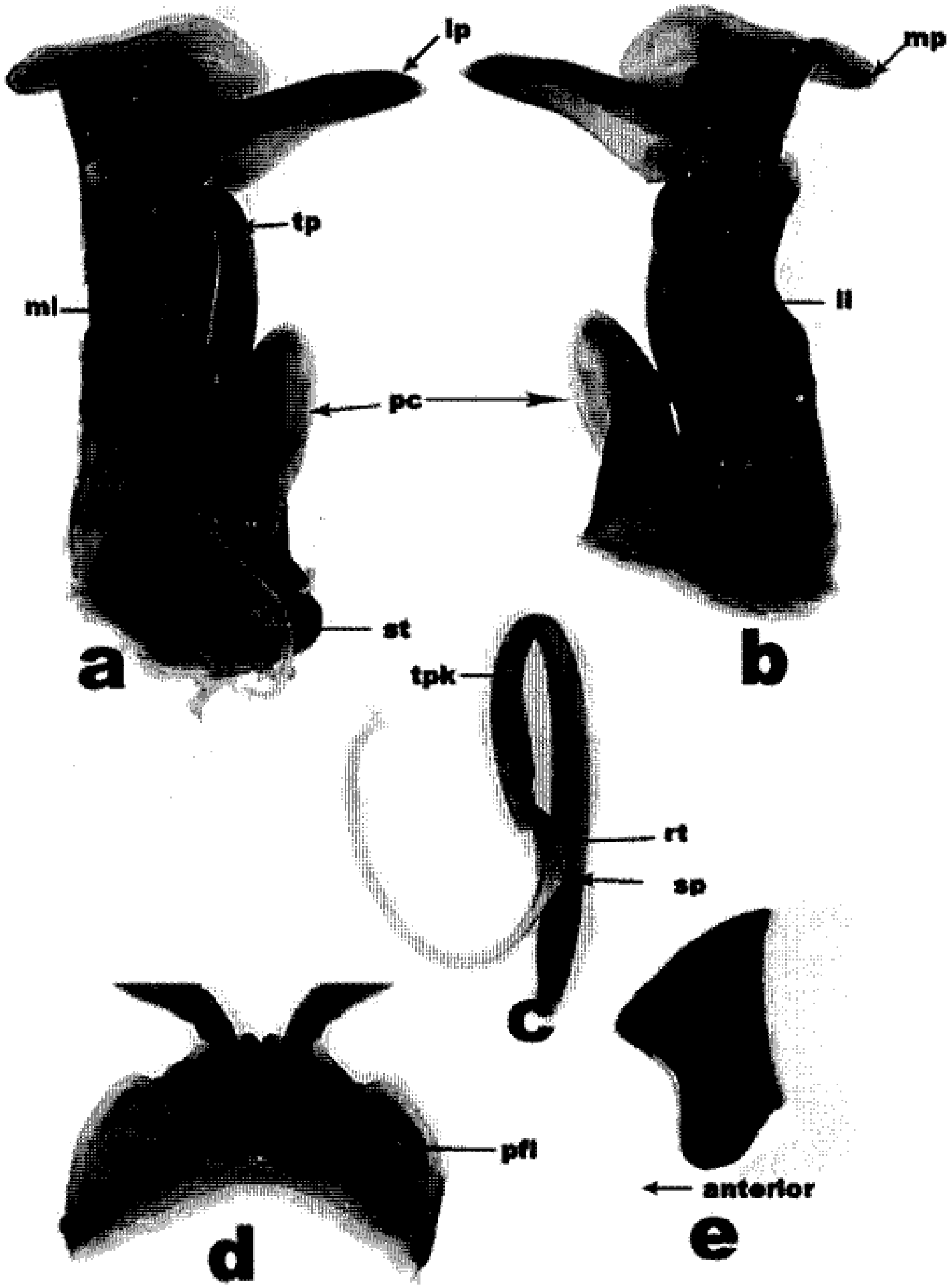

Fig. 9

FIGURE 9. *Brevitibius polyptychus* (HTO 18.229). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of proximal part of telopodite; **d,** oral view of prefemoral lobe of first pair of male legs; **e,** lateral view of collum. Abbreviations: ll, lateral leaf; lp, lateral process; ml, median leaf; mp, median process; pc, paracoxite; pfl, prefemoral lobe; rt, region of torsion; st, sternite; tp, telopodite; tpk, telopodite knee; sp = spine.

Key to the species of *Bicoxidens*

1. Apical region of telocoxite with a flattened median process that overlaps the opposite one; median leaf with an apical median axe-shaped process; telopodite with a long femoral lobe (Figs. 2a, 5a)..................2

- Apical region of telocoxite without a flattened median process; median leaf without apical axe-shaped process; telopodite with a short femoral lobe (Figs 1a, 3a, 4a, 6a, 7a, 8a) 3
2. Apical telocoxite with a horizontal lateral process; apically lateral leaf with a small, transverse, ear-shaped aboral projection (Fig. 5b) .... ***grandis***
- Apical telocoxite without lateral process; apical lateral leaf with a small rounded aboral lobe on distal margin (Fig. 2b) .... ***flavicollis***
3. Apical telocoxite T-shaped, with three median processes and a long lateral process. Middle median process overlaps with the process from the opposite telocoxite (Figs. 3a, 3b) .... ***friendi***
- Apical telocoxite not T-shaped, without three median or a long lateral process 4
4. Apical telocoxite not oval. Aboral lateral leaf lobe basally rounded and not produced into a lateral extension 5
- Apical telocoxite oval. Aboral lateral leaf lobe basally not rounded and produced into a lateral extension (Fig. 8a) .... ***nyathi*** sp. n
5. Apical telocoxite with two broadly rounded median processes that may be in touch 6
- Apical telocoxite with three narrowly rounded or overlapping median processes 7
6. Apical telocoxite with an overhanging folded lateral process above and not extending beyond knee bend; median processes do not touch; median leaf constricted subapically but without a basal lateral lobe (Figs. 4a, 4b) .... ***gokwensis*** sp. n.
- Apical telocoxite with a broadly rounded lateral process above and extending beyond knee bend; median processes reciprocally in touch, leaving a window between them; sub-apically (below setose area), median leaf constricted and with a basal lateral lobe (Fig. 6a) .... ***matopoensis*** sp. n
7. Apical telocoxite bird head-shaped with three median processes, the middle long, beak-like and overlapping the opposite one (Figs. 1a, 1b) .... ***brincki***
- Apical telocoxite not bird head-shaped, with two median processes that do not overlap. (Fig. 7a) .... ***nigerrimus***

Discussion

Taxonomy

As in other spirostreptid genera, gonopod characteristics are the most widely used in *Bicoxidens* taxonomy. Telocoxite and telopodite are the two components of a gonopod (Figs.1a, 1b), with the latter being more important in generic definition and the telocoxite morphology used to differentiate species.

In *Bicoxidens*, the telopodite is characteristically L-shaped (post knee) and lacks torsion. Additionally, the presence of a pair of furrows on either side of the anal valve is consistent within the genus and distinguishes it from other large African spirostreptids including *Doratogonus* Attems, 1914, *Spirostreptus* Brandt, 1833, *Archispirostreptus* Silvestri, 1895, *Odontostreptus* Attems, 1914, *Taitastreptus* Van den Spiegel, 2001, *Pseudotibiozus* Demange, 1870, *Brevitibius* Attems, 1950 and *Kartinikus* Attems, 1914. At present it appears that the presence of these furrows is the only reliable external character, other than gonopods, that characterises *Bicoxidens*.

Several other external body characteristics are of limited taxonomic value because they vary intra-specifically. These include body size and number of body rings. For specimens preserved in alcohol, colour (body, antennae and leg colour) was also not a reliable character because live colour was lost.

It is the structure and shape of the telocoxite in *Bicoxidens*, particularly the distal or apical parts that have lobes and processes which show consistent variation between species. However, just the presence and number of lobes or processes on the gonopods and sternite shape are of little taxonomic value. Although the telopodite is generally limited to generic differentiation it appears that the length of the femoral lobe, distal overlap between distal telocoxite processes, extent of looping and position in relation to tip of sternite are useful in defining *Bicoxidens* species or perceived species groups. The shape of the prefemoral lobe of the first pair of male legs may be a useful specific character, however, in *flavicollis* this shows intraspecific variation among populations.

B. flavicollis is the most common and widely distributed species in this genus, which occurs in diverse habitats south of Zambezi River. Different populations do not display wide size variation. However, body colour differs depending on geographical location. Although black is the most common colour, yellow and brown specimens have been recorded in the eastern highlands along the Zimbabwe-Mozambique border.

Besides being outside the known distribution range of *Bicoxidens* species (Fig. 10), *polyptychus* is superficially similar to the species in this genus. Its morphological characters are not consistent with the genus except those most likely influenced by environmental factors. The telopodite of *polyptychus* is unlike that of *Bicoxidens*, and does not fit the generic diagnosis.

We propose that *polyptychus* be assigned to another genus. Besides having a collum with a prominent anterior lobe with up to 9 complete and 2 incomplete folds; lacking two furrows on either side of the anal valve and having an arrow-head shaped paracoxite, the most remarkable differences are found on the telopodite, which has torsion unlike that of *Bicoxidens* (Fig. 9c). In addition, other external body dimensions fall outside the range for *Bicoxidens* species, *polyptychus* is larger with more body rings and greater body diameter.

B. polyptychus, described from Katanga Province, Democratic Republic of Congo, is therefore removed from *Bicoxidens* and tentatively placed in *Brevitibius*. Some external body characteristics of *polyptychus* also resemble some species of *Spirostreptus, Odontostreptus* and *Archispirostreptus*. Revisions of other spirostreptid genera are therefore necessary in order to establish the generic position of *polyptychus* and bring about taxonomic stability in the spirostreptids.

The results of the phylogenetic analysis also supports our assertion that *polyptychus* is not a *Bicoxidens*. This is illustrated in the cladogram by its early and strongly supported separation from *Bicoxidens* species (Fig.11). The wide geographical separation from *Bicoxidens* species provides additional support to these observations and conclusion.

Species Groups

Bicoxidens is a monophyletic group that is strongly supported in the consensus tree (Fig. 11). The distal telocoxites are distinct and characteristic of each species. Three species groups are apparent.

Group B is the most speciose. The gonopods of Group B species have a characteristic distal telocoxite with a rounded lateral process (except for *nyathi*) and at least two median processes. These species also have a short femoral process on the telopodite, two complete collum folds and a prominent lateral leaf lobe. In all the species the distal telopodite (post femur) of gonopods overlap above the apex of sternite.

B. grandis forms a strongly supported clade with *friendi* (Group A), this *friendi-grandis* clade has a T-shaped distal teloxoxite and is a sister group of Group B species.

B. flavicollis forms a widely distributed monotypic group (Group C), a sister taxon of all other *Bicoxidens* species (Fig. 11). The distal telocoxite has a characteristic flattened and tapering median process that completely overlaps the opposite one. The gonopod is similar to that of *grandis* in that both species have axe-shaped processes on the median leaf and a long femoral process, both lack a large lateral leaf lobe (Figs. 2a, 5a).

The morphological similarities of *flavicollis* and *grandis* gonopods may be a result of homoplasy. Hamer and Slotow (2000) reported possible homoplasies in the related genus *Doratogonus*.

Character and data matrix for cladistic analysis of *Bicoxidens*

1. Shape of tip of prefemoral extension 1^{st} leg pair of male: 0—arrow-head shaped; 1—broadly rounded; 2—spade shaped
2. Number of telocoxite processes: 0—2; 1—3; 2—4; 3—1
3. Telocoxite median process overlap: 0—no overlap: 1—overlap;
4. Hammer-shaped process on median leaf: 0—absent; 1—present;
5. Lateral leaf lobe extending from telocoxite: 0—absent; 1—long bulb/flask haped, broadly rounded basally; 2—small diagonal ear shaped; 3—small rounded, nipple shaped; 4—long acutely rounded, small basally
6. Telopodite post femur: 0—not parallel and not overlapping; 1—overlapping and parallel; 2—overlapping not parallel
7. Extent of looping: 0—no looping; 1—incomplete; 2—complete
8. Telopodite tip overlap: 0—do not overlap; 1—at or above sternite; 2—on opposite gonopod
9. Femoral lobe length: 0—absent; 1—short not extending to femoral bend; 2—long extending to femoral bend
10. Sternite apex: 0—not as 1 and 2; 1—below overlapping telopodites; 2—same level as sternite tip or past overlapping telopodites

TAXON	CHARACTER STATES
	1 10
S. sebae	0000000000
polytychus	2000000000
friendi	2210111112
grandis	2011211122
nigerrimus	2300121111
brincki	2310121211
flavicollis	1311322222
matopensis n.sp.	2110111211
gokwensis n.sp.	1300112211
nyathi n.sp.	1100421111

Faunistics and Distribution

Bicoxidens species occur in diverse habitats, ranging from dry savanna to relatively wet miombo woodland. Figure 10 shows the area south of Zambezi River, covering Zimbabwe, as the centre of *Bicoxidens* radiation.

According to Nyamapfene's (1981) analysis of rainfall-vegetation relationships in Zimbabwe, montane vegetation and miombo woodland dominate the eastern highlands which receive more than 1000 mm of reliable rainfall per year. Central areas are mainly savanna and miombo woodland; they receive about 750 mm per year. The southern areas and Zambezi Valley are dry savanna, which receive less than 650 mm of erratic rainfall per year. These conditions may have heavily influenced speciation and distribution of *Bicoxidens* species.

All *Bicoxidens* species occur between the Zambezi and Limpopo Rivers except for *brincki*, which has also been recorded in the Kruger National Park, South Africa, and *flavicollis*, which has been collected in Maguge, Mozambique. *Bicoxidens* species show strict habitat fidelity, the patchiness of preferred habitats in the savanna coupled with their poor dispersal ability possibly being the cause of the genus radiation in Zimbabwe.

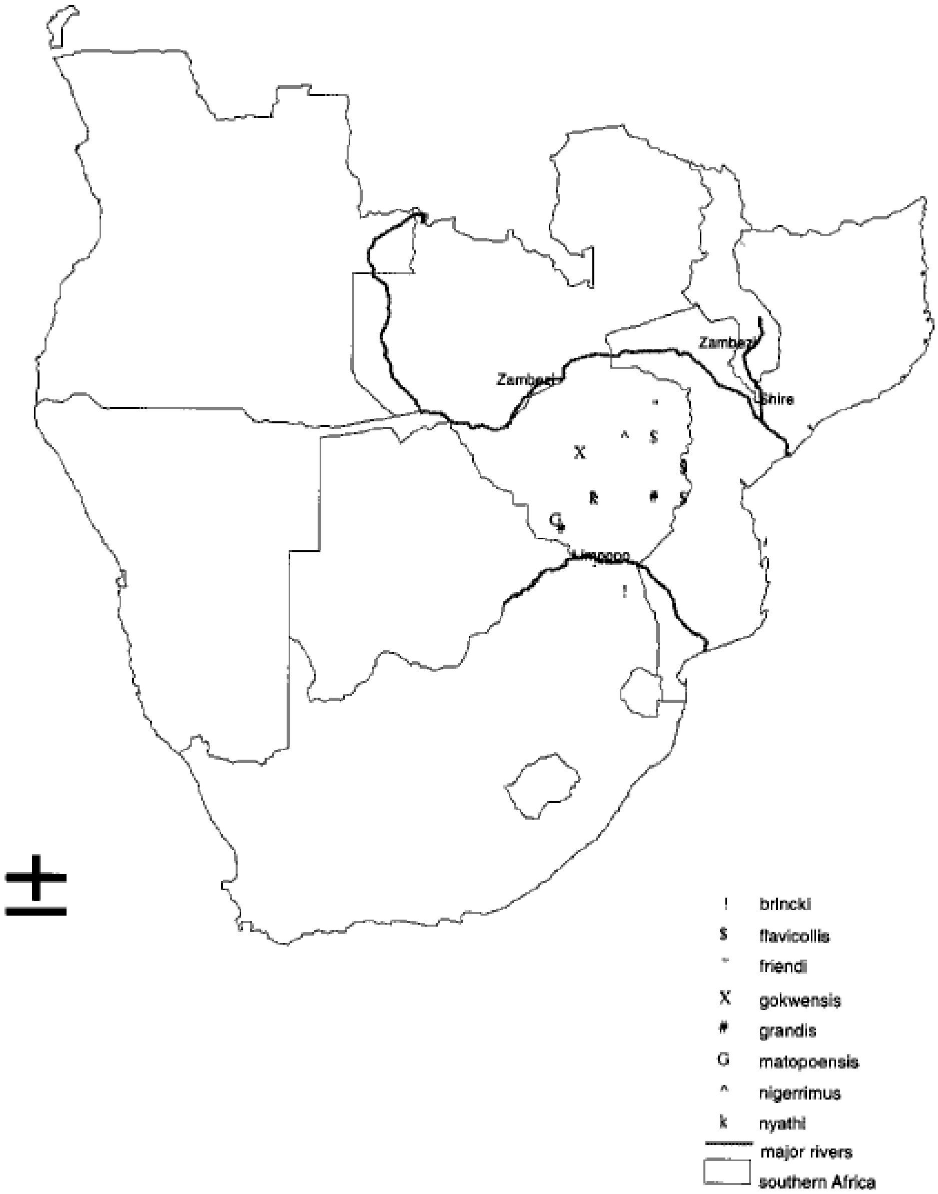

FIGURE 10: Distribution of Bicoxidens species

Unlike larger spirostreptids, *Bicoxidens* species are relatively less mobile and occur in small groups in the preferred moist and sheltered microhabitats. The surface activity of small species appears to be restricted to short periods during the wet season. All these factors and attributes would restrict gene flow, increase or maintain genetic distance between populations and enable taxa to remain or become genetically isolated and distinct.

The restricted distribution is remarkable and appears to support the argument that rainfall and vegetation are major factors that influence distribution patterns of *Bicoxidens* species. The smaller species, *flavicollis*, *nigerrimus*, *nyathi*, *matopoensis* and *gokwensis*, seem to occur in regions that have more woody vegetation and receive more rainfall.

Although rivers are known barriers to several animal taxa, it is unlikely that Zambezi and Limpopo Rivers alone could have been sufficient barriers to *Bicoxidens* dispersal. Hamer and Slotow (2000) suggested that a dispersal corridor across the Limpopo River may exist, linking the northern and southern populations of some species of *Doratogonus*. *B. brincki* may be one of many taxa that could have exploited similar corridors. However, the Zambezi River and the sudden change of biome could have restricted the spread of the genus northwards into Zambia. The Zambezi Valley is large, dry and generally a less habitable environment; therefore, it is likely to represent a greater challenge to *Bicoxidens* dispersal northwards.

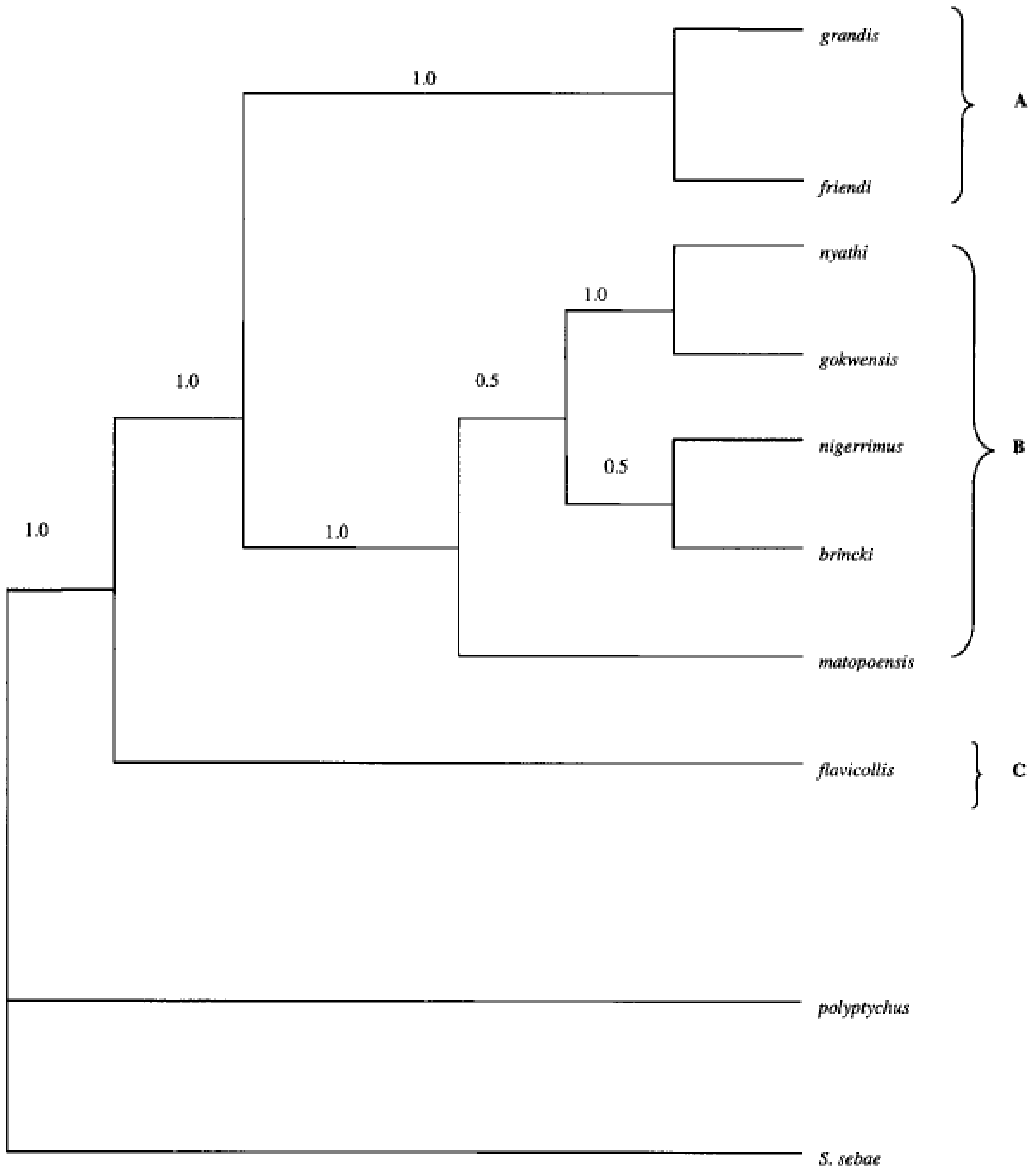

FIGURE 11. A consensus tree of *Bicoxidens* species using *S. sebae* as an outgroup. The numbers indicate the number of times the groups to the right of each fork occur among the trees out of 1.00 trees.

Until more areas in southern Africa are surveyed and material in museums studied, any conclusions on distribution patterns and speciation of taxa will be difficult to defend. It is estimated that several species of *Bicoxidens* are yet to be described and new distribution records await discovery. This is corroborated by the three new species described here and new distribution records of *flavicollis* in Mozambique and *brincki*, *nigerrimus* and *grandis* from south and western Zimbabwe (Mwabvu, 2005).

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A new species of *Bicoxidens* Attems, 1928 (Diplopoda, Spirostreptida, Spirostreptidae) species from northern Zimbabwe

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Abstract

Bicoxidens aridis **sp. n.** is described from five male specimens collected from northern Zimbabwe. Besides being the smallest member of the genus, *B. aridis* has a hook-shaped distal telocoxite, a telopodite with a long postfemur and a proximal clockwise coil. The discovery of this species suggests that the geographical range of the genus may extend further north into Zambia.

Keywords

Millipede, gonopod, telocoxite, proplica, metaplica, telopodite, endemic, southern Africa.

Introduction

According to Mwabvu et al. (2007), many southern African millipedes are unknown to science because several habitats have not been surveyed and because large quantities of material held in museums has not been studied. Our knowledge of the region's millipede diversity and distribution is therefore incomplete (Mwabvu et al. 2007).

The genus *Bicoxidens* is endemic to southern Africa (Mwabvu 2000). It has been recorded in savanna woodland, riverine vegetation and forests south of the Zambezi River (Mwabvu et al. 2007). The distribution of *brincki* Schubart, 1966 extends southwards from Zimbabwe across the Limpopo River into the Kruger National Park, South Africa, and *flavicollis* Attems, 1928 extends eastwards from Zimbabwe to Maguge in western Mozambique (Mwabvu et al. 2007), but otherwise the genus seems to be restricted to Zimbabwe, particularly the central, eastern and southern regions (Fig. 3). Details of localities and synonymies of known species are provided in Mwabvu et al. (2007).

The genus is characterized by a telopodite which has neither antetorsal process nor torsotope, but which may have one or two lobes at the femur and terminally. Until now *Bicoxidens* had not been recorded from the Zambezi Valley, which led to the suggestion that the hot and arid conditions in the valley are less habitable and, therefore, restricted the spread of the genus northwards (see Mwabvu et al. 2007). However, a recent study of millipedes held in the Natural History Museum, uncovered a new species from the Zambezi Valley in northern Zimbabwe.

Material and methods

The material examined is housed in the Royal Museum of Central Africa, Tervuren, Belgium (MRAC) and the Natural History Museum, Bulawayo, Zimbabwe (NMZ).

Methods follow Mwabvu et al. (2007), and terminology follows Hoffman (2008). Specimens were studied using a Carl Zeiss Stereo microscope (Stemi DV4) and photographed using auto montage software (Leica Microscope MZ12s with 3 CCD Toshiba Camera). Adobe Photoshop CS (version 8) was used to manipulate the images and prepare the plate. In addition, images of the telopodite were produced using a JEOL JSM-6480LVscanning electron microscope. Material for electron microscopy was prepared following Barnett et al. (1991). ArcGis (Arcmap 9.1) was used to prepare the distribution map of species.

Description

Bicoxidens aridis **Mwabvu, sp. n.**
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Type material. Holotype: ZIMBABWE: 1 ♂, Mbizi Pan [1628C4], 12. XII. 1983, Putterill G. (NMZ/D156).

Additional material examined. ZIMBABWE: 1 ♂, Nyamapanda [16° 90' S, 32° 80' E], XII.1998, Mwabvu T. (MRAC 20554); 2 ♂, Mushumbi Pools [1630B1], 22-25.XI.1997, (NMZ/D819); 1 ♂, Chimutsi (NMZ/D272).

Etymology. Specific name refers to the fact that the species occurs in a dry, low rainfall region.

Diagnosis. Distal telocoxite folded towards apical proplica, producing a hook shape and a median cavity (Figs 1a, 1b); lateral margins of proplica and metaplica setose; postfemur of telopodite as long as proplica, with a proximal clockwise coil distal to the femoral lobes, and without looping at the extremity (Fig. 2).

Description

Dimensions. Body length 73-88 mm; minimum and maximum body width 3-4 mm and 3.5-6 mm, respectively; antenna length 4-5 mm, extending up to the 3rd body ring; leg length 3-4 mm.

Number of body rings. 54-56.

Colour. Body light to dark brown; head light brown; antennae dark brown to black; posterior part of metazonite dark brown or black; prozonite cream; legs light brown.

Gnathochilarium. With long setae along distal margin of the stipes and lingual lamella; one small papilla behind and between the larger two.

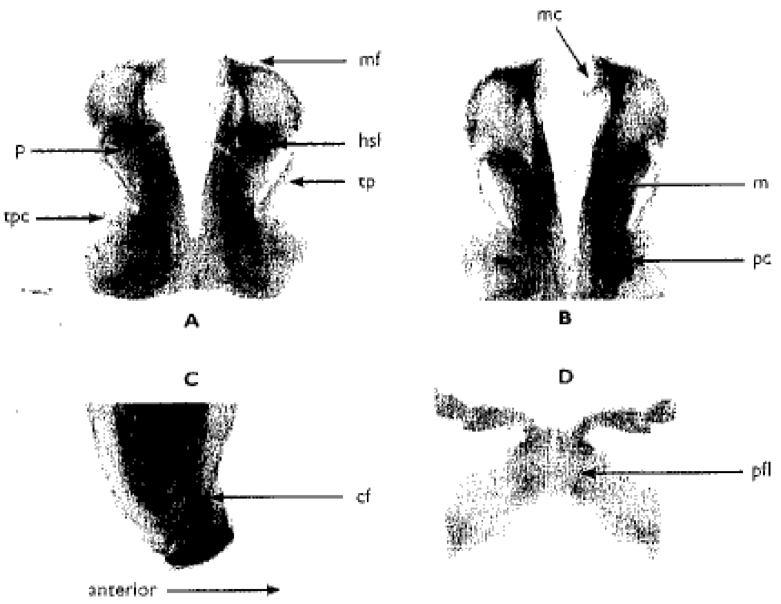

Figure 1. *Bicoxidens aridis* sp. n. **A**, oral view of gonopods; **B**, aboral view of gonopods; **C**, lateral view of collum; **D**, oral view of prefemoral lobe of first pair of male legs. Abbreviations: **p**, proplica; **hsl**, heart-shaped lobe; **m**, metaplica; **mc**, median cavity; **tp**, telopodite; **tpc**, telopodite coil; **mf**, metaplica fold; **cf**, collum fold; **pfl**, prefemoral lobe; **pc**, paracoxite.

First ozopore. On 6th body ring close to or on sigilla row.

Collum. Anterior corner rounded or square in shape, not produced into a lateral lobe, with 2-6 submarginal folds (Fig. 1c).

First pair of legs. Tarsal claws straight, but gently curved apically; prefemoral processes proximally parallel, but not touching medially, with laterally directed nipple-shaped apical lobes that are widely separated distally (Fig. 1d).

Sigilla. One row of large circles.

Midbody ring. Diameter of metazonite greater than prozonite, prozonte with up to 16 striae that are further apart posteriorly; limbus with straight edge.

Gonopod. (Figs 1a, 1b, 2) 4 mm long, with a triangular sternite; paracoxite rounded apically and basally fused to metaplica. Distally, metaplica of telocoxite hook shaped, laterally rounded and folded towards and overhanging apical region of proplica of telocoxite forming a median cavity (Figs 1a, 1b). Lateral margins of proplica and metaplica setose. Orally proplica with an apical heart-shaped lobe which conceals the telopodite at the knee (Fig. 1a).

Proximal half of telopodite broader than distal (postfemoral) half. Length of postfemoral region of telopodite equal to that of proplica. Telopodite bends laterally and produces a tight clockwise coil distal to the femoral lobes, above level of the paracoxite

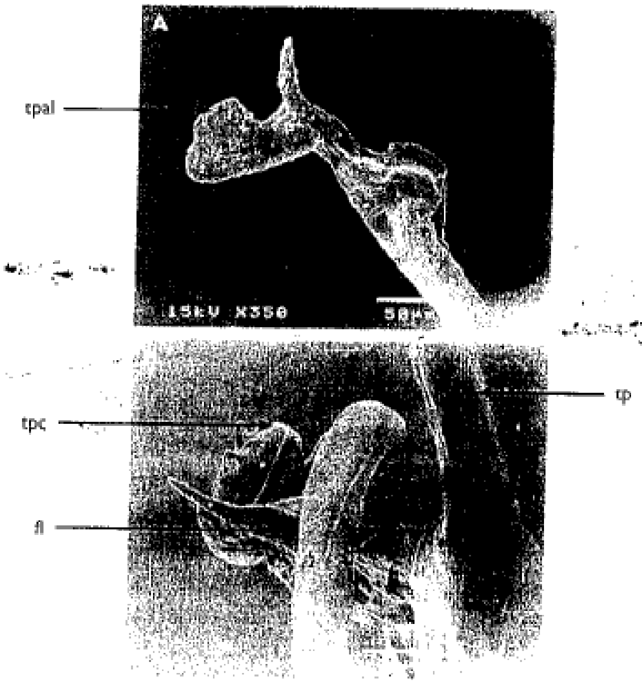

Figure 2. *B. aridis* sp. n. **A,** telopodite apex; **B,** telopodite coil. Abbreviations: tp, telopodite; fl, femoral lobe, tpc, telopodite coil; tpal, telopodite apical lobe.

(Figs 1a, 2b). Postfemur of telopodite extends distally towards the telocoxal apex and crosses the post knee part proximal to the coil and femoral lobes (Fig. 1a). Telopodite without apical looping, but with two unequal lobes at the extremity (Fig 2a).

Distribution. Appears to be widespread in the Zambezi Valley and northern Zimbabwe, a dry savanna region characterised by high temperatures and low, unreliable rainfall (Nyamapfene, 1991).

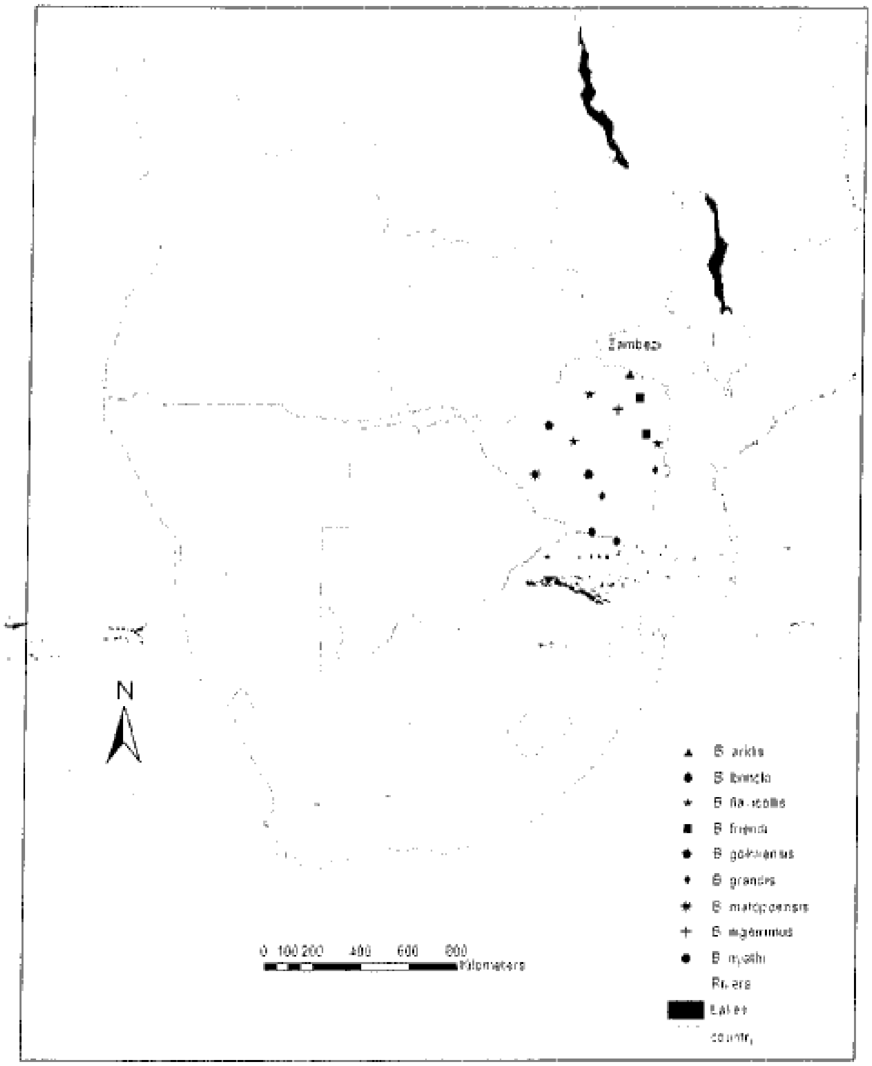

Figure 3. Distribution of *Bicoxidens* species

Comparisons

In terms of body width, *B. aridis* is the smallest among the known species in the genus. Other major differences relate to the structure and shape of the apical gonopod, and the clockwise coil of the telopodite at the femur.

Although the apical folding of the metaplica is more pronounced and produces a median cavity in *aridis*, folding of this structure is not unique to *aridis*; varying degrees of folding of the distal telocoxites was reported by Mwabvu et al. (2007) in *brincki*, *friendi* Mwabvu, 2000, *gokwensis* Mwabvu, 2007, *matopoensis* Mwabvu, 2007 and *nyathi* Mwabvu, 2007. However, the characteristic median cavity and telopodite coil are present in *aridis* only.

Unlike congeners, the distal telocoxite of *aridis* lacks lateral processes such as those found in *friendi*, *grandis* Lawrence, 1965, *nyathi* and *nigerrimus* Attems, 1928 or median processes similar to those found in *brincki*, *flavicollis*, *gokwensis*, *grandis*, *matopoensis* and *nyathi*.

Distally the proplica has a heart-shaped lateral lobe which covers the telopodite at the knee (Fig. 1a); which appears to prevent the telopodite from slipping out of the gonoschisma. A similar function was suggested for the apical lobe of the proplica which is found in *flavicollis* and *grandis* (see Mwabvu et al. 2007).

Unlike other species, the aboral surface of the metaplica of *aridis* does not have a lobe or projection at the level of the apical proplica. Additionally, the lateral margins of the metaplica and proplica are setose, while in other species only the apical region of the proplica is setose.

The post knee region of the telopodite of *aridis* is approximately twice as long as the proplica, in addition, the post knee telopodite is not L-shaped nor deflected medially at the level of the paracoxites or sternite (Figs 1a, 1b) as is the case in congeners (see Mwabvu et al. 2007). The telopodite typically produces a single clockwise coil just after the femoral lobes and lacks terminal bending or looping, making the shape of the telopodite unique to *aridis*.

An additional couplet would have to be added to the key to *Bicoxidens* species in Mwabvu et al. (2007) in order to accommodate *aridis*. This becomes the first couplet because the shape of the distal region of the telocoxite and the structure of the telopodite distinguish *aridis* from congeners.

1 Apical metaplica hook-shaped and with a median cavity (Figs. 1a, 1b), without produced lateral or median processes; post knee telopodite not L-shaped (Fig. 1a), with a clockwise coil after the femoral lobes and without looping at the extremity (Fig. 2) .... ***Bicoxidens aridis* sp. n.**

– Apical metaplica not hook-shaped and without a median cavity; with produced lateral or median processes; post knee telopodite L-shaped, without a clockwise coil after the femoral lobes and with looping at the extremity........ .... **2** (all other *Bicoxidens* species)

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CHAPTER 2

A TAXONOMIC REVIEW OF THE SOUTHERN AFRICAN MILLIPEDE GENUS, *Bicoxidens* Attems, 1928 (DIPLOPODA: SPIROSTREPTIDA: SPIROSTREPTIDAE) WITH THE DESCRIPTION OF THREE NEW SPECIES AND A TENTATIVE PHYLOGENY.

A NEW SPECIES OF *Bicoxidens* ATTEMS, 1928 (DIPLOPODA, SPIROSTREPTIDA, SPIROSTREPTIDAE) SPECIES FROM NORTHERN ZIMBABWE.

LIST OF ERRATA

Chapter 2: **A taxonomic review of the southern African millipede genus, *Bicoxidens* Attems, 1928 (Diplopoda: Spirostreptida: Spirostreptidae) with the description of three new species and a tentative phylogeny.**

1. **Minimum and maximum body width**

The values are definitely wrong. The correct minimum and maximum body width ranges for *B. brincki* should be 6–9 and 8–11 mm, respectively.

2. **Page 15, minimum and maximum body width**

The minimum and maximum body width for *B. nyathi* should be 5 and 7 mm, respectively.

3. **"Telocoxite and telopodite are the two components of a gonopod". This is a gross simplification.**

The correct statement should read: The telocoxite and telopodite are the most taxonomically useful components of gonopods in *Bicoxidens*.

4. Reasons for synonymising *B. nasti* and *B. flavicollis*

After studying more material and after using SEM *B. nasti* and *B. flavicollis* were synonymised because similarities in the genitalia were enough to consider them the same species.

5. Distribution map of *Bicoxidens* species

The distribution map of *Bicoxidens* species (below) is an improved version of Figures 10 and 3 in the published taxonomic revision of *Bicoxidens* (Mwabvu *et al*. 2007), and in the published description of *B. aridis* (Mwabvu *et al*. 2009), respectively (Chapter 2 in the thesis). The recent map includes all the available distribution data for the genus.

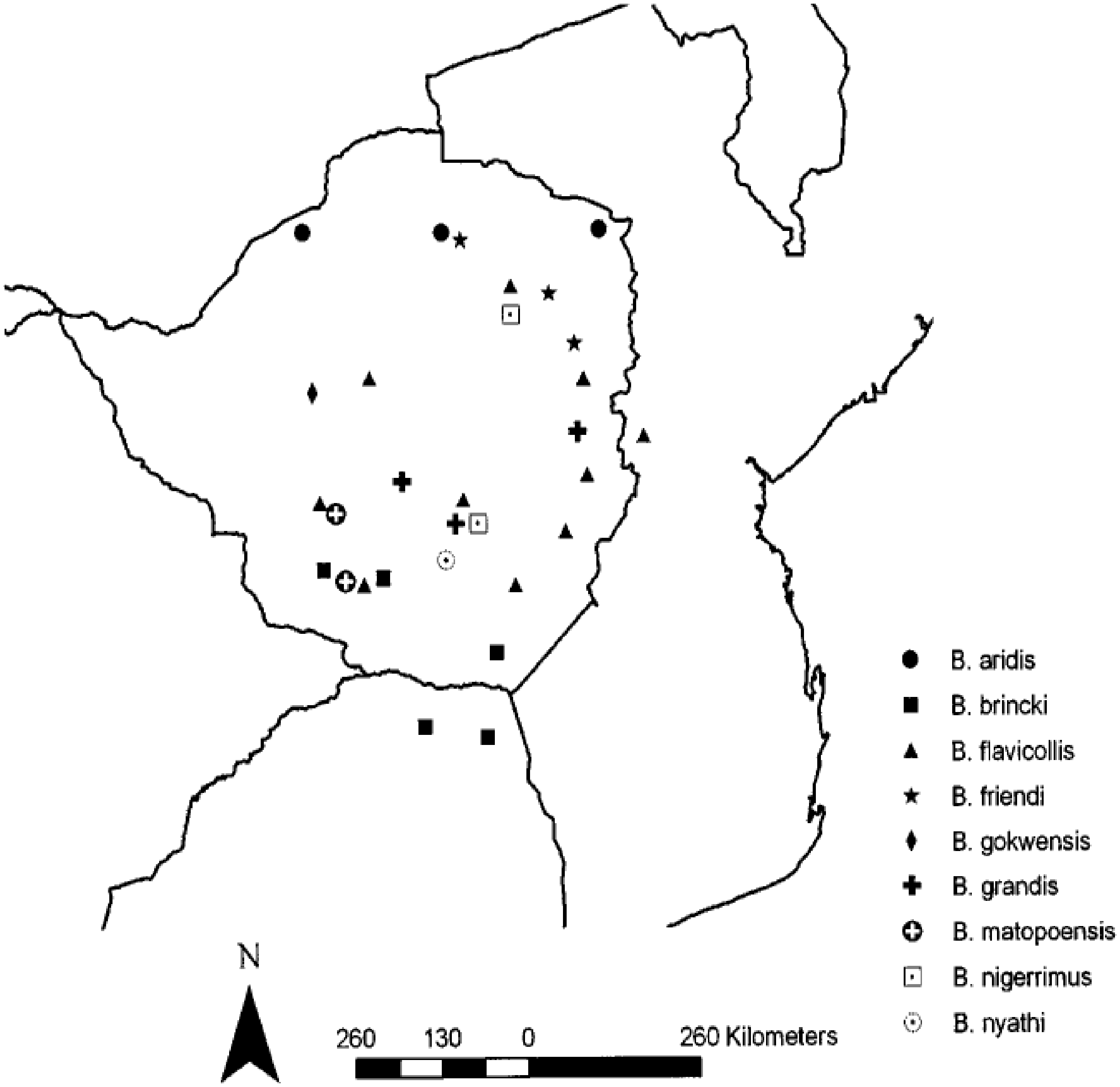

FIGURE 10. Distribution of *Bicoxidens* species.

CHAPTER 3

A REVISION OF THE TAXONOMY AND DISTRIBUTION OF *Spirostreptus* Brandt 1833 (DIPLOPODA, SPIROSTREPTIDA, SPIROSTREPTIDAE) WITH DESCRIPTIONS OF A NEW SPECIES AND A NEW GENUS OF SPIROSTREPTID MILLIPEDE.

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A revision of the taxonomy and distribution of *Spirostreptus* Brandt 1833 (Diplopoda, Spirostreptida, Spirostreptidae) with descriptions of a new species and a new genus of spirostreptid millipede

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Abstract

The giant millipede genus *Spirostreptus* Brandt 1833 is revised to include six species from Africa, south of the Congo River. The six species formerly included in the genus were *S. heros* Porat 1872, *S. kruegeri* Attems 1928, *S. sebae* Brandt 1833, *S. tripartitus* (Cook & Collins 1893), *S. unciger* Attems 1928 and *S. kymatorhabdus* Attems 1914. *Spirostreptus kymatorhabdus* is here removed from *Spirostreptus* and accommodated in the new genus *Namibostreptus*. A new species, *S. batokensis* Mwabvu from Zimbabwe, is described. A key to the species of *Spirostreptus* species based on gonopod morphology is presented. Despite the remarkable similarity between the gonopods of *S. heros* and *S. kruegeri*, the two species are distinct. *Spirostreptus* has strict fidelity to the savanna biome, with overlapping distributions of species, thus making conservation of many species in one biome possible.

Key words: savanna, millipedes, gonopod, identification key, conservation, southern Africa

Introduction

Millipedes constitute a major part of soil macrofauna (Crawford 1992) both in terms of numbers of species and biomass (Dangerfield 1990). They enhance organic matter breakdown (Bond & Sierwald 2002; Sierwald & Bond 2007) and mix organic matter with upper soil layers (Edwards *et al.* 1970). The high densities of millipedes that emerge from the soil during the rainfall season and their relatively large body size suggest a much greater role as detritivores in tropical environments than previously estimated. Crawford (1992) ranked millipedes behind earthworms and termites as one of the major groups important in the breakdown of organic matter. Dangerfield and Telford (1989) estimated that millipedes in tropical miombo woodland would consume close to 30.6 % of annual litter fall.

Millipedes prefer moist microhabitats, which are often patchy, and because millipedes are unable to completely close their spiracles, their ability to disperse over long distances is limited. Therefore many millipede species are isolated and occur in small areas (Hopkin & Read 1992), which makes them vulnerable to habitat disturbance and extinction (Hamer & Slotow 2000; 2002), and this also means that they are suitable bioindicators for ecological studies. Despite being conspicuous, important in ecological processes, diverse (552 species in southern Africa: Hamer 1999, 2000) and habitat specific, millipedes remain neglected and under-utilised in biodiversity/conservation studies. This is largely due to lack of up to date data on diversity and distribution (Hamer & Slotow 2000), and the scarcity of millipede taxonomists (Hamer 1997).

Because of the threats to invertebrate diversity due to habitat alteration (New 1995; Hamer 1997), it is essential that surveys and taxonomic studies on millipedes are conducted to establish species diversity and distribution. The number of millipede species recorded in southern Africa could increase substantially once

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forested habitats have been sampled, existing and new material studied, and taxa revised (Hamer 1997). The efforts would provide useful data for invertebrate conservation programmes and enhance the understanding of the factors and processes that may influence speciation and distribution.

Seventy-nine millipede genera have been recorded in southern Africa (Hamer 1997). Twenty-three belong to four families in the Order Spirostreptida (Hamer 1999); most of these genera are endemic to the region (Hamer 1997). Among the 23 genera are the large, yet poorly studied and under-collected genera *Archispirostreptus* Silvestri 1895, *Spirostreptus* Brandt 1833, *Limnostreptus* Hoffman 2008, *Choristostreptus* Hoffman 2008 and *Plagiotaphrus* Attems 1914. These genera belong to the Tribe Spirostreptini based on a prostatic groove which branches into two or three small distal processes (Hoffman 2008). The species composition of the Spirostreptini has been the subject of intense scrutiny, with the validity of several taxa questioned (Hoffman 1971, 2008). In addition, the actual distributions of most of these taxa are doubtful or unknown (see Hoffman 1971, 2008).

Prior to the redefinition by Hoffman *et al.* (2001), *Spirostreptus* was considered problematic because of ambiguous generic limits. Hoffman *et al.* (2001) regarded Krabbe's (1982) list of 39 *Spirostreptus* species too inclusive, and suggested that she had included many species that were not congeneric.

Krabbe (1982) listed nine species under *Triaenostreptus* Attems 1914: *T. benedictus* (Kraus 1958), *lykophorus* (Attems 1935) and *tripartitus* from Angola and the Democratic Republic of Congo, *lawrencei* (Hoffman 1971) from Malawi, *kymatorhabdus* from Namibia and the more southern *heros*, *sebae*, *unciger* and *kruegeri*. According to Krabbe (1982), *unciger* was recorded from the Transvaal (Limpopo Province, South Africa); *kruegeri* from the Transvaal (Limpopo Province) and Guborone (Botswana); *sebae* from Mazowe (Zimbabwe) and Beira (Mozambique); and *heros* from the Kalahari (Botswana) and Kimberley (North West Province, South Africa). Since the publication of Krabbe's (1982) list, new locality records for *heros*, *sebae*, *unciger* and *kruegeri* have been added following collecting surveys and processing of museum material.

The redescription and identification of *S. sebae* (see Golovatch & Hoffman 2000; Hoffman *et al.* 2001) as the type species for the genus, which in turn is the type genus of the family, had implications for the nomenclature of spirostreptids. Firstly, *Triaenostreptus* became a subjective junior synonym of *Spirostreptus* and, therefore, Triaenostreptinae and Triaenostreptini were rendered invalid (Hoffman *et al.* 2001), as was suggested earlier by Hoffman (1979). Secondly, the authors confirmed synonymy of *T. triodus* Attems 1928 with *S. heros*, and *T. petersi* Attems 1928 with *S. sebae*.

Although the improved understanding of *Spirostreptus* has stabilised the taxonomy of Spirostreptida (Hoffman *et al.* 2001), problems at the species level remain because earlier species descriptions were based on few characters of taxonomic value (Hoffman 1979). Therefore, some taxa may not be valid or correctly assigned to genera because their description may have been based on homoplastic characters. A partial solution is the recent erection of two new genera, *Limnostreptus* and *Choristostreptus*, by Hoffman (2008) for *benedictus* and *lykophorus*, and *lawrencei*, respectively. This leaves *S. sebae*, *heros*, *unciger*, *kruegeri*, *tripartitus* and *kymatorhabdus* as the valid species in *Spirostreptus* prior to this revision. The recent collection of new material provided the opportunity to revise the genus *Spirostreptus* and examine its distribution.

According to Attems (1928), *Spirostreptus* is defined by a broad distal telocoxite that surpasses the lateral margins of the proplica, the presence of a digitiform lateral lobe produced from the lateral edge of the telocoxite (aboral to the knee bend of the telopodite) and three widely separated sclerites that form the prebasilar plate of the gnathochilarium. Based on this diagnosis, Hoffman's (1971, 2008) suggestion that some of the species are incorrectly assigned to *Spirostreptus* appears to be well founded and requires further investigation.

The main objectives of the study were to revise *Spirostreptus*, produce a key to species based on gonopod morphology, establish distribution patterns and clarify relationships between the species.

Materials and methods

This study relied on material from museums and recent surveys. Museum abbreviations used are as follows:

SAM	South Africa Museum, Cape Town, South Africa
MRAC	Royal Museum of Central Africa, Tervuren, Belgium
NMSA	Natal Museum, Pietermaritzburg, South Africa
NMZ	Natural History Museum, Bulawayo, Zimbabwe
ZMB	Museum für Naturkunde, Humboldt Universität, Berlin, Germany
ZMUC	Natural History Museum (Zoological Museum), University of Copenhagen, Copenhagen, Denmark
USNM	National Museum of Natural History, Washington, USA

Generally the methods followed those described in Mwabvu *et al.* (2007). Although colour would have changed in preserved specimens, body, leg and antenna colour were recorded for all specimens. Body rings (except head and anal valve) were counted. Body length was measured using a soft wire placed against the line of ozopores. Where the body rings were separated (as was the case for most preserved material) the body was reconstructed and length measured as before. Minimum and maximum body widths were measured using Vernier calipers. All the measurements are in millimeters. Although the measurements were mostly based on male specimens, females were also used when they were available. The male gonopods were dissected out, examined and photographed.

The telocoxite and telopodite of the male gonopod were examined. The telopodite was separated from the telocoxite to allow detailed examination. The absence/presence, size, shape and number of branches/processes/lobes, angle between lobes and relative length of various gonopod structures were compared and recorded.

Material was studied using a Nikon AZ100 stereo-microscope and a Carl Zeiss Stemi D4 stereo-microscope. Photographs were taken using NIS-elements D software and auto montage software (Leica Microscope MZ12s with 3 CCD Toshiba Camera), and the final images and plates were prepared using Adobe Photoshop CS (version 8). ArcGis (Arcmap 9.1) was used to prepare the distribution map of species.

Specimen data are presented as stated on the labels. Where the co-ordinates for the localities were not provided on the label, Google Earth (2009 Tele Atlas version) was used to estimate the co-ordinates.

This revision will follow the new terminology advanced by Hoffman (2008), who proposed the following terms for the gonocoxite structures: proplica for median leaf; metaplica for lateral leaf; gonoschima for gonocoel; and for the telopodite: torsotope for region of torsion; and antetorsal process for femoral process.

Results

Taxonomy

Genus *Spirostreptus* Brandt 1833

Spirostreptus Brandt 1833, p. 203 (type species: *Spirostreptus sebae* Brandt 1833; by subsequent designation of Pocock, 1894, p. 388); *Spirostreptus*: Attems 1914, 1928; Hoffman 1965, 1979, 2008; Krabbe 1982; Golovatch & Hoffman 2000; Hamer 1998, 1999; Hoffman *et al.* 2001; Mwabvu 2005b, 2006

Triaenostreptus Attems 1914, p. 149 (type species *Spirostreptus triodus* Attems 1909, by subsequent designation of Jeekel, 1970, p. 139); Attems 1928; Golovatch & Hoffman 2001; Hoffman 1971, 1979, 2008; Krabbe 1982; Hamer 1998

Diagnosis: Large spirostreptid millipedes, body length 162–344 mm; antennae 9–13 mm; minimum and maximum body width 4–15 mm and 11–19 mm, respectively.

Prozonite 1–3 mm wide and metazonite 1–2 mm wide.

Number of body rings 60–73.

Three separate sclerites form the prebasilar plate of the gnathochilarium.

Collum with an anterior lobe, black or dark brown in colour, with 2–5 complete folds and 0–7 incomplete folds.

Body black or brown in colour. Legs, antennae and anal valve colour generally lighter shades of body colour, often light brown.

Prozonite yellowish to brown; metazonite with one row of sagilla. Ozopores begin on 5th or 6th body ring.

Gonopod 6–9 mm long; sternite triangular; paracoxite fused tightly to the metaplica, apically horizontal. Telocoxites approximately parallel to each other, medial edge straight and close together.

Proplica approximately 2/3 of gonopod length; proplica broad sub-apically, setose apically. Proplica with a central groove flanked by sharply raised lateral and medial edges.

Thumb-like lateral lobe present between the distal telocoxite lobe and apical proplica, lateral lobe directed towards paracoxite at an angle to lateral edge of distal lobe.

Distal telocoxite enlarged and laterally produced into rounded golf club-shaped lobe (Figs 1a, 2a, 3a, 4a, 5a, 6a).

Metaplica with a small window through which part of pre-knee telopodite is visible (Figs 1b, 2b, 3b, 4b, 5b, 6b).

Telopodite knee and origin of antetorsal process concealed under apex of proplica. Antetorsal process tapering; post knee telopodite coils or spirals proximally, becoming lamellate before narrowing distally into a long thin extension with a trifurcate ending. Antetorsal process straight, S-shaped or crescent-shaped, with terminal spine (Fig. 7).

Distribution: Known from southern Africa (Angola, Botswana, Democratic Republic of Congo, Mozambique, Namibia, South Africa, Zambia and Zimbabwe).

Remark: Although Hoffman (2008) did not use the presence of the distal lobe and the slanting digitiform lateral lobe to define *Spirostreptus* in his key to the genera of Spirostreptini, we think that these characters are taxonomically more informative at the genus level than the form of the antetorsal process.

The distribution of the genus shows large gaps even in habitats similar to those from which the genus is known. These gaps are mainly in less accessible regions which suggest that current understanding of the distribution is a result of collecting bias rather than a true fragmentation.

Spirostreptus heros Porat 1872

Figs 1, 7a

Spirostreptus heros Porat 1872, p. 29; Hoffman *et al.* 2001; Mwabvu 2005a; Hoffman 2008
Spirostreptus triodus Attems 1909, p. 46, figs 76–79.
Triaenostreptus triodus: Attems 1928; Hoffman 1971, 2008; Krabbe 1982; Hamer 1998; Hoffman *et al.* 2001

Type material: Holotype: BOTSWANA: 1 ♂, Kalahari [22°36'S, 23°34'E]. (ZMB 4968).

Additional material examined: BOTSWANA: 1 ♂, 1 ♀, Gemsbok National Park, Kalahari [22°36'S, 23°34'E], 20.iv.1970, B. Lamoral (NMSA 16152); 1 ♂, 1 ♀, Kalahari [22°36'S, 23°34'E], 2005, (NMSA 20570). SOUTH AFRICA: **North West Province:** 2 ♂, Malopo [25°43'S, 24°17'E], 13.i.2001, R. Slotow & M. Hamer (NMSA 20495, 20498). **Northern Cape Province:** 1 ♂, 1 ♀, Northern Cape [27.697°S, 21.355°E], (NMSA 20551); 1 ♂, Northern Cape [27.697°S, 21.355°E], (NMSA 20495). NAMIBIA: 2 ♂, 5 ♀, Okawungo [18°18'S, 19°15'E], 29.iii.2002, G. Plotner (ZMB 13737, 13738, 13739 & 13742). ZIMBABWE: 1 ♂, Beitbridge [22°02'S, 30°00'E], (NMZ/D835).

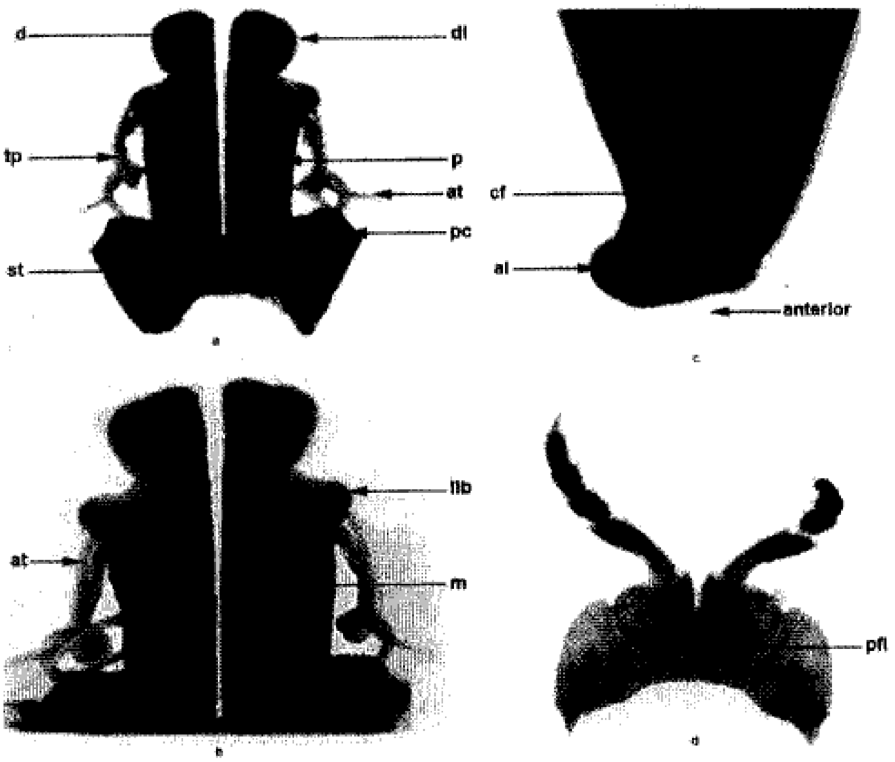

FIGURE 1. *Spirostreptus heros* (NMSA 20495). **a**, oral view of gonopods; **b**, aboral view of gonopods; **c**, oral view of prefemoral lobe of first pair of male legs; **d**, lateral view of collum. Abbreviations: p, proplica; m, metaplica; llb, lateral lobe; dl, distal lobe; d, depression; tp, telopodite; at, antetorsal process; pc, paracoxite; st, sternite; cf, collum fold; al, anterior lobe; pfl, prefemoral lobe.

Diagnosis: Lateral and medial edges of proplica parallel; proplica without abrupt widening subapically; angle between lateral lobe and distal lobe equal to or less than a right angle; antetorsal process S-shaped (Figs 1a, 1b, 7a).

Description: *Size*: Body length 184–344 mm; minimum and maximum body width 8–14.5 mm and 13.5–19 mm; antenna length 10–13 mm.

Number of body rings: 59–68.

Colour: Body black; legs and antennae black or dark brown.

Collum: Anterior produced laterally into a narrow lobe, with 2–5 complete folds and 0–3 incomplete folds (Fig. 1d).

Pre-femoral process of 1st pair of male legs: Proximally parallel and rounded, medial nipples distally narrow and strongly deflected laterally (Fig. 1c).

Gonopod: (Figs 1a, 1b) 7–9 mm long; telocoxites parallel, but not in contact.

Sternite short, wide and apex not extending distally to level of paracoxite apex.

Proplica tapering apically. Apex of proplica conceals proximal lateral lobe. Proplica does not overlap distal lobe (Fig. 1a).

Metaplica without lobes or humps, wider proximal to telopodite knee (Fig. 1b).

Lateral lobe extends beyond lateral edges of proplica and distal lobe. Aborally, lateral lobe proximally narrow, rounded distally (Figs 1a, 1b).

Distal lobe laterally and apically rounded; medial edge of distal lobe concave, forming a shallow invagination. Surface of distal telocoxite lobe smooth; distal lobe not extending beyond lateral edge of proplica apex (Fig. 1a). Orally, the distal lobe may have a shallow central depression.

Telopodite with antetorsal process which extends past paracoxite, post-knee telopodite with an open coil. Antetorsal process S-shaped (Figs 1a, 1b, 7a).

Distribution: Known from southern Botswana, north-western South Africa, northern Namibia and southern Zimbabwe.

Remarks: The smooth surface texture and shape of the distal lobe of the gonopods resemble the form in *batokensis*, *unciger* and *kruegeri* rather than *sebae* and *tripartitus*.

The gonopods of *heros* and *kruegeri* are the most similar. However, in *heros* the angle between the lateral lobe and distal lobe is equal to or less than a right angle while in *S. kruegeri* it is wider. Additionally, in *heros* the lateral edge of the proplica is straight, without abrupt widening subapically while in *kruegeri* the proplica is wide subapically. The antetorsal process in *heros* is S-shaped unlike in *kruegeri* where it is concave (Figs 7a, 7b). The distal nipple on the lateral lobe in some specimens of *kruegeri* has not been observed in *heros*. In addition, the medial edges of the telocoxites are straight and largely parallel along the whole length in *heros* as opposed to *kruegeri* where they are widely separated at the level of the lateral lobe (Figs 1a, 2a).

Spirostreptus kruegeri (Attems 1928)

Figs 2, 7b

Triaenostreptus kruegeri Attems 1928, p. 367, figs 315–317; Hoffman 1971; Krabbe 1982; Hamer 1998
Spirostreptus kruegeri: Mwabvu 2005a; Hoffman 2008

Type material (not examined): SOUTH AFRICA: **Gauteng Province**: Krugersdorp (SAM).

Additional material examined: SOUTH AFRICA: **Gauteng Province:** 1 ♂, Pretoria [25°44'S, 28°11'E], 1961, (NMSA 8896). **Limpopo Province:** 1 ♂, Makalali Game Reserve [24°11'S, 30° 37'E], x.1998, M. Hamer (NMSA 22051); 1 ♂, Klipfontein, N. Transvaal [2428A2], 4.xii.1979 (NMZ/D97); 1 ♂, Phalaborwa [23°51'S, 31°12'E], i.1998, S. Piper (NMSA16196). **North West Province:** 1 ♂, Pilanesberg National Park [25°15'S, 27°06'E], 30.x.2000, R. Slotow (NMSA 15816); 1 ♂, Pilanesberg National Park [25°15'S, 27°06'E], 12.xii.1999, R. Slotow (NMSA 20478); 1 ♂, Pilanesberg National Park [25°15'S, 27° 06'E], 1999, J. Londt (NMSA 20513); 1 ♂, Pilanesberg [25°15'S, 27°06'E], 21.i.1999, (NMSA15816); 1 ♂, Botsalano Game Reserve [25°34'S, 25°42'E], 7.i.2000, (NMSA 22053); 1 ♂, Madikwe Game Reserve [25°21'S, 26°32'E], iii.2000, R. Slotow (NMSA 20497); 1 ♂, Madikwe [25°21'S, 26°32'E], ii.2000, R. Slotow (NMSA 20479). **Northern Cape Province:** 1 ♂, Northern Cape [28.577°S, 22.489°E], (NMSA 22052). NAMIBIA: 1 ♂, 1 ♀, Palmfontain Farm [1914CB], 25.ii.1969, B. Lamoral (NMSA 9965). ZIMBABWE: 1 ♂, Humani Ranch HQ [2032A3], 13.iv.1987 (NMZ/D502); 1 ♂, Maphisa [21°00'S, 28°27'E], 1998, T. Mwabvu (NMSA 20539); 1 ♂, Doddieburn Ranch, West Nicholson [2129A4], 18.xii.85, (NMZ/D362, NM/D381); 1 ♂, Doddieburn Ranch, West Nicholson [2129A4], 5.ix.86, F. Nyathi (NMZ/D387); 1 ♂, Manana Hospital [20°56'S, 29°00'E], 14.12.1996, F. Nyathi (NMZ/D838); 1 ♂, Hippo Valley [21°10'S, 31°32'E], xi.1998, T. Mwabvu (NMSA 20543); 1 ♂, West Nicholson [21°03'S, 28°21'E], 17.xii.1974 (NMZ/D574); 1 ♂, Chivi [20°30'S, 30°50'E], xi.1998, T. Mwabvu (NMSA 16196).

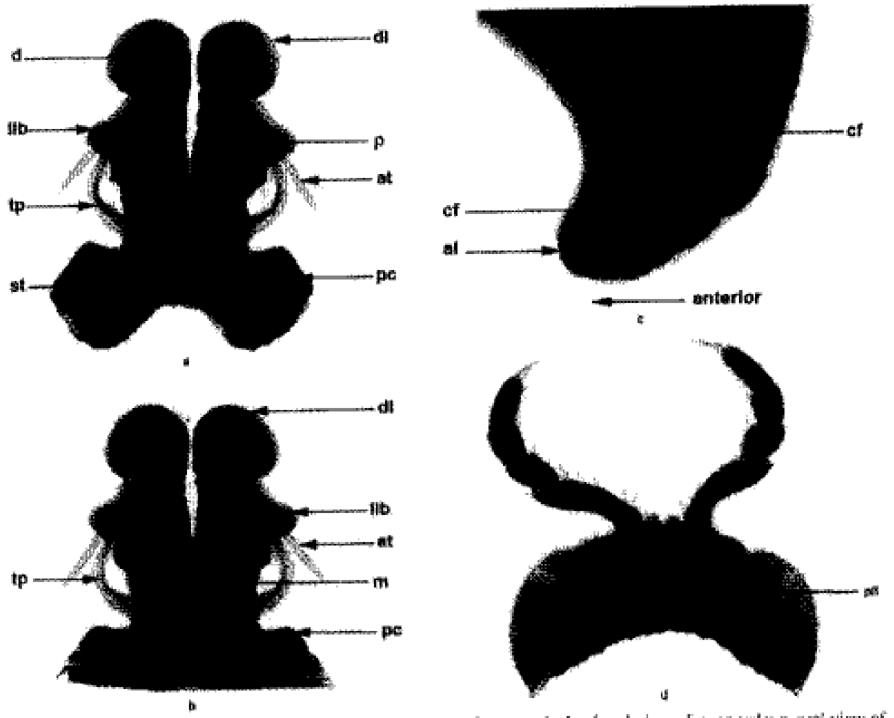

FIGURE 2. *Spirostreptus kruegeri* (NMZ/D362). **a**, oral view of gonopods; **b**, aboral view of gonopods; **c**, oral view of prefemoral lobe of first pair of male legs; **d**, lateral view of collum. Abbreviations: p, proplica; m, metaplica; llb, lateral lobe; dl, distal lobe; d, depression; tp, telopodite; at, antetorsal process; pc, paracoxite; st, sternite; cf, collum fold; al, anterior lobe; pfl, prefemoral lobe.

Diagnosis: Telocoxites wider apart at the level of the apex of the proplica; proplica and metaplica abruptly widen subapically; lateral lobe may have an apical nipple; lateral lobe strongly slanting towards paracoxite away from the distal lobe, at greater than right angle; apically lateral lobe deflected aborally; antetorsal process crescent-shaped distally (Figs 1a, 1b, 7b).

Description: *Size*: Body length 220–240 mm; minimum and maximum body width 5–9 mm and 11–15 mm; antenna length 9–12 mm.

Number of body rings: 63–73.

Colour: Body brown and black; legs reddish brown or brown; antennae brown.

Collum: Rounded anterior lobe slightly produced ventrally, with 3–4 complete and 0–7 incomplete folds (Fig. 2d).

Pre-femoral process of 1st pair of male legs: Proximally parallel with a short and broad, laterally deflected distal nipple (Fig. 2c).

Gonopod: (Figs 2a, 2b) 6–8 mm long. Sternite long, reaching level of paracoxite apex. Telocoxites further apart at the level of the proplica apex.

Proplica widens abruptly subapically and tapers apically. Raised lateral edge of proplica pronounced and extending further than medial edge. Proplica concealing lateral lobe proximally.

Metaplica without lobes, wider with humps proximal to lateral lobe, and with a prominent distal hump.

Lateral lobe strongly slanting towards paracoxite (away from distal lobe) and extending beyond lateral edges of proplica and distal lobe, proximally constricted and rounded distally (Fig. 2b). Lateral lobe deflected aborally, may end in a prominent apical nipple which is clearly seen in aboral view.

Lateral and medial edges of distal lobe rounded distally, with shallow depression on the surface.

Telopodite with open coil or spiral, antetorsal process crescent-shaped distally, may reach paracoxite apex (Figs 2a, 2b).

Distribution: Known from north and north-central South Africa, southern Zimbabwe, Gaberone, Botswana and northern Namibia.

Remarks: The texture of the distal lobe of the gonopod is similar to that of *batokensis*, *unciger* and *heros*, however the resemblance to *heros* is greater. Besides having overlapping distributions, *heros* and *kruegeri* have similar body and gonopod characteristics, particularly the shape and surface texture of the distal telocoxite lobe. The major differences in the gonopods of *heros* and *kruegeri* are the proximity of the telocoxites, the shapes of the subapical proplica and antetorsal process, the angle between the lateral and distal lobes, the height of the sternite in relation to the paracoxite apex, and the nature of the telopodite coil. Subapically the proplica is abruptly wider and angular in *kruegeri*, unlike in *heros*. A difference in the width of the metaplica is also evident between the two species (see remarks under *heros*).

According to the literature (Hamer 1998), the type material of *S. kruegeri* is in the SAM. However, this material is missing, presumed lost, from the SAM collection, and is not in other collections in the southern African region. Suggestions that the material could be in the Naturhistorisches Museum, Vienna, Austria could not be confirmed.

***Spirostreptus sebae* Brandt 1833**

Figs 3, 7c

Spirostreptus sebae Brandt 1833, p.203, figs 40–45; Golovatch & Hoffman 2001; Hoffman *et al.* 2001; Mwabvu 2005a; Hoffman 2008

Triaenostreptus petersi Attems 1928, p. 367; Hoffman 1971, 2008; Krabbe 1982; Hamer 1998; Hoffman *et al.* 2001

Type material: Holotype: MOZAMBIQUE: 1 ♂, Tete, Peters (ZMB 477).

Additional material examined: MOZAMBIQUE: 1 ♂, Tete, Peters (ZMB 2179). ZIMBABWE: 1 ♂, Tobwe School, Kamativi [18°18'S, 27°02'E], 3.viii.1985, J. M. Sango (NMZ/D248); 1 ♂, Rifa Camp [1628B2], 8.xii.1995, (NMZ/D799); 1 ♂, Chapoto Village [1530C2], 21.iii.1997, S. Nyathi (NMZ/D820); 1 ♂, Mzola Camp [1827C2], 4.xii.1997, (NMZ/D847); 1 ♂, Gweru [19°27'S, 29°48'E], 17.xii.2002, T. Mwabvu (NMSA 20500); 1 ♂, Mount Darwin [16°46'S, 31°34'E], 1998, T. Mwabvu (NMSA 22050); 1 ♂, Karoi [16°48'S, 29°41'E], 1999, T. Mwabvu (NMSA 22048); 1 ♂, Gokwe [18°02'S, 28°08'E], i.1999, T. Mwabvu (NMSA 20488); 1 ♂, Chipangali [20°10'S, 28°40'E], 2001, M. Perrin (NMSA 20416); 2 ♂, Chihota [18°40'S, 31°30'E], 11.ii.2006, T. Mwabvu (NMSA 21938); 2 ♂, Chegutu [18°20'S, 30°20'E], 19.xii.2008, T. Mwabvu (NMSA 21940); 2 ♂, Marange [19°00'S, 32°40'E], 23.xii.2008, T. Mwabvu (NMSA 21967); 1 ♂, Bulawayo [20°10'S, 28°40'E], 1998, T. Mwabvu (NMZ uncatalogued); 1 ♂, Selous [18°04'S, 30°26'E], 1998, T. Mwabvu (NMZ uncatalogued); 1 ♂, Gokwe [18°02'S, 28°08'E], 1999, T. Mwabvu (NMZ uncatalogued); 1 ♂, Guruve [16°43'S, 30°18'E], 1998, T. Mwabvu (NMZ uncatalogued); 1 ♂, Mushumbi Pools [16°10'S, 30°33'E], 1998, T. Mwabvu (NMZ uncatalogued); 1 ♂, Centenary [16°44'S, 31°04'E], 1998, T. Mwabvu (NMZ uncatalogued); 1 ♂, Raffingora [17°02'S, 30°26'E], 1998, T. Mwabvu (NMZ uncatalogued); 1 ♂, Mutoko [17°30'S, 32°20'E], 1998, T. Mwabvu (NMZ uncatalogued); 1 ♂, Esigodini [20°17'S, 28°56'E], 1998, T. Mwabvu (NMZ uncatalogued); ZAMBIA: 2 ♂, 5 ♀, Lusaka [15°24'S, 28°15'E], 12.xii.2008, M. Bingham & T. Mwabvu (NMSA 22048).

Diagnosis: Apical medial edge of proplica extended into a narrow medial tip which touches distal lobe of telocoxite proximally; distal lobe tilted anteriad, lateral width of distal lobe 0.5 times greater than length, apex of distal lobe horizontal (Fig. 3a). Apical metaplica with horizontal hump, medial hump and central cone reaching apex giving two prong appearance (Fig. 3b).

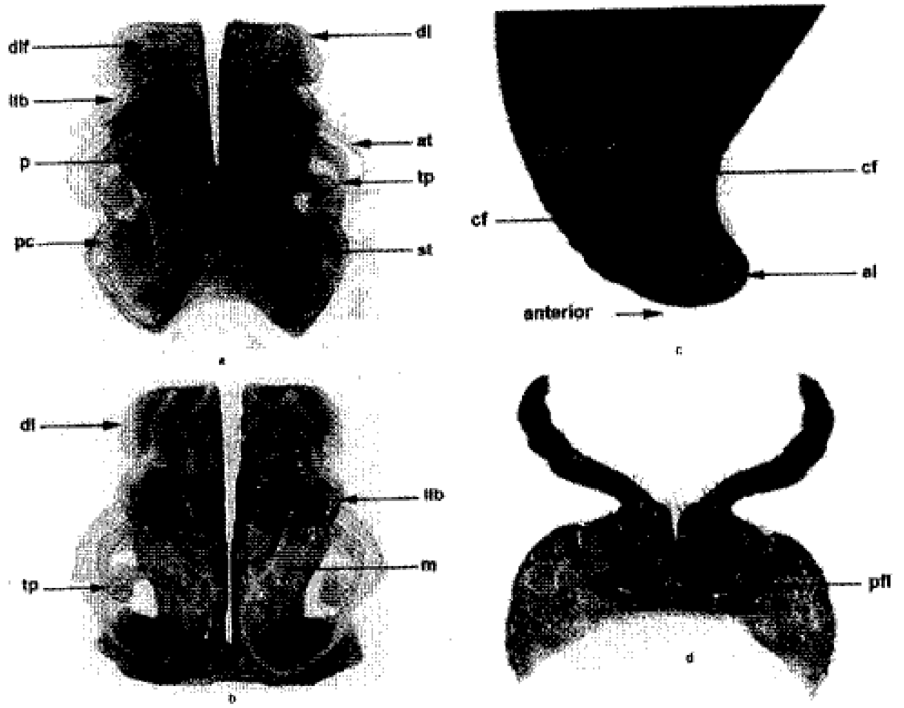

FIGURE 3. *Spirostreptus sebae* (NMZ/D820). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum. Abbreviations: p, proplica; m, metaplica; llb, lateral lobe; dl, distal lobe; dlf, distal lobe fold; tp, telopodite; at, antetorsal process; pc, paracoxite; st, sternite; cf, collum fold; al, anterior lobe; pfl, prefemoral lobe.

Description: *Size*: Body length 162–215 mm; minimum and maximum body width 7–11.5 mm and 11–14 mm; antenna length 8–12 mm.

Number of body rings: 57–63.

Colour: Body black or dark brown; legs and antennae brown or black.

Collum: Anterior lobe slightly produced ventrally, with 3–4 complete and 1–2 incomplete folds.

Pre-femoral process of 1st pair of male legs: Proximally oval, with a strongly laterally deflected medial nipple.

Gonopod: (Figs 3a, 3b) 6 mm long. Sternite apex extended distally to the level of paracoxite apex.

Telocoxites approximately parallel, wider apart distal to sternite apex.

Proplica wide sub-apically, medial edge extended apically into a narrow medial tip which may touch the distal lobe of telocoxite proximally.

Metaplica wider proximal to telopodite knee, with humps along the length. Distally metaplica with horizontal hump, raised medial edge and central cone giving a two prong appearance; central cone extending distally to the apex of the distal lobe, the central cone may have perpendicular folds (Fig. 3b).

Finger-like lateral lobe folded and rounded apically. Lateral lobe extends slightly beyond lateral margins of proplica and distal lobe.

Lateral edge of distal lobe extending to or beyond the lateral margin of proplica apex. Surface of distal lobe rough, with folds extending to edges, lateral width of distal lobe 0.5 times greater than length.

Telopodite with antetorsal process extending past paracoxite or may bend medially and crossing the metaplica. Antetorsal process strongly curved into a crescent shape; post knee telopodite with loose coil (Figs 3a, 3b, 7c).

Distribution: Known from central, northern, north-eastern, eastern and western parts of Zimbabwe, Beira and Tete (Mozambique) and Lusaka (Zambia).

Remarks: The gonopods of *sebae* closely resemble those of *tripartitus*. In these species the gonopods are smaller and the surface of the distal lobe is rough with several folds, unlike in *unciger, batokensis, heros* and *kruegeri*. Despite the similarities, the distal lobe of *tripartitus* differs from *sebae* by being smaller and more rounded (see remarks under *tripartitus*).

***Spirostreptus tripartitus* Cook & Collins 1893**

Figs 4, 7f

Spirostreptus tripartitus Cook & Collins 1893, p. 31, figs 17–22; Hoffman 2008
Triaenostreptus tripartitus; Attems 1928; Hoffman 1971; Krabbe 1982

Type material: Syntypes: CONGO: 2 ♂ (USNM 2384).

Additional material examined: ANGOLA: 1 ♂, Egito near Benguela [12°33'S, 13°24'E], 1975, (ZMUC uncatalogued).

Diagnosis: Gonopods with angular distal lobe, and with oral surface with folds and a prominent diagonal groove; distal lobe length equal to width (Fig. 4a).

Description: *Size*: Body length 176 mm; minimum and maximum body width 7–9 mm and 11–14 mm.

Number of body rings: 66–72.

Colour: Body black or brown; legs and antennae red-brown.

Collum: With narrow anterior lobe slightly produced ventro-laterally, 3–4 complete folds and an incomplete fold (Fig. 4d).

Pre-femoral process of 1st pair of male legs: Proximally rounded, with a long slightly laterally deflected nipple (Fig. 4c).

Gonopod: (Figs 4a, 4b) 6 mm long. Sternite short, not reaching the level of paracoxite apex.

Telocoxites parallel, not touching, wider apart distal to sternite apex (at the level of proplica apex).

Proplica wide and angular subapically (Fig. 4a).

Metaplica wider proximal to telopodite knee, distally metaplica with small horizontal hump, raised medial edge and a small central, conical apex giving a two prong appearance.

Lateral lobe tightly fused to distal lobe and apical proplica, folded and rounded distally. Lateral lobe extending slightly beyond the lateral edges of subapical proplica and distal lobe.

Distal lobe extends to or beyond the lateral edge of proplica apex, lobe as long as it is wide. Orally, distal lobe surface with folds and a deep diagonal groove (Fig. 4a). Distal lobe overlaps lateral lobe proximally.

Telopodite with crescent-shaped antetorsal process which does not extend to or past paracoxite apex, strongly bent medially but not crossing metaplica (Figs 4a, 4b, 7f); post knee telopodite with loose spiral.

Distribution: Benguela, west coast of Angola and from an unknown locality in Democratic Republic of Congo.

Remarks: Gonopod morphology suggests that *tripartitus* is closest to *sebae*. Like *sebae*, the distal lobe has surface folds, however, *tripartitus* is distinguished by a prominent diagonal groove (Fig. 4a) on the distal lobe surface and the smaller size of the distal lobe. In *sebae* the distal lobe is wider (lateral width) than it is long and the apex is horizontal, unlike in *tripartitus* (see remarks on *sebae*).

According to the literature (Krabbe 1982) the holotype of *S. tripartitus* is in the United States National Museum, Washington, USA. However, only a syntype was made available for examination. Therefore the syntype, material from Angola and the original description were used in the study.

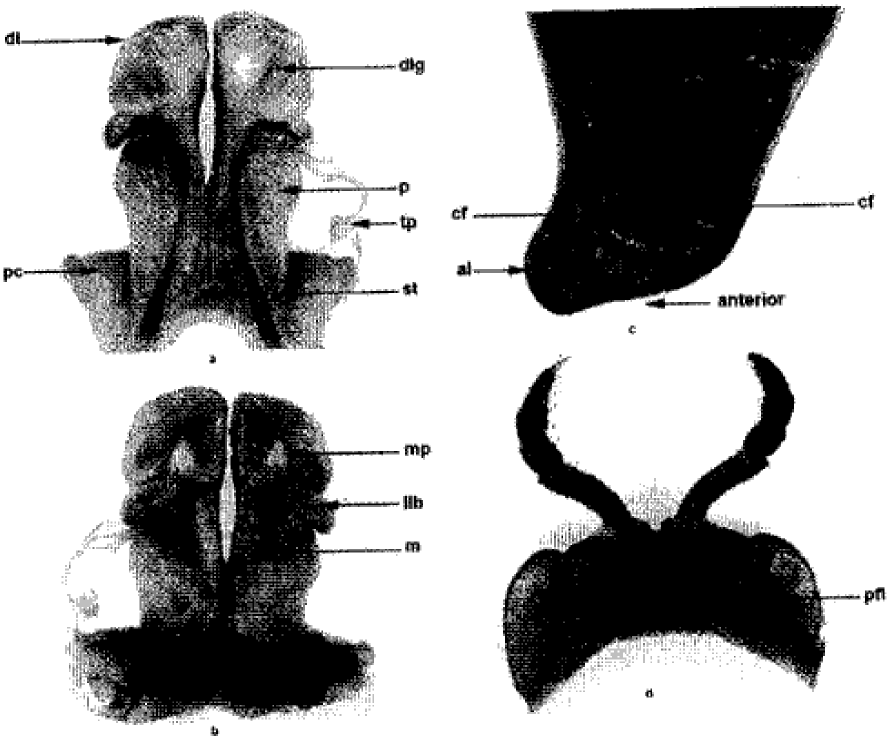

FIGURE 4. *Spirostreptus tripartitus* (USNM 2384). **a**, oral view of gonopods (without left telopodite); **b**, aboral view of gonopods (without left telopodite); **c**, oral view of prefemoral lobe of first pair of male legs; **d**, lateral view of collum. Abbreviations: p, proplica; m, metaplica; llb, lateral lobe; mp, metaplica prong; dl, distal lobe; dlg, distal lobe groove; tp, telopodite; pc, paracoxite; st, sternite; cf, collum fold; al, anterior lobe; pfl, prefemoral lobe.

Spirostreptus unciger **(Attems 1928)**

Figs 5, 7d

Triaenostreptus unciger Attems 1928, p. 365, figs 318–320; Hoffman 1971; Krabbe 1982; Hamer 1998
Spirostreptus unciger: Hoffman 2008

Type material (not examined): SOUTH AFRICA: **North West Province:** Vryburg (SAM).

Additional material examined: SOUTH AFRICA: **Gauteng Province:** 1 ♂, Pretoria [25°44'S, 28°11'E], x.1961, H. Fiedler (NMSA 8896); 1 ♂, Pretoria [25°44'S, 28°11'E], 2004, (NMSA 21939). **Mpumalanga Province:** 1 ♂, 1 ♀, Barberton, Mpumalanga [25°47'S, 31°03'E], xii.1909, Miss de Beer (NMSA 18990). **North West Province:** 2 ♂, Barakolalo [25°16'S, 25°54'E], 14.i.2000, M. Hamer & R. Slotow (NMSA 21975). **Unknown locality:** 1 ♂, iv.1966, G. Lombard (NMSA 9609).

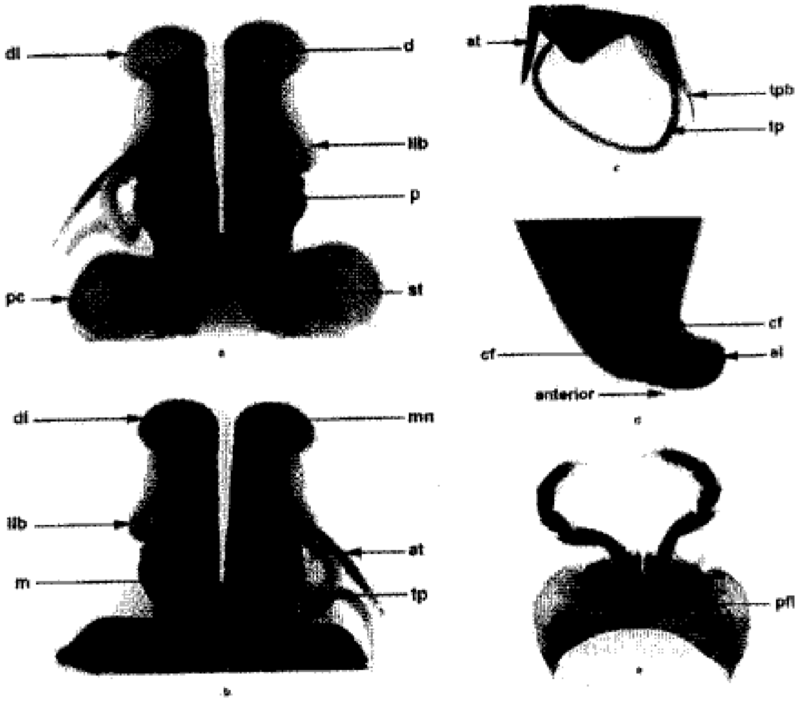

FIGURE 5. *Spirostreptus unciger* (NMSA 8896). **a**, oral view of gonopods; **b**, aboral view of gonopods; **c**, telopodite; **d**, oral view of prefemoral lobe of first pair of male legs; **e**, lateral view of collum. Abbreviations: p, proplica; m, metaplica; llb, lateral lobe; mn, metaplica nipple; dl, distal lobe; d, depression; tp, telopodite; tpb, telopodite branch; at, antetorsal process; pc, paracoxite; st, sternite; cf, collum fold; al, anterior lobe; pfl, prefemoral lobe.

Diagnosis: Lateral lobe very wide proximally, distal part lying tightly against lateral edge of apical proplica (Fig. 5a); telopodite with distal side branch (Fig. 5c).

Description: *Size*: Body length 230–250 mm; minimum and maximum body width 5–8 mm and 11–15 mm; antenna length 12–13 mm.

Number of body rings: 67–73.

Colour: Body black or brownish; legs brown; antennae black or brown.

Collum: Anterior produced laterally into a narrow, rounded lobe, with 3 complete and 1–2 incomplete folds (Fig. 5e)

Pre-femoral process of 1st pair of male legs: Proximally U-shaped with short, apical nipple slightly deflected laterally (Fig. 5d).

Gonopod: (Figs 5a, 5b) 7–8 mm long. Sternite apex extends distally to level of paracoxite apex.

Proplica tapering apically, wider at the level of telopodite spiral. Proplica not overlapping the distal lobe, resulting in much of proximal lateral lobe being visible orally; lateral edge of proximal half of proplica raised more sharply than medial edge.

Distally, metaplica with a rounded hump and nipple-shaped apical extension proximal to distal lobe apex; metaplica width approximately constant along the length except at the level of lateral lobe, a deep depression present at the level of lateral lobe.

Free lateral lobe short and finger-like distally. Proximally lateral lobe broad and vertical. Lateral lobe lying tightly against proplica, does not extend beyond lateral edges of proplica or distal lobe (Fig. 5a). Distally lateral lobe widely separated from distal lobe.

Telocoxites parallel, slightly wider apart distal to sternite apex, medial edge straight, distal lobe not extending beyond lateral edge of proplica apex.

Post knee telopodite with a side branch distal to coil (Fig. 5c); antetorsal process of telopodite straight, extending past the origin of side branch (Fig. 7d).

Distribution: Known only from north-western and north-eastern South Africa

Remarks: The broad and vertical proximal part of the lateral lobe and the side branch on the telopodite distinguish *unciger* from congeners (Figs 5c, 7d). The distal lobes of the gonopods are as in congeners, however, the shape and surface texture suggest closer affinities with *heros*, *batokensis* and *kruegeri*. The position of the lateral lobe in relation to the proplica and distal lobe, and the wide separation of the apical proplica from the distal lobe are unique to *unciger*.

The type material of *S. unciger* is supposed to be in the SAM but is missing from this collection and from other institutions in southern African.

Spirostreptus batokensis **Mwabvu, sp. n.**

Figs 6, 7c

Type material: Holotype: ZIMBABWE: 1 ♂, Batoka Gorge [1726C3], 28.vii.1995, F. Nyathi (NMZ/D835).

Etymology: Refers to the type locality, Batoka Gorge, Zimbabwe.

Diagnosis: Distal lobe subtriangular (Fig. 6a).

Description: *Size*: Body length 215 mm; minimum and maximum body width 6 mm and 13 mm; antenna length 11 mm.

Number of body rings: 60.

Colour: Body black; legs and antennae black.

Collum: Anterior slightly produced into a short rounded lateral lobe, with 4 complete folds and 3 incomplete folds (Fig. 6d).

Pre-femoral process of 1^{st} pair of male legs: Proximally rounded, medial nipples distally narrow and strongly deflected laterally (Fig. 6c).

Gonopod: 6 mm long; telocoxites parallel, but separated.

Sternite apex not reaching the level of paracoxite apex.

Proplica wider subapically and tapering apically. Apically proplica concealing the proximal lateral lobe. Proplica not overlapping the distal lobe (Fig. 6a).

Metaplica with humps, wider proximal to telopodite knee (Fig. 6b).

Lateral lobe slanting steeply, not extending beyond the lateral edge of the distal lobe or widest part of proplica. Aborally, lateral lobe proximally wide; rounded distally (Figs 6a, 6b).

Distal lobe rounded and narrow apically, proximally wider than apex (subtriangular), surface of distal telocoxite lobe smooth with a depression; proximal distal lobe width not extending beyond lateral edge of subapical proplica (Fig. 6a).

Telopodite with short crescent-shaped antetorsal process; antetorsal process not reaching paracoxite apex; post knee telopodite with an open coil (Figs 6a, 6b, 7c).

Distribution: Known only from type locality near Victoria Falls in western Zimbabwe.

Remarks: Like congeners this species has a laterally rounded distal lobe. Although the gonopod is smaller (approximately the same size as that of *sebae* and *tripartitus*), the surface texture of the distal telocoxite lobe resembles more closely that of *heros*, *unciger* and *kruegeri* than *sebae* and *tripartitus*. The subtriangular shape of the distal lobe distinguishes *batokensis* from the congeners (Fig. 6a).

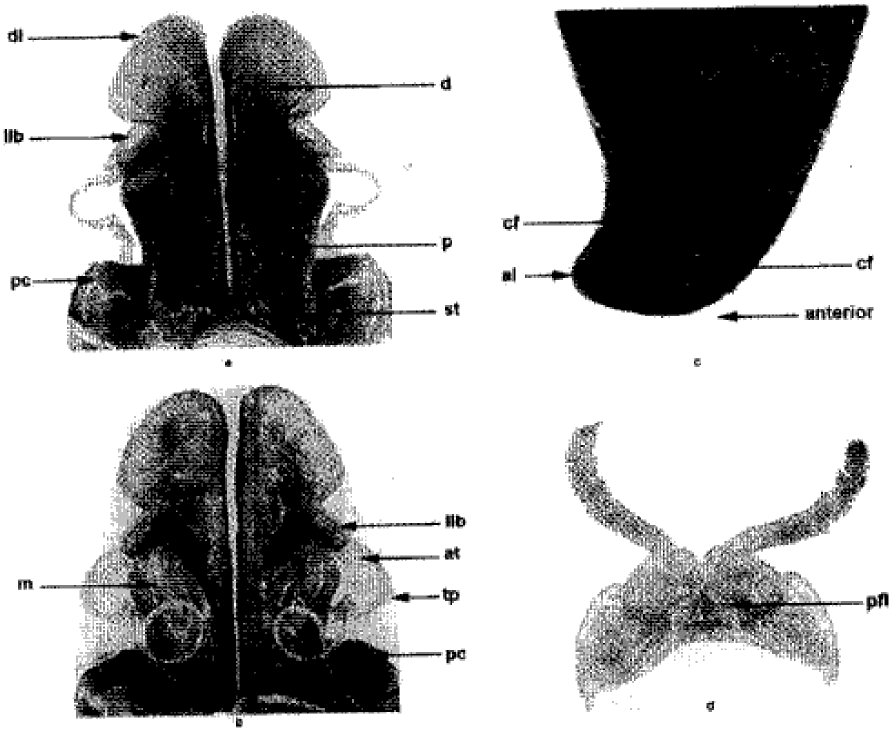

FIGURE 6. *Spirostreptus batokensis* (NMZ/D585). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum. Abbreviations: p, proplica; m, metaplica; llb, lateral lobe; dl, distal lobe; d, depression; tp, telopodite; at, antetorsal process; pc, paracoxite; st, sternite; cf, collum fold; al, anterior lobe; pfl, prefemoral lobe.

Species removed from *Spirostreptus*

Namibostreptus gen. n.

Type species: *Spirostreptus kymatorhabdus* Attems 1914

Etymology: Named for Namibia, the country of provenance of the type species (Gender: Masculine).

Diagnosis: Proplica length approximately half that of gonopod (Fig. 8a). Apical proplica with an acute medial tip; proplica wide, with a concavity apically; distal metaplica with large proximal convex lateral lobe, short lateral process and short laterally deflected end process. Convex lobe extending beyond the lateral edge of proplica. End process of distal metaplica at approximately right angle with the short lateral process.

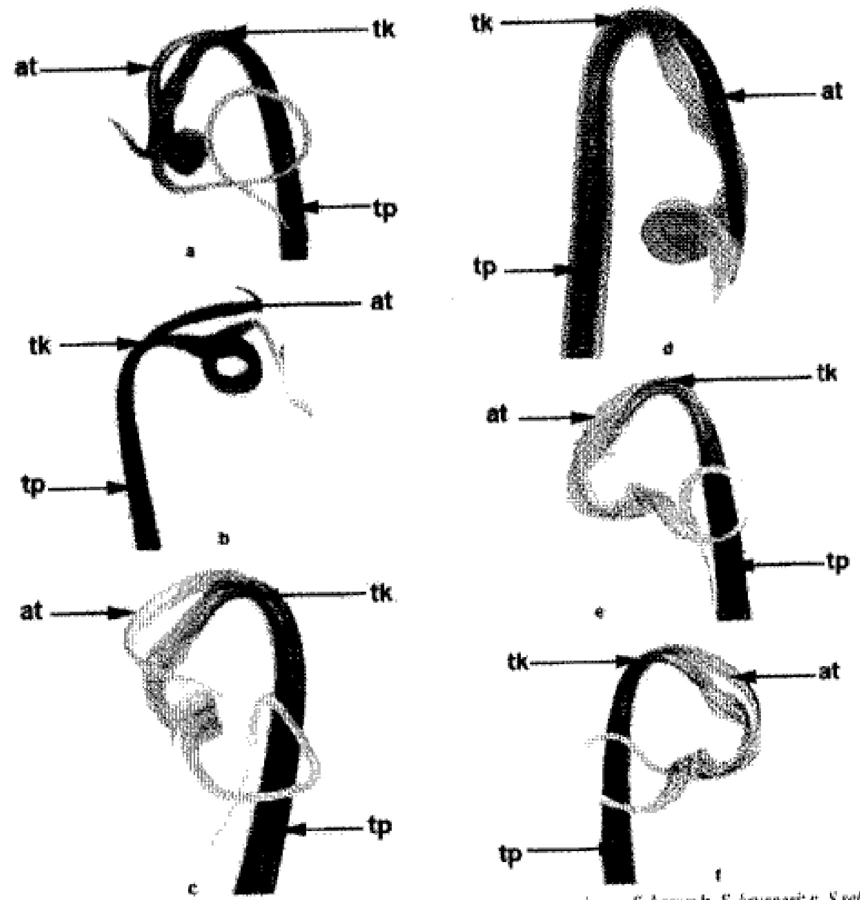

FIGURE 7. Shape of antetorsal process of the telopodites of *Spirostreptus* species. **a**, *S. heros*; **b**, *S. kruegeri*; **c**, *S.sebae*; **d**, *S. unciger*; **e**, *S.batokensis*; **f**, *S. tripartitus*. Abbreviations: tp, telopodite; tk, telopodite knee; at, antetorsal process.

Namibostreptus kymatorhabdus (Attems 1914)

Fig. 8

Spirostreptus kymatorhabdus Attems 1914, p. 151, figs 147–149; Hoffman 2008
Triaenostreptus kymatorhabdus: Attems 1928; Hoffman 1971; Krabbe 1982; Hamer 1998

Type material: Holotype: NAMIBIA: 1 ♂, Walfishbay [22°38'S, 14°39'E], Colonial-Gesellschaft (ZMB 2043).

Additional material examined: NAMIBIA: 1 ♂, Lubbert (ZMB 5197); 1 ♂, Daan Viljoen Game Park 30 km north of Windhoek [22°32'S, 17°41'E], 24.ii. 1978, O. Lomholdt & E. Wederkinch (ZMUC uncatalogued).

Diagnosis: See generic diagnosis.

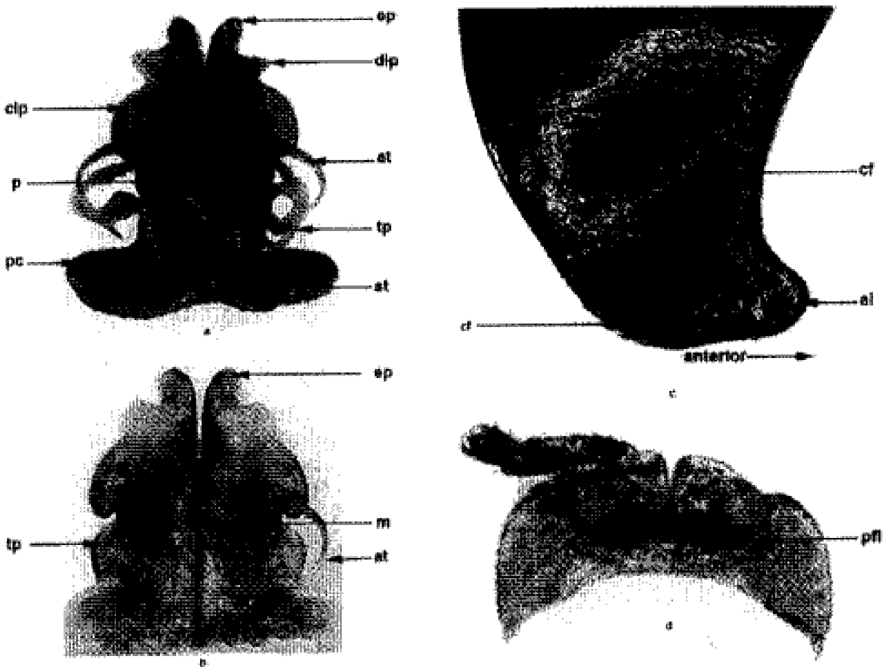

FIGURE 8. *Namibostreptus kymatorhabdus* (ZMB 2043). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c**, oral view of prefemoral lobe of first pair of male legs; **d**, lateral view of collum. Abbreviations: p, proplica; m, metaplica; clb, convex lateral lobe; dlp, distal lateral process; ep, end process; tp, telopodite; at, antetorsal process; pc, paracoxite; cf, collum fold; al, anterior lobe; pfl, prefemoral lobe.

Description: *Size*: Body length 210 mm; minimum and maximum body width 9–11 mm and 11–12 mm; antenna length 8–12 mm.

Number of body rings: 62–74.

Colour: Body black or dark brown; legs and antennae brown.

Head: Regularly spaced striations present behind and between the lateral edges of eyes; gnathochilarium with a triangular median prebasilar sclerite.

Collum: Anteriorly produced into a short rounded lateral lobe, with 3–4 complete and 2 or more incomplete folds.

First ozopore: On 6th body ring.

Pre-femoral process: Proximally rounded with a short laterally deflected medial nipple (Fig. 8c).

Gonopods: (Figs 8a, 8b) 8–9 mm long. Gonopod surface smooth, without ridges or humps; distal telocoxite with an end process. Orally medial edges of telocoxite parallel, raised and folded laterally, fold becomes broader distally, ending in a flat end process.

Sternite triangular, reaching the level of the paracoxite apex; paracoxite apically horizontal and tightly fused to the metaplica.

Proplica about half the length of gonopod: apical proplica broad with a concavity and acute medial tip.

Lateral and medial edges of proplica pronounced subapically, with shallow central groove, lateral edge more pronounced than medial edge. Orally distal depression separates proplica from the larger convex lateral lobe of the distal telocoxite.

Metaplica with a broad, convex-shaped lateral lobe (wider than it is long and distal to proplica apex) which extends beyond lateral edge of proplica; a smaller distal lateral process parallel to paracoxite apex present proximal to end process. Metaplica with a window through which part of telopodite is visible. Wide depression present adjacent to the convex lobe, distal to the point of emergence of telopodite.

Telopodite long, with a trifurcate ending. Antetorsal process crescent-shaped and tapering (Figs 8a, 8b), extending past paracoxite apex. Distally, antetorsal process with a terminal spine, bending medially past lateral edge of proplica; post knee telopodite lamellate with a loose coil preceding abrupt narrowing.

Distribution: Known only from the west coast of Namibia and near Windhoek (Namibia).

Remarks: The lack of a lateral lobe and the lack of a laterally rounded distal lobe, the shorter proplica, and the abrupt narrowing of the telopodite (distal to the telopodite coil) are character states that do not support placement in *Spirostreptus*. Based on Hoffman's (2008) diagnosis of the Spirostreptini, *kymatorhabdus* is a member of the tribe, the telopodite structure and the prostatic groove resemble member genera. However, the shape and size of the distal coxite of the gonopod of *kymatorhabdus* differ from other Spirostreptini genera by having a unique convex lobe. Therefore, we erect *Namibostreptus* to accommodate *kymatorhabdus*, this bringing the number of genera in Spirostreptini to six.

Taxonomy and species relationships

Spirostreptus is a homogeneous and probably monophyletic genus. The distal telocoxite of *Spirostreptus* species which is enlarged into a laterally rounded golf club-shaped lobe (Figs 1a, 2a, 3a, 4a, 5a, 6a), and the lateral lobe lying between the distal lobe and apical proplica distinguish the genus from the other African spirostreptid genera.

As in other spirostreptid genera, the telocoxite provides the most useful characters in species diagnosis. The shape and surface texture of the laterally rounded distal lobe and the shape of the apical and subapical proplica are probably the taxonomically most informative gonopod characters in *Spirostreptus*.

Although the telopodite distinguishes genera such as *Doratogonus* Attems 1914 (Hamer 2000) and *Bicoxidens* Attems 1928 (Mwabvu 2000; Mwabvu *et al.* 2007), this is not necessarily the case of *Spirostreptus*. For example, the S-shape of the antetorsal process distinguishes *heros* from congeners, while other *Spirostreptus* species have a crescent-shaped or straight antetorsal process (Fig. 7). In *S. unciger* the distal side branch of the telopodite (Fig. 5c) forms the basis of the species diagnosis. Therefore the structure of the telopodite is useful in separating species in *Spirostreptus*.

The gonopod of *Namibostreptus kymatorhadbus* differs from *Spirostreptus* species by lacking both a laterally rounded distal lobe and a finger-like lateral lobe, and the proplica is approximately half the length of the gonopod (Fig. 8a); similarities to *Spirostreptus* are superficial.

Although separating *heros* and *kruegeri* was difficult, there are sufficient morphological differences in the gonopods, particularly the shape of the antetorsal process and subapical proplica, to support the species status of these taxa. Therefore, existing species concepts are maintained pending the availability of DNA sequence data.

Key to species of *Spirostreptus*

1. Gonopod distal telocoxite lobe bulbous and smooth, without surface folds, with an anterior depression.................... 2
\- Gonopod distal telocoxite lobe not bulbous or smooth, with surface folds, without an anterior 3
2. Telopodite with a distal side branch (Fig. 5c).. *unciger*
\- Telopodite without a distal side branch 4
3. Apical proplica tapering with narrow medial tip: distal lobe 0.5 times as wide as it is long, tilted towards anterior, without diagonal groove, apex horizontal.. *sebae*

- Apical proplica not tapering, without a medial tip, wide subapically; distal lobe as wide as it is long, with deep diagonal groove, apex rounded (Fig. 4a) .... *tripartitus*

4. Distal telocoxite lobe subtriangular .... *batokensis* **sp. n.**
- Distal telocoxite lobe not subtriangular 5

5. Proplica not wider or angular subapically, lateral and medial edges parallel proximal to apex; lateral lobe without apical nipple; lateral lobe-distal lobe angle acute or a right angle; antetorsal process S-shaped .... *heros*
- Proplica wider and angular subapically, lateral and medial edges not parallel proximal to apex; latera lobe may have apical nipple; lateral lobe-distal lobe angle obtuse; antetorsal process crescent-shaped (Figs 2a, 7b)........ *kruegeri*

Faunistics and distribution

Generally, *Spirostreptus* occurs in the savanna biome in southern Africa north of the Orange River. There are records neither from forests nor grasslands, nor at high altitudes. The genus is widely distributed in relatively hot, low rainfall areas. Five of the six species were recorded from the eastern half of southern Africa (Fig. 9). *Spirostreptus heros* occurs westwards into Namibia and Botswana; and *kruegeri* has also been recorded from northern Namibia. The only other record of the genus in the western region of southern Africa is *S. tripartitus* from western Angola.

Three species (*S. kruegeri*, *unciger*, and *heros*) were recorded from South Africa north of the Orange River; *sebae*, *heros* and *kruegeri* have been collected from Zimbabwe; *sebae* is the only species of the genus recorded north of the Zambezi River in Zambia; and *heros* is the only species that occurs in Botswana. Among the six species only two were recorded on the coast: *tripartitus* from western Angola and *sebae* from Beira, Mozambique. *Spirostreptus kruegeri* is the most widely distributed species.

Major river systems in the region do not appear to have restricted the distribution of the genus (Fig. 9). However, some species have an apparently relatively narrow distribution. *Spirostreptus batokensis* from western Zimbabwe, *S. tripartitus* from Angola and *S. unciger* from northern South Africa are examples of species recorded from a restricted area. Vegetation and climatic factors may be the major factors influencing the distribution of the species. The distribution of *S. sebae* in miombo woodland is distinct from the pattern of *heros*, *kruegeri* and *unciger*, which are confined to the relatively hot and dry habitats in southern Zimbabwe, northern and western South Africa, southern Botswana and Namibia.

Discussion

Hoffman (1971) reported intraspecific variation in gonopod structures of widely distributed species. In *Spirostreptus*, intraspecific variability of gonopods is not significant; in particular the shape of the distal lobe, proplica and metaplica were consistent between and within populations in all species. However, some degree of plasticity was observed in the orientations of the antetorsal processes, the apical shapes of the lateral lobes and the surface texture of the lateral lobes, particularly in *kruegeri*. Because *kruegeri* is widespread, subtle differences in gonopod features are expected among populations.

The occurrence of species of *Spirostreptus* in the savanna biome only suggests that it is a specialist genus compared to the widely distributed genera, such as *Doratogonus* and *Archispirostreptus*. For a milipede with a large body size and relatively greater mobility the distribution of *Spirostreptus* is unexpected. We suggest the potential to disperse into and survive in different biomes to be greater in *Spirostreptus* than in genera of smaller body size, such as *Bicoxidens* or *Doratogonus*. It is possible that the current distribution of *Spirostreptus* is a collecting artifact, and that the absence of the species in some biomes may not be real. Several areas, particularly north of the Zambezi River, in Mozambique and in the western region of southern Africa have not been extensively surveyed. The recent collection of *S. sebae* in Zambia corroborates our sampling artifact hypothesis.

There may be other possible reasons why *Spirostreptus* is not as widely distributed as the other giant millipede genus *Archispirostreptus*, whose range extends from southern Africa to East and West Africa, or even the slightly smaller *Doratogonus* which is widely distributed in the southern Africa region, including the eastern highlands (see Hamer 2000; Hamer & Slotow 2000). Although the influence of altitude on the distribution of *Spirostreptus* is unknown, the absence of *Spirostreptus* from the eastern highlands suggests an effect. Despite extensive millipede surveys in forests in the east African highlands and the eastern highlands of Zimbabwe, *Spirostreptus* has never been recorded. Therefore, it seems reasonable to hypothesise that the distribution of *Spirostreptus* is influenced by altitude, climatic factors and associated vegetation type. Rainfall and vegetation type have been reported to affect the distribution of *Doratogonus* (Hamer & Slotow 2000). That *S. heros*, *kruegeri* and *unciger* occur only in dry savanna supports our conclusion that climatic factors and vegetation type do affect the distribution of species of *Spirostreptus*.

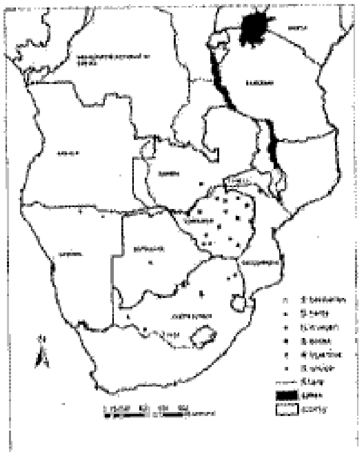

FIGURE 9. Distribution of *Spirostreptus* species

Although *Spirostreptus* is widespread in southern Africa, individual species occur in specific areas in the savanna biome. This is probably because the savanna biome is heterogeneous (Druce *et al.* 2007) and millipede species have specific habitat requirements and low dispersal ability (Hopkin & Read 1992). In Zimbabwe, *sebae* occurs in miombo woodland and neither in dry savanna nor montane vegetation. In addition, *S. sebae* has not been recorded south of the Limpopo River despite extensive surveys. This indicates the absence of the species in South Africa, rather than collecting bias. However, *S. kruegeri*, *heros* and *unciger* occur and coexist in the dry savanna in South Africa. This further affirms that the preference for specific vegetation type and climatic conditions influence the distribution of the species.

Although river systems are recognised barriers to animals, the Zambezi and Limpopo Rivers do not seem to restrict the spread of *Spirostreptus* species. Hamer and Slotow (2000) suggested that the existence of dispersal corridors across the Limpopo River may link populations of *Doratogonus* species. Similar corridors may have facilitated the spread of *heros*, *kruegeri* and *sebae* into suitable habitats.

Because species of *Spirostreptus* coexist in the savanna biome, small areas (for example parts of north-western South Africa and southern Zimbabwe) could be targeted for conservation. Therefore, we conclude that more species of *Spirostreptus* could be conserved in a relatively small area than species of *Doratogonus* (see Hamer & Slotow 2000) and *Archispirostreptus*. Additionally, the savanna biome which covers 46 % of southern Africa (Druce *et al.* 2007) is widespread, making *Spirostreptus* less threatened by habitat destruction than genera found in rarer habitats, such as forests.

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CHAPTER 3

A REVISION OF THE TAXONOMY AND DISTRIBUTION OF *Spirostreptus* Brandt 1833 (DIPLOPODA, SPIROSTREPTIDA, SPIROSTREPTIDAE) WITH DESCRIPTIONS OF A NEW SPECIES AND A NEW GENUS OF SPIROSTREPTID MILLIPEDE.

LIST OF ERRATA

Chapter 3: **A revision of the taxonomy and distribution of *Spirostreptus* Brandt 1833 (Diplopoda, Spirostreptida, Spirostreptidae) with descriptions of a new species and a new genus of spirostreptid millipede.**

1. **Phylogenetic Analysis of *Spirostreptus* species**

Materials and Methods

Character and data matrices were constructed using male gonopod characters. A phylogenetic analysis was performed using PARS 3.6 and CONSENSE 3.6 (both in the phylogeny inference program, PHYLIP) to produce an extended majority rule consensus tree. The reliability of the tree was tested using bootstrap analysis with the use of 1000 replicates. *Orthoporoides pyrhocephalus* (C. L. Koch 1865) was selected as the outgroup because it has a gonopod structure similar to the ingroup.

Results and Discussion

The phylogenetic analysis separates the ingroup into two groups, the strongly supported monophyletic *Spirostreptus* species group (Group A) and the monotypic *Namibostreptus* (Fig. 10).

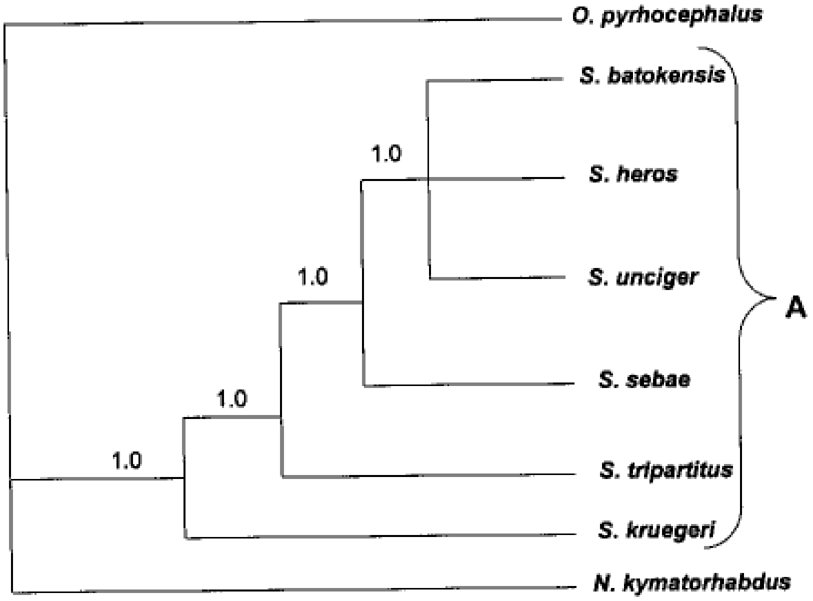

Figure 10. A consensus tree of *Spirostreptus* species using *Orthoporoides pyrhocephalus* as an outgroup. The numbers indicate the number of times the groups to the right of each fork occur among the trees out of 1.00. The letter A to the right of species names represents the monophyletic *Spirostreptus* species group.

Group A includes all the valid species of *Spirostreptus*, which are characterized by laterally rounded distal lobes (Figs. 1a, 2a, 3a, 4a, 5a, 6a), thus corroborating our observation that the taxa are closely related. However, the relationships among *Spirostreptus batokensis*, *heros* and *unciger* are not resolved. Although gonopod morphology is useful in species diagnoses, the number of morphological characters may be inadequate in phylogenetic analysis of species (Scotland *et al.* 2003). The small number of gonopod characters (nine in this study) is marginally higher than the number of taxa (seven) in the ingroup, this is probably why the clade is unresolved. Using more characters and different character sources (including non-gonopod and genetic characters) could produce robust phylogenies, particularly in closely related taxa (Collin, 2003).

The phylogenetic results also supported the erection of the new genus *Namibostreptus* to accommodate *N. kymatorhabdus*, which was removed from *Spirostreptus*. The gonopod of *N. kymatorhabdus* differs from *Spirostreptus* species by lacking both a laterally rounded distal lobe and a finger-like lateral lobe, and the proplica is approximately half the length of the gonopod (Fig. 8a).

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Appendix 1: Character matrix for cladistic analysis of *Spirostreptus*

1. Proplica: 0—four fifths of gonopod length; 1—half of gonopod length; 2—two thirds of gonopod length
2. Lateral lobe: 0—absent; 1—present
3. Distal lobe: 0— absent; 1—present
4. Distal lobe shape: 0— without distal lobe; 1 — subtriangular; 2 — not subtriangular
5. Distal lobe folds: 0— without distal lobe; 1—absent; 2—present
6. Distal lobe diagonal groove: 0— without distal lobe; 1—absent; 2—present
7. Distal lobe depression: 0— without distal lobe; 1—absent; 2—present
8. Telopodite distal side branch: 0—absent; 1—present
9. Antetorsal process shape: 0—without antetorsal process; 1—straight; 2—crescent shaped; 3—S-shaped

Appendix 2: Data matrix for cladistic analysis of *Spirostreptus*

Taxon	**Character states**
8	**9**
O. pyrocephalus	000000000
S. batokensis	211111202
S. heros	211211203
S. kruegeri	211211202
S. sebae	211221102
S. tripartitus	211222102
S. unciger	211211211
N. kymatorhabdus	100000000

2. Distribution map of *Spirostreptus* species

The distribution map of *Spirostreptus* species (below) is a modified version of Figure 9 in the published taxonomic revision of *Spirostreptus* (Mwabvu *et al.* 2009) (Chapter 3 in the thesis). The map includes all the known localities from which the species have been recorded.

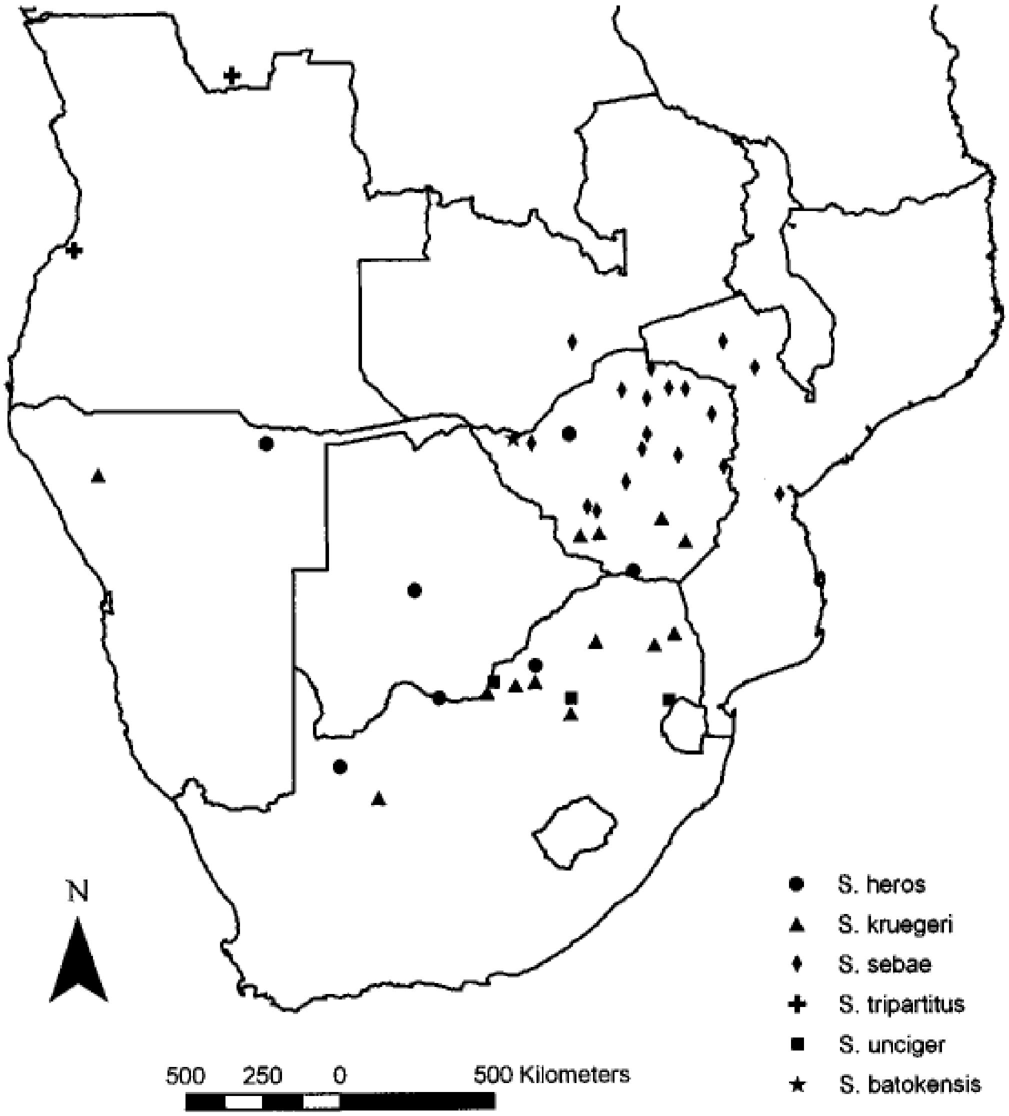

FIGURE 10. Distribution of *Spirostreptus* species.

3. Distribution map of *Namibostreptus kymatorhabdus*

The new distribution map of *Namibostreptus kymatorhabdus* (below) is an addition to the published taxonomic revision of *Spirostreptus* (Chapter 3 in the thesis). The genus *Namibostreptus* was erected to accommodate *kymatorhabdus* which had been incorrectly assigned to *Spirostreptus* (Mwabvu *et al.* 2009). The map includes all the known localities from which *N. kymatorhabdus* has been recorded.

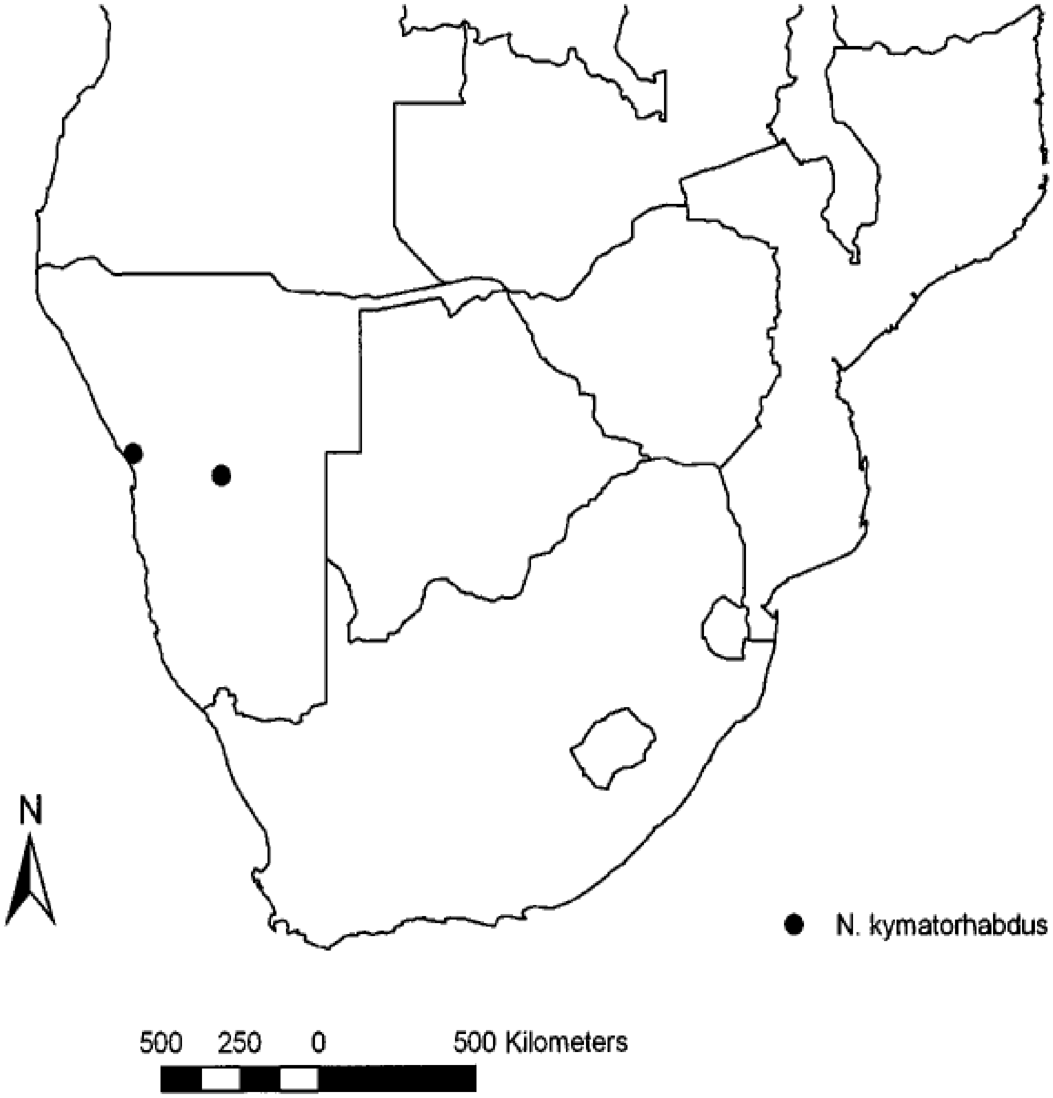

FIGURE 11. Distribution of *Namibostreptus kymatorhabdus*.

4. **Diagnosis: “Telocoxites wider apart at the level of the apex of the proplica”.**

They are wider apart at the level of the proplica (distally) than proximally (i.e. close to the gonopod sternite.

5. **Page 46, *S. tripartitus* holotype?**

The holotype was not available. Only the syntype was studied.

CHAPTER 4

A REVIEW OF THE TAXONOMY AND DISTRIBUTION OF *Plagiotaphrus* Attems 1914 (DIPLOPODA, SPIROSTREPTIDA, SPIROSTREPTIDAE).

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A review of the taxonomy and distribution of *Plagiotaphrus* Attems 1914 (Diplopoda, Spirostreptida, Spirostreptidae)

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Abstract

Plagiotaphrus is a monophyletic genus which formerly included three species, *P. sulcifer* Attems 1914 (the type species), *P. improvisus* (Attems 1934) and *P. longius* Attems 1928. *Plagiotaphrus longius* is a *nomen dubium* and is here excluded from the genus. A key to the species based on gonopod morphology is also presented. The distribution of *Plagiotaphrus* is disjunct. Given that several localities in Africa have not been surveyed it is likely that *Plagiotaphrus* species occur in more localities.

Key words: savanna, millipedes, gonopod, conservation, southern Africa, central Africa

Introduction

The important role played by millipedes in breaking down organic matter and improving soil structure has been extensively reported (see Crawford 1992; Dangerfield & Telford 1989; Sierwald & Bond 2007; Edwards *et al.* 1970). Given that several biomes are under threat because of human activities (New 1995) several millipede species face possible extinction because millipedes have poor dispersal abilities and because there are many endemics (Hopkin & Read 1992; Hamer & Slotow 2002).

Some of the most conspicuous and yet poorly known millipedes in the tropics belong to the Tribe Spirostreptini. Hoffman (2008) diagnosed the Spirostreptini as having a gonopod telopodite with a distally bifid or trifid prostatic groove, with each branch ending separately. The Spirostreptini are known for their relatively large body size; they include *Spirostreptus* Brandt 1833, *Plagiotaphrus* Attems 1914, *Archispirostreptus* Silvestri 1895, *Limnostreptus* Hoffman 2008 and *Choristostreptus* Hoffman 2008. A key to these genera is presented in Hoffman (2008). Recently, Mwabvu *et al.* (2009) added a new genus, *Namibostreptus* Mwabvu *in* Mwabvu, Hamer, Slotow & Barraclough, 2009, thus bringing to six the number of genera in the tribe.

The genus *Plagiotaphrus* is not adequately described (Krabbe 1982). It has fewer species than the closely related genera (*Spirostreptus* and *Archispirostreptus*) and these are, in addition, poorly known: hence the taxonomic validity of the genus is questionable. In addition, *Plagiotaphrus* is probably the least studied member of the Spirostreptini. Only three species, *P. improvisus* (Attems 1934) from central Angola, *P. longius* Attems 1928 from Umtali (Mutare) in eastern Zimbabwe and *P. sulcifer* Attems 1914 (the type species) from a doubtful locality in East Africa, have been described.

The unknown or doubtful localities of type species, the paucity of new material and the inaccessibility of several areas, particularly in central and the western half of Africa, have hindered efforts to collect and study *Plagiotaphrus*. Therefore, the actual species richness in the genus may be several times more than the number of species described; and the known distribution patterns may reflect a collecting bias. This implies that the

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known diversity and distribution of the taxa are probably inaccurate. Therefore, any attempts to explain evolutionary processes or interpret apparent distribution patterns using current data would be futile. Until recently, each of the species was known from only one locality and was described from one specimen. The availability of new material from previously unsurveyed localities has allowed a review of the genus.

The objectives of this review are to ascertain the taxonomic validity and generic limits of *Plagiotaphrus*, evaluate the validity of the species currently assigned to the genus, present a key to the species and describe their distribution.

Materials and methods

Material from museum collections was used in this study. Museum abbreviations are as follows:

NHMW	Naturhistorisches Museum, Wien, Austria
NMSA	Natal Museum, Pietermaritzburg, South Africa
SAM	South African Museum, Cape Town, South Africa
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main, Germany

Body, leg and antenna colour were recorded and body rings were counted. Body length was measured using a soft wire placed against the line of ozopores. Minimum and maximum body widths were measured just behind the head and at about midlength, respectively, using Vernier calipers.

Gonopods were dissected out, examined and photographed. The telocoxite and telopodite of the gonopod were separated and examined.

Material was studied using a Carl Zeiss Stereo Microscope (Stemi DV4) and photographed using automontage software (Leica Microscope MZ12s with 3 CCD Toshiba Camera). The final images and plates were prepared using Adobe Photoshop CS (version 8). ArcGis 9.1 (ESRI) was used to prepare a distribution map of species.

Terminology follows Hoffman (2008).

Results

Taxonomy

Genus *Plagiotaphrus* Attems 1914

Type species: *Plagiotaphrus sulcifer* Attems 1914, p. 160, figs 165–171
Megaskamma Attems 1934, p. 13, from Angola. Synonymy by Hoffman 1971
Plagiotaphrus: Attems 1914, 1928; Schubart 1951, 1966; Hoffman 1971, 2008; Krabbe 1982; Hamer 1998, 1999; Mwabvu *et al.* 2009

Diagnosis: Proplica approximately 9/10 of gonopod length; end process short and apically convex; telopodite with a tongue-like lobe distal to the origin of antetorsal process.

Description: Body length 158–172 mm; minimum and maximum body width 7–9 mm and 11–13 mm, respectively.

Body rings 56–62.

Body black; legs and antennae brown.

Collum produced into an anterior lobe, with 3–4 complete and 1–3 incomplete folds.

Sternite conical with rounded apex.

Apical proplica acute/conical; proplica setose apically/subapically (Figs 1a, 2a); proximal proplica groove flanked by raised edges; proplica aproximately 9/10 of gonopod length.

Distal metaplica with rounded median hump adjacent to proximal lateral process (Figs 1a, 1b, 2a, 2b).

Lateral process slanting posteriad, proximally broad and tapering distally.

End process short and apically convex.

Telopodite with a tongue-like lobe distal to the origin of antetorsal process; telopodite spirals distal to telopodite knee, apically with 2 or 3 small lobes at extremity.

Origin of antetorsal process distal to telopodite knee; antetorsal process long, with a spine at extremity.

Distribution: Chire (probably Shire, Malawi); central Angola; northern Zimbabwe.

Remarks: The new records of *P. sulcifer* from northern Zimbabwe and its overlapping distribution with *Archispirostreptus tumuliporus* (Karsch 1881) and *Spirostreptus sebae* Brandt 1833 suggest that the genus is widely distributed and probably occurs in localities (in the savanna) where other giant millipedes have been recorded.

The shapes and sizes of the proplicae, metaplicae, end processes, metaplical processes and antetorsal processes of the gonopods differentiate the Spirostreptini genera. The gonopods of *Plagiotaphrus* species resemble those of *Limnostreptus* and *Choristostreptus* more than those of other genera in the tribe. The length of the proplica is approximately 9/10 that of the metaplica; and the antetorsal process is longer with its origin distal to the telopodite knee in these genera, unlike in the gonopods of *Spirostreptus* and *Archispirostreptus*. The distal telocoxite of the gonopods is enlarged and laterally produced into a rounded lobe in *Spirostreptus*. In *Archispirostreptus* the distal telocoxite extends into a finger-like end process; in addition, the antetorsal processes of the gonopods have distal spikes.

Plagiotaphrus sulcifer Attems 1914

Fig. 1

Plagiotaphrus sulcifer: Attems 1914, p. 160, figs 165–171.
Plagiotaphrus sulcifer: Attems 1914, 1928; Hoffman 1971; Krabbe 1982; Hamer 1999

Type material (not examined): EAST AFRICA: Chire (MALAWI, Shire?): [13⁰S, 33⁰51'E]

Additional material examined: ZIMBABWE: 1 ♂, Makuvatsine Secondary school, Guruve [16⁰14'S, 30⁰38'E], 1.xii.1998, T. Mwabvu (NMSA 20506). 1 ♂, Cirad Camp, Mushumbi [16⁰S, 30⁰E], 19.iii.1997, F. Nyathi (NMZ/D830); 1 ♂, Mahuwe, Guruve [16⁰39'S, 30⁰42'E], 1.xii.1998, T. Mwabvu (NMSA 20486).

Diagnosis: Subapical proplica without a rounded lateral lobe; apical proplica narrow and convex medially (Fig. 1a); antetorsal process crescent-shaped distally (Figs 1b, 1e).

Description: *Size*: Body length 158–172 mm; minimum and maximum body width 7–9 mm and 11–13 mm.

Number of body rings: 57–62.

Colour: Black.

Collum: Produced into a rounded anterior lobe, with 3–4 complete folds and 2–3 incomplete folds (Fig. 1d).

Prefemoral process of 1st pair of male legs: Proximally broad with nipple-shaped and apically acute extension (Fig. 1c).

Gonopod: (Figs 1a, 1b) Sternite conical, with a rounded apex, apex not reaching level of paracoxite apex; paracoxite triangular, apically acute and not tightly fused to metaplica (Figs 1a, 1b).

Proplicae proximally grooved. Apical proplica overlapping proximal lateral process; medial edge of apical proplica convex (Fig. 1a); medial edge of subapical proplica with a short medial lobe which is concealed by oral fold of metaplica.

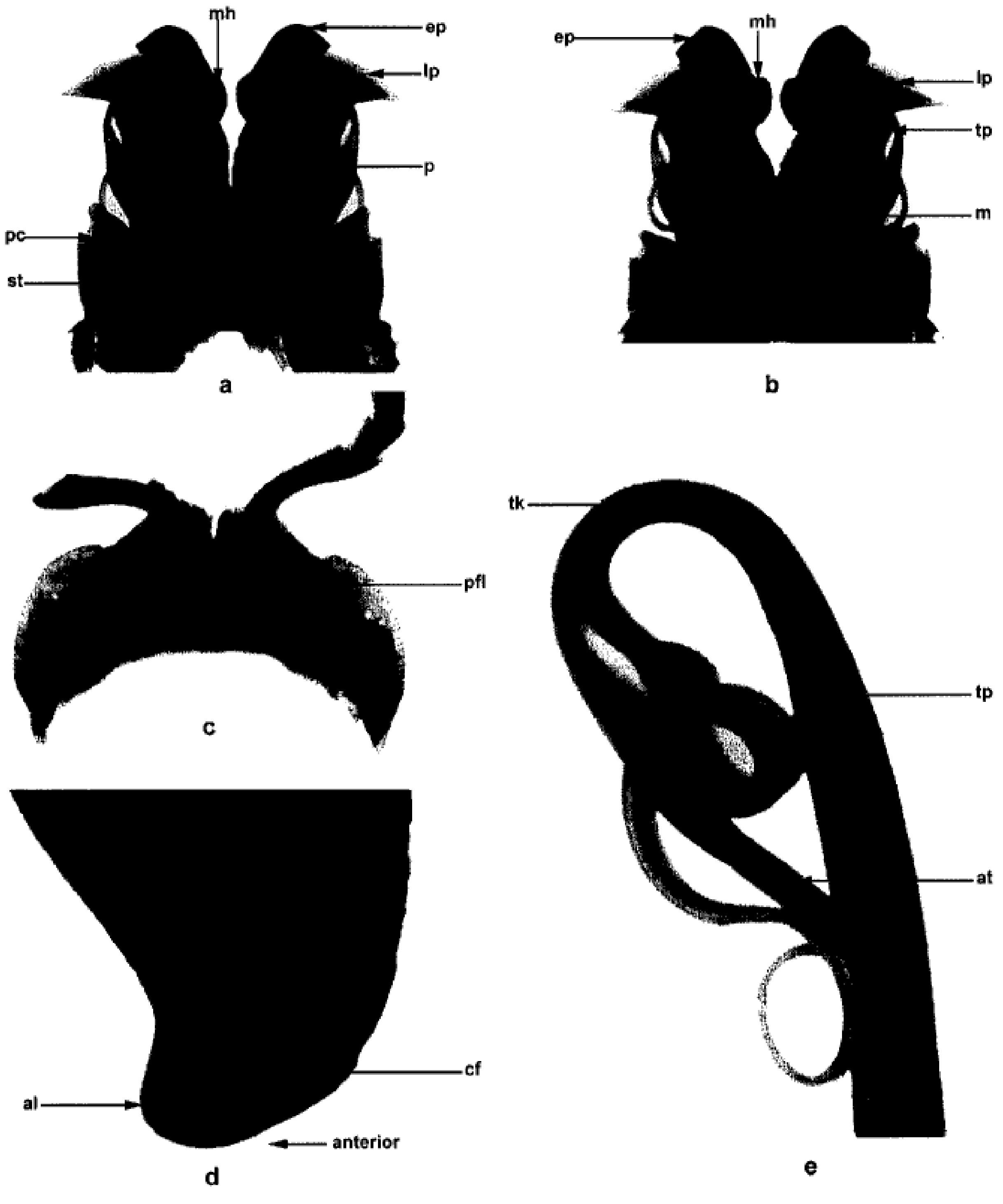

FIGURE 1. *Plagiotaphrus sulcifer* (NMZ/D830). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum; **e,** telopodite. Abbreviations: p, proplica; m, metaplica; mh, median hump; lp, lateral process; ep, end process; tp, telopodite; tk, telopodite knee; tl, tongue-like lobe; at, antetorsal process; pc, paracoxite; st, sternite; cf, collum fold; al, anterior lobe; pfl, prefemoral lobe.

Medial edge of proximal half of oral fold of metaplica raised (Fig. 1b). Distal metaplica with a broad and apically rounded lobe; rounded lobe is adjacent to proximal lateral process. Rounded lobe produced into a rounded median hump.

Lateral process with surface folds.

End processes deflected laterally onto proplica apex. Distal medial edge of end process convex (Figs 1a, 1b).

Post-knee telopodite with two spirals; telopodite trifid at extremity. Antetorsal processes distally crescent-shaped and extends laterally past paracoxite apex.

Distribution: Known only from Chire, East Africa (probably Shire in Malawi) and from northern Zimbabwe.

Remarks: The exact locality where *P. sulcifer* was first collected was given as Chire, East Africa; Krabbe (1982) and Hoffman (1971) suggested that this could be Shire in Malawi. This seems plausible given that *P. sulcifer* has been collected in northern Zimbabwe (Fig. 3). This is the only species in the genus to have been collected from more than one locality. The location of the type material is unknown (Krabbe 1982). Although Krabbe (1982) gave NHMW as the institution likely to be housing the material, the museum does not have the material. It is presumed lost.

Plagiotaphrus improvisus (Attems 1934)

Fig. 2

Megaskamma improvisa: Attems 1934, p. 13, figs 14–17; Synonymy by Hoffman 1971
Plagiotaphrus improvisus: Hoffman 1971

Type material (not examined): ANGOLA: 1 male, near Cuanza river, Biė District, [12°S, 17°30'E], i.1932, F. Haas (SMF 1694).

Diagnosis: Apical proplica tapering and acute, subapically produced into a large, rounded lateral lobe at the level of telopodite knee (Fig. 2a); antetorsal process describes a semi-circle and crosses the proplica (Fig. 2b).

Description: (based on Attems 1934)

Size: Maximum body width 10.5 mm.

Number of body rings: 56.

Colour: Body dark brown; legs dark red-brown.

Collum: Produced into an anterior lobe, with 3 complete folds and an incomplete fold.

Prefemoral process of 1st pair of male legs: Rounded laterally, nipple-shaped and acute apically (Fig. 2c).

Gonopod: (Figs 2a, 2b) Sternite triangular; paracoxite rounded.

Proplicae wider at level of telopodite knee; apical proplica tapering, acute and overlapping proximal lateral process. Subapical proplica extended into a setose, rounded lateral lobe (Fig. 2a).

Medial edge of end process convex distally.

Post-knee telopodite broad proximally, with a spiral distal to paracoxite, distal half narrows with two short branches at extremity; antetorsal processes not reaching paracoxite apex, strongly curved (describing a semi-circle), extend medially and cross proplica (Fig. 2b).

Distribution: Known only from type locality, General Machado, central Angola.

Remarks: According to Hoffman (1971) and Krabbe (1982), the type material is in the SMF, however, the material is not in the collection. The material is said to have been sent to Krabbe in 1975 and it was not returned to the collection. Krabbe (1982) acknowledged having studied the gonopods after finding them in NHMW.

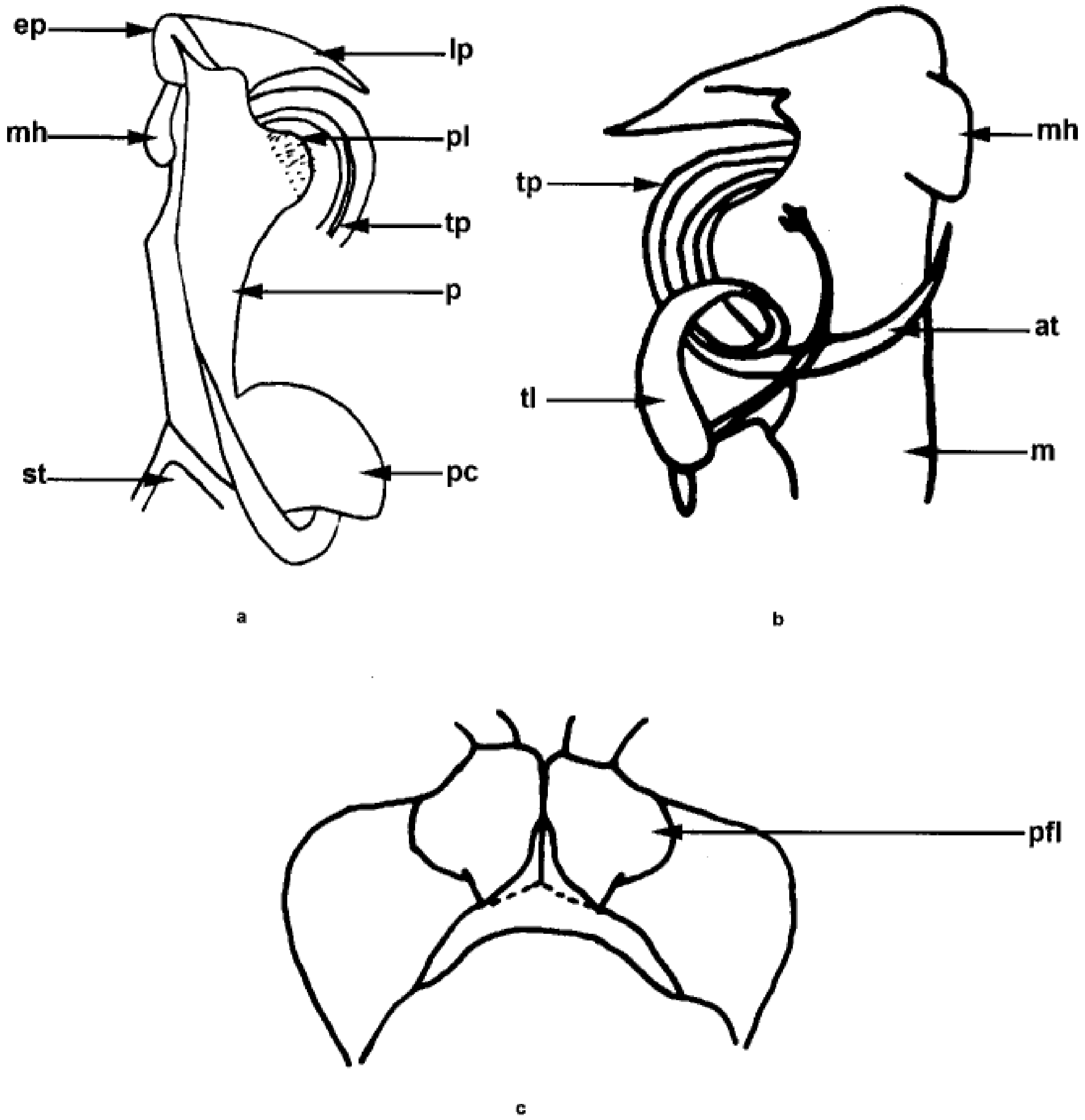

FIGURE 2. *Plagiotaphrus improvisus* (adapted from Attems 1934). **a,** oral view of gonopods; **b,** aboral view of gonopods; **c,** oral view of prefemoral lobe of first pair of male legs. Abbreviations: p, proplica; pl, proplical lobe; m, metaplica; mh, median hump; lp, lateral process; ep, end process; tp, telopodite; tl, tongue-like lobe; at, antetorsal process; pc, paracoxite; st, sternite; pfl, prefemoral lobe.

Species *nomen dubium*

Plagiotaphrus longius Attems 1928, p. 369–370, from Mutare (Umtali), Zimbabwe.

The description of this species was based on a female (SAM 13741) and its generic position and taxonomic validity is doubtful (see Hoffman 1971; Hamer 1998). Until males (and more females) are collected and the gonopods are compared to congeners, *longius* remains doubtful.

According to Attems (1928), the type material is in the SAM. However, the material is missing from the collection and is not in other southern African museums.

Key to species of *Plagiotaphrus*

1. Apical proplica convex medially, narrow and setose (Figs 1a, 1b); subapical proplica not produced into a rounded lateral lobe at level of telopodite knee; antetorsal process crescent-shaped distally (Fig. 1e) ....*sulcifer*
- Apical proplica not convex medially, apically tapering and acute (Fig. 2a); subapical proplica produced into a setose, rounded lateral lobe at level of telopodite knee (Fig. 2a); antetorsal process strongly curved into a semi-circle (Fig. 2b) .... *improvisus*

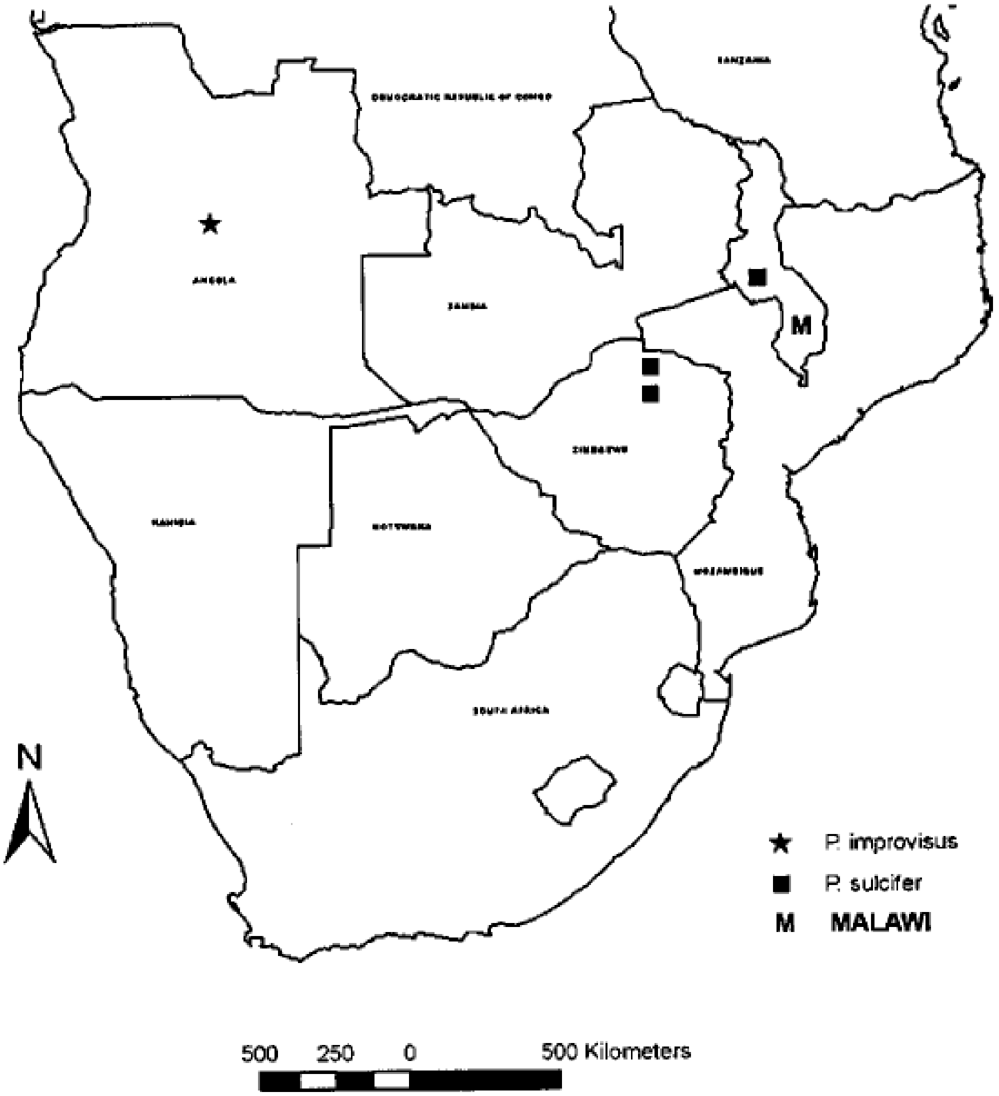

FIGURE 3. Distribution of *Plagiotaphrus* species.

Discussion

Plagiotaphrus is a valid genus of the tribe Spirostreptini with clearly defined synapomorphies; among these are the long proplicae of the gonopod, the presence of distal median humps, the apically convex end processes and a tongue-like lobe on the telopodite distal to the origin of the antetorsal process.

The exclusion of *longius* from the genus leaves *P. sulcifer* and *improvisus* as the only two included species. *Plagiotaphrus longius* is a doubtful taxon because the description was based on a female. Males of this taxon have never been collected; until males become available and their gonopods are compared to congeners, the validity of *longius* cannot be verified, therefore it is a *nomen dubium*. Although Attems (1928) reported that the external features of the female resemble *P. sulcifer*, the specimen described differs from valid *Plagiotaphrus* species by having more body rings. Similarities to *Plagiotaphrus* species are probably due to convergence.

Based on current data, *Plagiotaphrus* has a disjunct distribution (Fig. 3). Given that in northern Zimbabwe *Plagiotaphrus sulcifer* co-occurs with *Spirostreptus sebae*, which has been collected in several localities (see Mwabvu *et al.* 2009), *Plagiotaphrus* species probably occur in the same vegetation types where *sebae* was recorded. Although the isolated records of *Plagiotaphrus* species suggest a wide distribution in southern and central Africa, until more areas (particularly north of the Zambezi River and in Mozambique) have been surveyed, we cannot establish whether the known distributions of the species are real or a collecting artifact. The absence of *Plagiotaphrus* species from South Africa and from the eastern highlands of Zimbabwe (including Mutare, where *longius* was collected) (Fig. 3) suggest that they do not occur in these parts. However, the absence could also be because *Plagiotaphrus* species occur in small areas and would not have been collected in scattered sampling. Therefore, the distribution of the genus should be interpreted with caution because of inadequate sampling or lack of sampling in several localities. Because of our fragmentary knowledge of the taxa more data have to be collected before *Plagiotaphrus* species can be used in biodiversity conservation studies.

Acknowledgements

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CHAPTER 5

A REVISION OF THE TAXONOMY AND DISTRIBUTION OF *Archispirostreptus* Silvestri 1895 (DIPLOPODA, SPIROSTREPTIDA, SPIROSTREPTIDAE), AND DESCRIPTION OF A NEW SPIROSTREPTID GENUS WITH THREE NEW SPECIES.

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A revision of the taxonomy and distribution of *Archispirostreptus* Silvestri 1895 (Diplopoda, Spirostreptida, Spirostreptidae), and description of a new spirostreptid genus with three new species

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Abstract

As it is currently defined, *Archispirostreptus* includes two species groups (the southern African and the east African) with distinct kinds of gonopods. A new genus, *Cacuminostreptus* Mwabvu, is proposed to accommodate the southern African species which include *C. conatus* (Attems 1928) comb. n. and three new species, *C. vumbaensis* Mwabvu, *C. triangulatus* Mwabvu and *C. mazowensis* Mwabvu. Two new synonymies are established: *A. Cecchii* Silvestri 1897 = *A. phillipsii* Pocock 1896 and *A. transmarinus* Hoffman 1965 = *A. syriacus* (Saussure 1859). The species *A. arabs* Pocock 1895 is *incertae sedis*; and *A. sumptuosus* Silvestri 1896 is a *nomen dubium*. Identification keys to the genera and species based on gonopod morphology and distribution data are presented.

Key words: millipedes, distribution, gonopod, savanna, eastern highlands, East Africa, southern Africa, Horn of Africa

Introduction

In some terrestrial ecosystems millipedes are a major part of the soil macrofauna (Crawford 1992) in terms of numbers of species and biomass (Dangerfield 1990). Millipedes enhance organic matter breakdown (Bond & Sierwald 2002; Sierwald & Bond 2007) and mix organic matter with upper soil layers (Edwards *et al.* 1970). They are ranked behind earthworms and termites as one of the major groups involved in the breakdown of organic matter (Crawford 1992).

Despite being common, conspicuous (Hamer 1999; 2000) and ecologically important (New 1995), the diversity and distribution of spirostreptid millipedes are incompletely known. In addition, several African genera are of dubious taxonomic status. Although some genera have been revised (see Hamer 2000; Mwabvu *et al.* 2007; Mwabvu *et al.* 2009b), more African genera still need revision.

The tribe Spirostreptini, to which several large-sized African genera have been assigned based on the bifid or trifid prostatic groove (Hoffman 2008), is among the problematic taxa. According to Hoffman (2008), *Archispirostreptus* Silvestri 1895, *Choristostreptus* Hoffman 2008, *Limnostreptus* Hoffman 2008, *Plagiotaphrus* Attems 1914 and *Spirostreptus* Brandt 1833 can be grouped to form tribe Spirostreptini. Among these genera the definition and distribution of *Archispirostreptus* species are probably the most confusing (see Krabbe & Enghoff 1978). Hoffman (2008) suggested that *Archispirostreptus* may be heterogeneous, and Krabbe & Enghoff (1978) reported that the validity of some of the species of *Archispirostreptus* was doubtful. Although current data make *Archispirostreptus* the most widely distributed and speciose member of the tribe, these data are not beyond question.

A taxonomic revision of *Archispirostreptus* based on type material is necessary to define the taxa unequivocally (Hoffman 1965). However, this endeavour presents major challenges, including the unknown location or loss of type specimens of some of the species, including *Spirostreptus arabs* Pocock 1895, *A. Cecchii* Silvestri 1897 and *A. sumptuosus* Silvestri 1896. Additionally, some body segments and the male gonopods of some material are missing, thus making gonopod morphology (on which most millipede descriptions are based) unavailable to delineate taxa. Although this is not ideal, in the absence of holotypes or gonopods the revisions of some species will be based on published descriptions. These challenges are compounded by the limited material available, including the absence of new material, and the fact that many species are known from single localities and that most data labels only give the country of collection rather than the exact locality. In addition, some species descriptions lack detailed drawings of male gonopods or were based on female specimens (see Silvestri 1897). Having encountered similar problems, Krabbe (1982) listed as *nomina dubia* or *incertae sedis* several species that had been assigned to *Archispirostreptus*.

Although records are fragmentary, *Archispirostreptus* seems to be widely distributed. The genus has been recorded from southern Africa (South Africa, Mozambique, Zimbabwe and Malawi), East Africa (Uganda, Tanzania and Kenya), the Horn of Africa (Ethiopia, Eritrea and Somalia), Central Africa (Democratic Republic of Congo and Cameroon), West Africa (Senegal, Mali, Chad and Niger) and the Middle East (Israel, Yemen, Syria, Jordan, Saudi Arabia) (Hoffman 1965; Krabbe 1982; Shelley 2009).

Fifteen species and five subspecies have been described. *Archispirostreptus conatus* (Attems 1928) is found mainly in southern Africa. Although Krabbe (1982) reported that *A. gigas* (Peters 1855) has been recorded from Kruger National Park, South Africa and Tete, Mozambique, the species occurs mainly in East Africa. Other species from East Africa are *A. tumuliporus* (Karsch 1881) and *A. divergens* Krabbe & Enghoff 1978. *Archispirostreptus tumuliporus* has also been recorded from Senegal and Malawi. *Archispirostreptus syriacus* has been recorded from Yemen and Syria. *Archispirostreptus bottegi* Silvestri 1895, *A. Cecchii, A. dodsoni* Pocock 1899, *A. lugubris* Brölemann 1901, *A. phillipsii* Pocock 1896, *A. smithii* Pocock 1899 and *A. sumptuosus* are known from the Horn of Africa.

Hoffman (1965) listed *A. phillipsii, A. dodsoni, A. bottegi, A. beccarii* Silvestri 1895, *Cecchii* and *smithii* as poorly known species, and reported that the localities for *beccarii, bottegi* and *Cecchii* are doubtful. Although the paucity of material and poor species descriptions make the revision of *Archispirostreptus* difficult, comparisons of available material and published descriptions should clarify taxonomic validity and distribution of the species. This endeavour is important because of the increasing demand for accurate data on species diversity, distribution patterns and potential indicator species which could be utilised in biodiversity conservation (Hamer & Slotow 2000); and because new material from previously unsurveyed localities is available to update records. Additionally, the possibility of cryptic species among the material requires investigation.

Currently *Archispirostreptus* is identified by a gonopod telopodite with an antetorsal process with laciniate edges or small acute projections (Krabbe 1982; Hoffman 2008) or with a spine at the extremity of the antetorsal process. Based on this definition the gonopods of *Archispirostreptus* species have two different forms of the antetorsal process. One species group with a spine at the extremity of the antetorsal process seems to be closely related to *Spirostreptus*.

We hypothesise that *Archispirostreptus* is non-monophyletic, that some species are incorrectly assigned to the genus or are invalid or synonyms of older names and that some species have not been described. The objectives of this study are to revise the genus and ascertain the validity of known species; to describe new taxa; to develop a key to species identification, to establish biogeographic patterns, and to determine factors that may influence the distribution of *Archispirostreptus*.

Materials and methods

This study used material from various museums, private collections and from recent surveys. Museum abbreviations used are as follows:

BMNH	Natural History Museum, London, United Kingdom
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MRAC	Royal Museum of Central Africa, Tervuren, Belgium
NMZ	Natural History Museum, Bulawayo, Zimbabwe
NMSA	Natal Museum, Pietermaritzburg, South Africa
SAM	South African Museum, Cape Town, South Africa
ZMB	Museum für Naturkunde, Berlin, Germany
ZMH	Zoologisches Institut und Museum, Hamburg, Germany
ZMUC	Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark
NHMW	Naturhistorisches Museum, Vienna, Austria
MSNG	Civic Museum of Natural History "G. Doria", Genoa, Italy

Unless specified the methods follow Mwabvu *et al.* (2007). The characteristics of males and females (when available) were recorded. Although colour may have changed in preserved material, body, leg and antenna colour were recorded and body rings (including the collum and preanal ring) were counted. Body length was measured using a soft wire placed against the line of ozopores. Maximum body width was measured at about midlength, using Vernier calipers. All the measurements were in millimeters.

The gonopods of males were dissected out, examined and photographed. The two parts (telocoxite and telopodite) of the male gonopod were examined. The telopodite was separated from the telocoxite to allow detailed examination. The absence/presence, shapes of processes and angle between processes and relative sizes of gonopod structures were compared and recorded.

Material was studied using a Carl Zeiss Stereo Microscope and photographed using NIS-elements D software and auto-montage software (Leica Microscope MZ12s with 3 CCD Toshiba Camera). The final images and plates were prepared using Adobe Photoshop CS (version 8). ArcGis 9.1 (ESRI) was used to prepare the distribution map of species.

Terminology used follows Hoffman (2008).

Abbreviations used in the figures: al, anterior lobe; ap, apical metaplical process; app, apical metaplical projection; at, antetorsal process; cf, collum fold; lh, lateral horn; lp, lateral metaplical process; m, metaplica; p, proplica; pc, paracoxite; pfl, prefemoral lobe; pl, proximal lobe; st, sternite; tp, telopodite.

Results

Taxonomy

Genus *Archispirostreptus* Silvestri 1895

Archispirostreptus Silvestri 1895, p. 776.
Graphidostreptus: Attems 1909, p. 414; 1914
Archispirostreptus: Attems 1926a, 1928; Schubart 1951; Hoffman 1965, 1971, 1979, 1996, 2008; Krabbe & Enghoff 1978; Krabbe 1979, 1982; Hamer 1998, 1999; Golovatch & Hoffman 2000; Mwabvu 2005, 2006; Mwabvu *et al.* 2007

Type species: *Spirostreptus gigas* Peters 1855, p. 75–79

Diagnosis: Proplicae tongue-shaped; lateral metaplical process tapering distally; apical metaplical process long, finger-like and apically rounded or acute; antetorsal processes with laciniate edges distally.

Description: Large spirostreptid millipedes; body length 130–270 mm; antenna length 10–12 mm; maximum body width 7–19 mm.

Body rings 54–71.

Body black or brown; legs and antennae of same colour.

Prebasilar plate of gnathochilarium not reduced to separate sclerites.

Collum sometimes with anterior lobe, with 2–5 complete striae and 0–6 incomplete striae.

Proplicae tongue-shaped, setose and rounded apically, with central depression flanked by raised edges; proplica about 2/3 of gonopod length; lateral and medial edges of proplicae approximately parallel in most species (Figs 1a, 2a, 3a, 4a).

Proximal metaplicae without lobes or projections (Figs 3b, 4b, 5b, 6b, 7b, 8b, 9b,10b).

Lateral metaplical process without abrupt narrowing, proximally broad and tapering distally. Lateral metaplical process horizontal or slanting towards the apical metaplical process or paracoxite (Figs 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a, 9a, 10a).

Apical metaplical process long, finger-like and apically rounded (Figs 1a, 2a, 4a, 6a, 7a, 8a, 9a) or acute (Figs 3a, 10a).

Telopodite spiralling distal to telopodite knee, antetorsal process with laciniate edges or spikes distally (Figs 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a, 9a, 10a); telopodite with three small lobes at extremity.

Distribution: South, East, Central and West Africa; Middle East.

Remarks: The telopodite, the shape and size of the proplicae, the shapes of the lateral and apical metaplical processes, and the orientation of the lateral and apical metaplical processes of the gonopod distinguish *Archispirostreptus* from all other genera of Spirostreptini.

Archispirostreptus beccarii Silvestri 1895
Fig. 1

Archispirostreptus Beccarii Silvestri 1895, p. 490, fig. 8.
Graphidostreptus beccarii: Attems 1914
Archispirostreptus beccarii: Hoffman 1965; Krabbe1982

Type material: Syntypes: ABYSSINIA: 3♂, 5 ♀, Cheren (probably Keren) [15°42'N, 38°24'E], 1870, O. Beccari (MSNG uncatalogued)

Diagnosis: Apex of proplica conical; apical metaplical process wider at level of lateral metaplical process; lateral metaplical process wider and horizontal proximally, abruptly tapering distally (Figs 1a, 1b).

Description: *Size*: Body length 90–145 mm; maximum body width 9–12 mm.

Number of body rings: 54–56.

Colour: Like ash or brown.

Collum: Antero-lateral corners produced into small lobes, with 2–3 complete striae and 0–2 incomplete striae (Fig. 1d).

Pre-femoral process of 1st pair of male legs: Proximally broad and round, with laterally diverging and tapering distal medial extension (Fig. 1c).

Gonopod: (Figs 1a, 1b) Sternum triangular; paracoxite conical.

Proplicae wider proximally, conical apically and overlapping lateral metaplical process proximally.

Opposite metaplicae separated at level of paracoxite apex. Metaplicae narrow distally, widest apart at level of lateral metaplical process.

Lateral metaplical process wider proximally, horizontal and at right angle to apical metaplical process.

Apical metaplical processes wider apart distally. Medial edge of apical metaplical process convex distally.

Telopodite with an incomplete loop distally. Origin of antetorsal processes at telopodite knee.Apex of antetorsal process extending past apex of paracoxite.

Distribution: Known only from the type locality, Cheren, Abyssinia (Ethiopia).

Remarks: Although the gonopod is similar to that of *bottegi*, the gonopods of the two species differ in the shapes of the proplica apex, lateral metaplical processes and apical metaplical processes, and the number of telopodite spirals (Figs 1a, 2a).

The gonopod of *A. beccarii* is also similar to that of *A. dodsoni* in the shapes of the proplicae and apical metaplical processes.

Archispirostreptus bottegi Silvestri 1895
Fig. 2

Archispirostreptus Bottegi Silvestri 1895, p. 489, fig. 7.
Graphidostreptus bottegi: Attems 1914
Archispirostreptus bottegi: Hoffman 1965; Krabbe 1982

Type material: Syntypes: ETHIOPIA: 1♂, 1♀, Ogaden.Archeisa (Harra-es-saghir), 12.x.1892, V. Bottego (MSNG uncatalogued)

Diagnosis: Apex of proplica rounded; apical metaplical process wider apically, thumb-like; post-knee telopodite with two coils (Figs 2a, 2b).

Description: *Size*: Body length 120–130 mm; maximum body width 10–12 mm.

Number of body rings: 54–56.

Colour: Black.

Collum: Antero-lateral corners not produced into lobes, square shaped, with 2 complete striae (Fig. 2d).

Pre-femoral process of 1st pair of male legs: Triangular; proximally broad, with tapering distal extension (Fig. 2c).

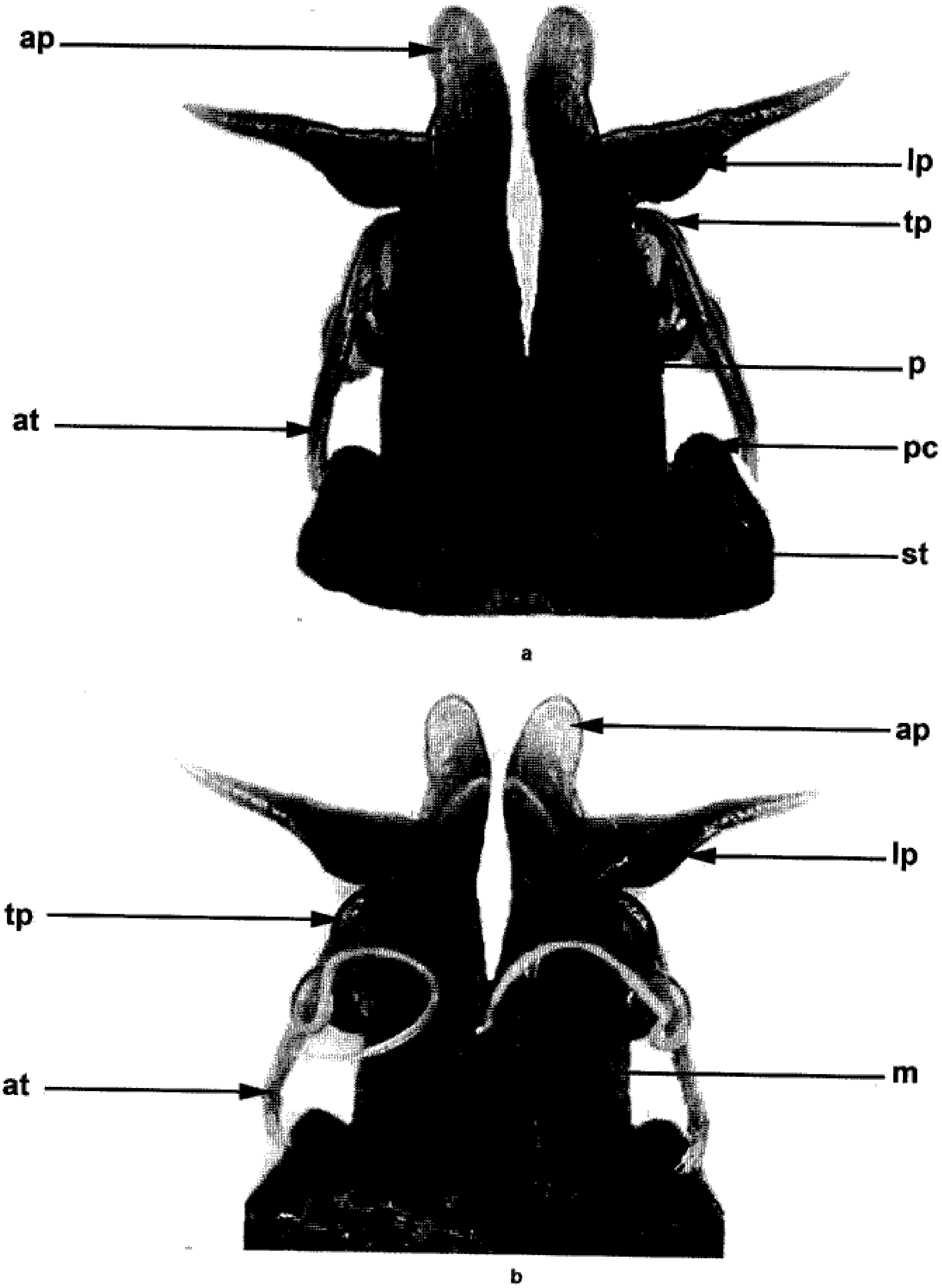

FIGURE 1a, b. *Archispirostreptus beccarii* (MSNG uncatalogued). **a,** oral view of gonopods; **b,** aboral view of gonopods.

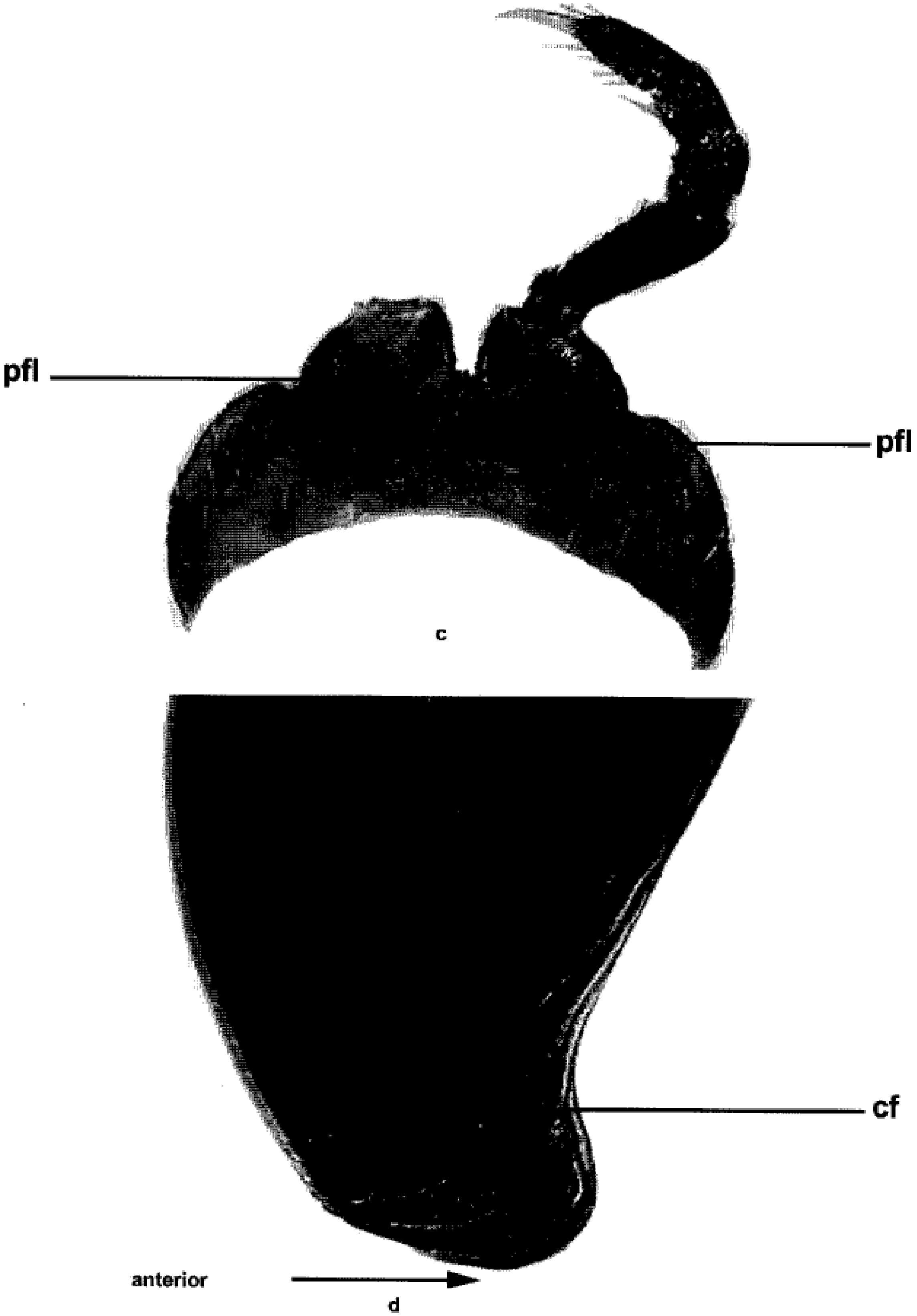

FIGURE 1c, d. *Archispirostreptus beccarii* (MSNG uncatalogued). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

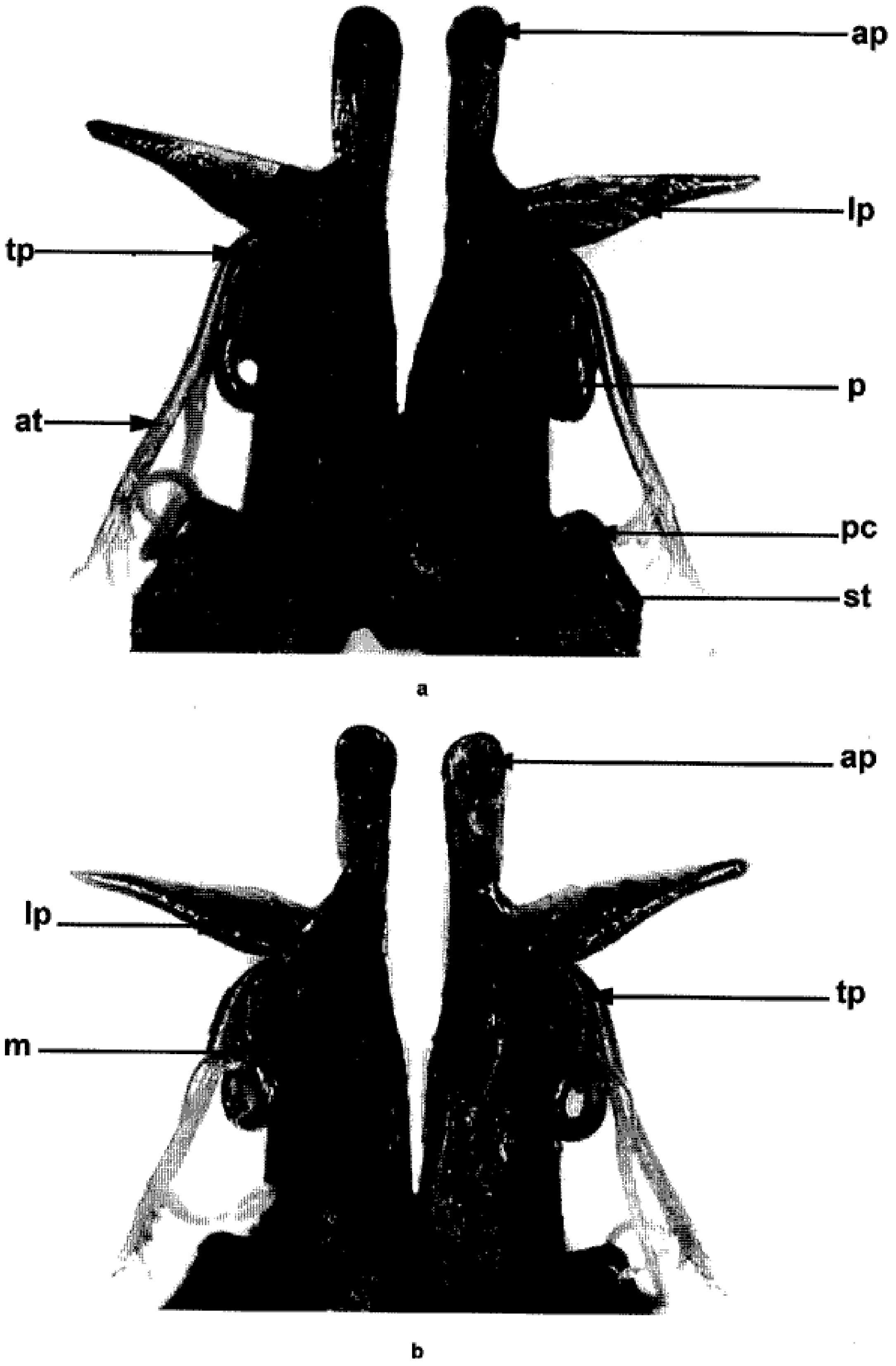

FIGURE 2a, b. *Archispirostreptus bottegi* (MSNG uncatalogued). **a,** oral view of gonopods; **b,** aboral view of gonopods.

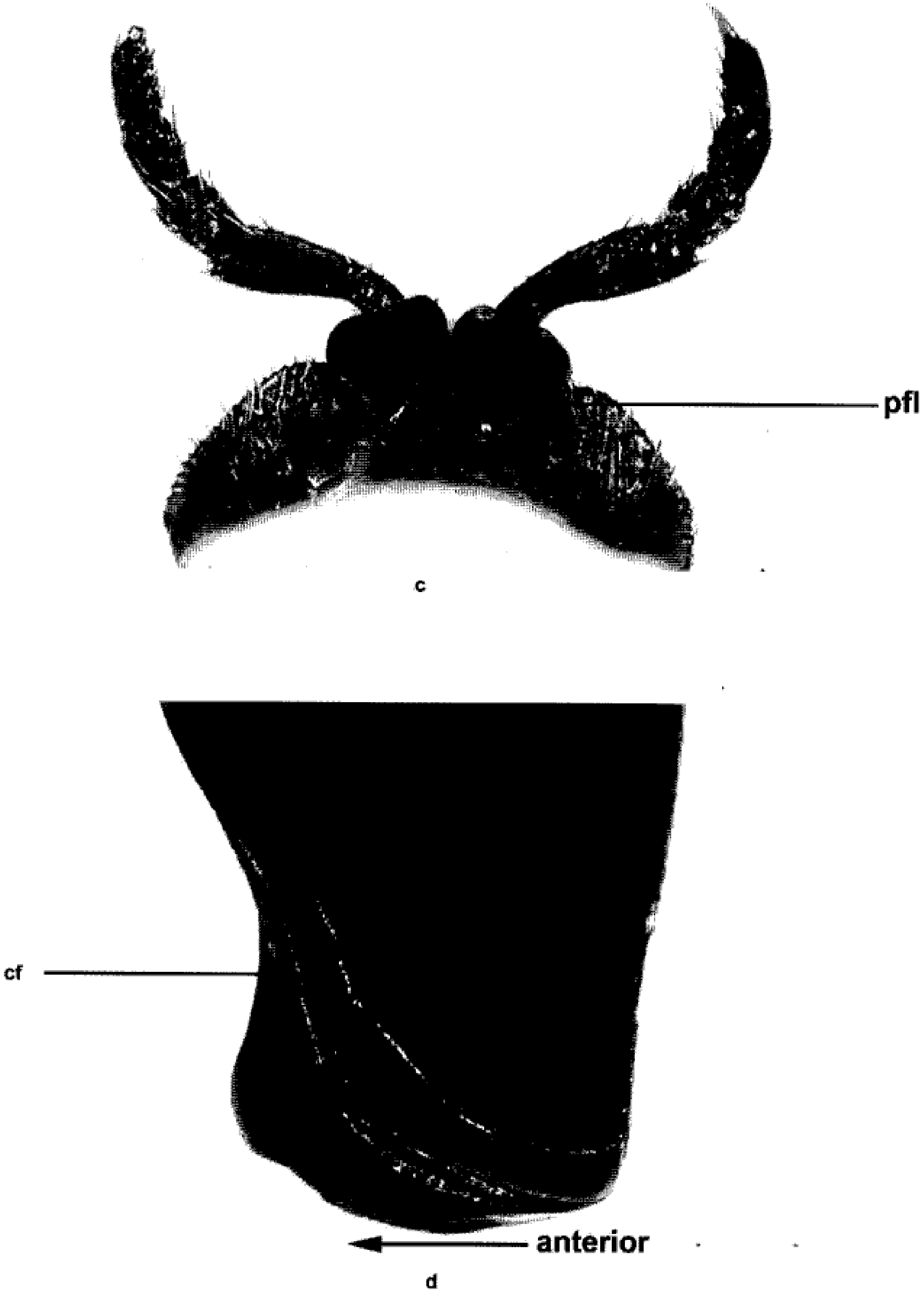

FIGURE 2c, d. *Archispirostreptus bottegi* (MSNG uncatalogued). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

Gonopod: (Figs 2a, 2b) Sternum triangular; paracoxite conical.

Proplica width same along length; apex of proplica finger-like and overlapping proximal lateral metaplical process.

Opposite metaplicae separate at level of paracoxite apex.

Lateral metaplical process horizontal, tapering distally and at right angle to apical metaplical process.

Apical metaplical processes thumb-shaped and parallel and about 2/3 length of lateral metaplical process.

Telopodite with two post-knee spirals, distal spiral at level of paracoxite.

Origin of antetorsal process at knee; apex of antetorsal process extending past apex of paracoxite, with long spikes.

Distribution: Known only from Ogaden, Ethiopia.

Remarks: The gonopods of *A. bottegi* and *A. beccarii* are distinguished by the apical shapes of the proplicae and apical metaplical processes, and the number of spirals of the telopodite. *Archispirostreptus bottegi* has a telopodite with two spirals and long spikes on the antetorsal process (see remarks under *A. beccarii*).

Archispirostreptus divergens **Krabbe & Enghoff 1978**

Fig. 3

Archispirostreptus divergens Krabbe & Enghoff 1978, p. 247–249, figs 1–5.
Archispirostreptus divergens: Krabbe 1982

Type material: Holotype: KENYA: 1♂, Lake Baringo Lodge c 100 km from Nairobi [0°59'N, 36°03'E], 21-22.vii.1977, H. Gonget (ZMUC uncatalogued). Paratype: KENYA: 1♂, same data as holotype (ZMH A89/78)

Diagnosis: Medially diverging and overlapping apical metaplical processes (Figs 3a, 3b).

Description: *Size*: Body length 130–150 mm; maximum body width 12–14 mm.

Number of body rings: 56–62.

Colour: Body black; legs and antennae red-brown.

Collum: Antero-lateral corners not produced into lobes, with 2–3 complete striae and 0–2 incomplete striae (Fig. 3d).

Pre-femoral process of 1st pair of male legs: Proximally broad and parallel, with laterally diverging and tapering distal extension (Fig. 3c).

Gonopod: (Figs 3a, 3b) Sternum wide proximally, dome-shaped apically; paracoxite rounded and not fused tightly to metaplica.

Proplicae with shallow central groove. Apex of proplica acute, overlapping lateral metaplical process proximally and with a spinous medial lobe.

Metaplicae wide proximally; opposite metaplicae wider apart at level of lateral metaplical process; oral fold of metaplica overlapping proximal lateral metaplical process and apical proplica. Medial edge of oral metaplica raised sharply at level of lateral metaplical process.

Lateral metaplical process slightly tilted anteriad, ending in distal spine. Lateral metaplical process proximally narrow, widens abruptly before tapering distally. Lateral metaplical process and apical metaplical process at obtuse angle.

Apical metaplical processes strongly diverging and overlapping medially leaving a proximal window (Fig. 3a).

Antetorsal process of the telopodite extends distally past the paracoxite apex.

Distribution: Known only from Lake Baringo, Kenya.

Remarks: The overlapping apical metaplical processes of the gonopods are unique to *A. divergens*. Other species of *Archispirostreptus*, except *A. phillipsii*, have erect and almost finger-like apical metaplical processes.

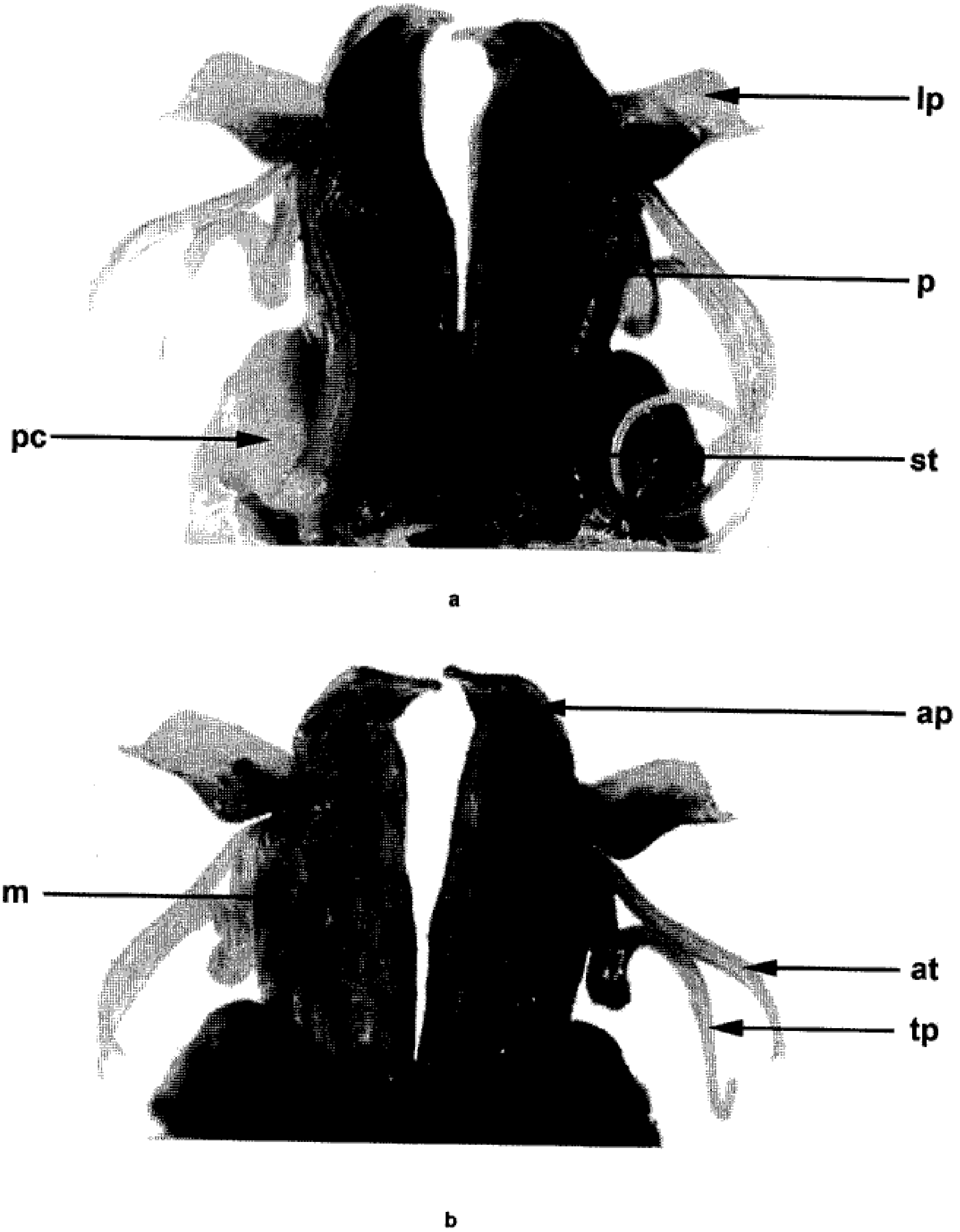

FIGURE 3a, b. *Archispirostreptus divergens* (ZMH A89/78). **a,** oral view of gonopods; **b,** aboral view of gonopods.

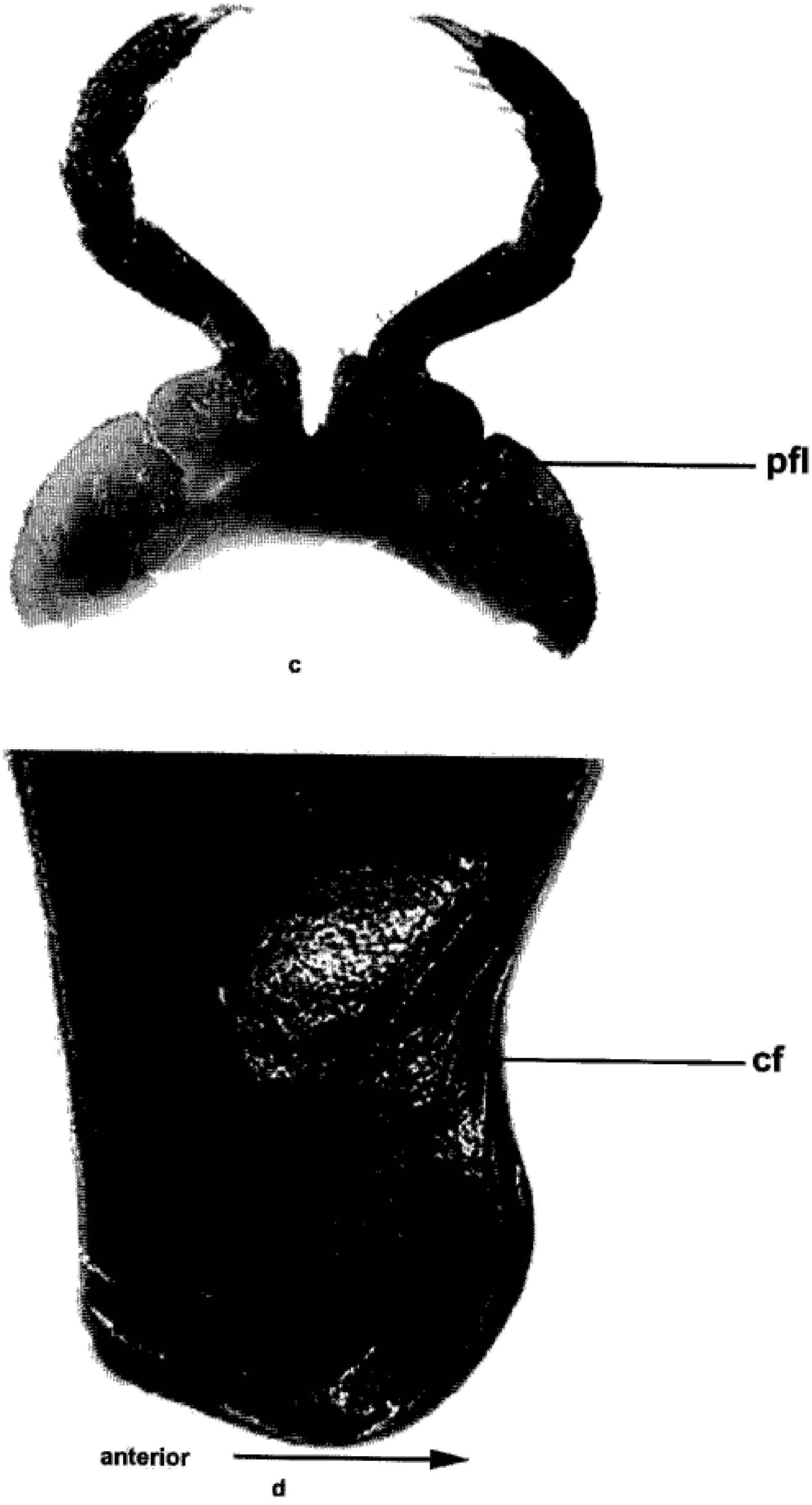

FIGURE 3c, d. *Archispirostreptus divergens* (ZMH A89/78). **c**, oral view of prefemoral lobe of first pair of male legs; **d**, lateral view of collum.

Archispirostreptus dodsoni Pocock 1899
Fig. 4

Archispirostreptus dodsoni Pocock 1899, p. 405.
Graphidostreptus dodsoni: Attems 1914
Archispirostreptus dodsoni: Hoffman 1965; Krabbe 1982

Type material: Holotype: SOMALIA: 1 ♂, Sheikh Husein, Arusha, Galla Country, 3.x.1894, Dr A. Donaldson Smith (BMNH 1897.11.10.87).

Additional material examined: SOMALIA: 1 ♂, 1 ♀, West of Shebali River, 1899, Dr Donaldson-Smith (BMNH 1897.11.10.88).

Diagnosis: Distal lateral metaplical process gently slanting towards paracoxite; proximal lateral metaplical process and proximal apical metaplical process at obtuse angle (Fig. 4a).

Description: *Size*: Body length 220–270 mm; maximum body width 18–19 mm.

Number of body rings: 69–71.

Colour: Dark brown.

Collum: Square shaped without anterior lobe, with 3–5 complete striae and 2–3 incomplete striae.

Pre-femoral process of 1st pair of male legs: Proximally broad with long tapering apical extension (Fig. 4c).

Gonopod: (Figs 4a, 4b) Sternum rounded apically; paracoxite apex horizontal.

Proplica width approximately constant along length; apical proplica overlapping part of proximal lateral metaplical process.

Metaplicae wide proximally, surface smooth.

Lateral metaplical process wide proximally, horizontal and acute apically, without abrupt change in width.

Apical metaplical process narrowly rounded apically. Proximal apical metaplical process and lateral metaplical process at obtuse angle (Fig. 4b).

Apex of antetorsal processes reaching paracoxite.

Distribution: Known from Ethiopia (Krabbe 1982) and Somalia.

Remarks: The shapes of the lateral metaplical processes and the apical proplicae of the gonopod of *A. dodsoni* closely resemble *A. beccarii*, however, the two species differ in body size. The prefemoral lobes of the first pair of male legs are similar to those of *A. smithii*, however, the gonopods of the two species differ in the orientation of the lateral metaplical processes. Proximally, the lateral metaplical processes of the gonopod of *A. smithii* are horizontal; the distal halves are tapering and deflected towards the apical metaplical process. In *A. dodsoni* the lateral metaplical process is horizontal and tapering without bending distally.

Archispirostreptus gigas (Peters 1855)
Fig. 5

Spirostreptus gigas Peters 1855, p. 536, figs 1–2.
Archispirostreptus gigas: Silvestri 1895; Schubart 1951; Hoffman 1965; Krabbe & Enghoff 1978; Krabbe 1982; Hamer 1998, 1999
Graphidostreptus gigas: Attems 1914; Attems 1928
Further synonymy in Krabbe (1982)

Type material (not examined): MOZAMBIQUE: 1 ♂, Tete.The location of the type material is unknown.

Additional material examined: KENYA: 1 ♂, 2 ♀, Tsavo, Taita Discovery Center [03° 25' S, 38° 46'E], 6.xii.2000, Van den Spiegel D. (MRAC 20254); 1 ♂, 1 ♀, Ngaia Forest [0° 24' N, 38° 02'E], 3.xii.2002, Van den Spiegel D. (MRAC 20764).

Diagnosis: Lateral metaplical process short and broad with a short terminal spine; lateral metaplical process at acute angle with apical metaplical process; lateral and medial edges of apical metaplical process convex proximally; lateral metaplical process darker proximally than distally; apical metaplical process darker laterally and proximally than medially or distally (Figs 5a, 5b).

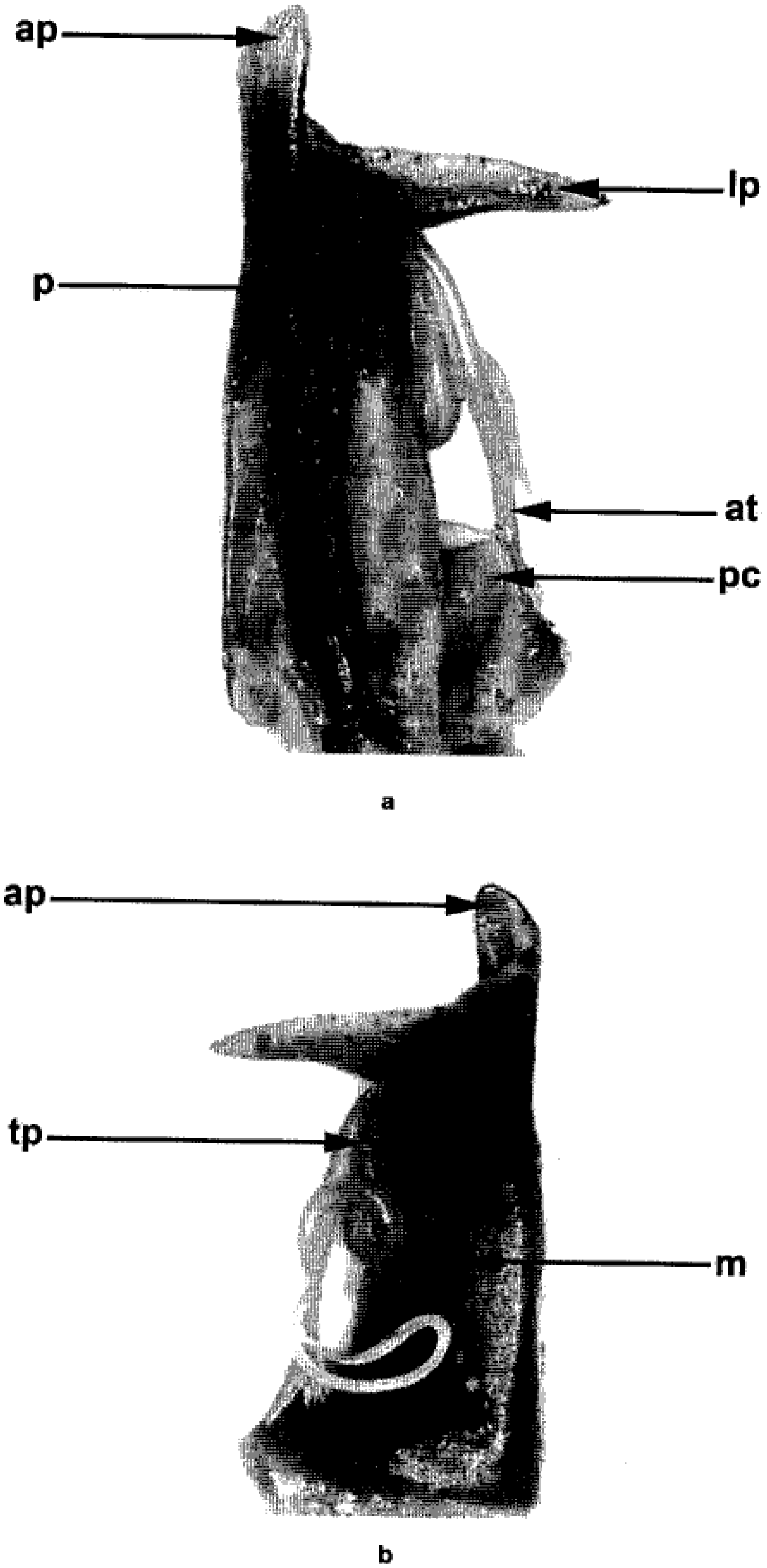

FIGURE 4a, b. *Archispirostreptus dodsoni* (BMNH 1897.11.10.87). **a,** oral view of gonopods; **b,** aboral view of gonopods.

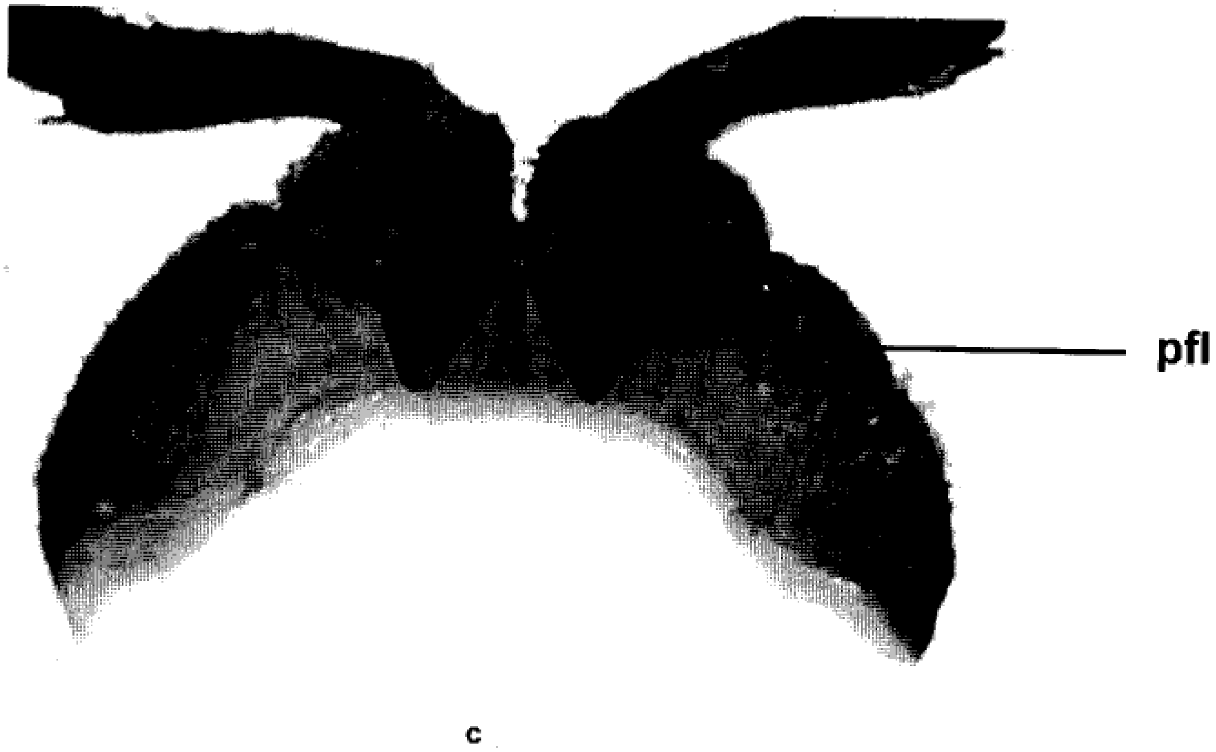

FIGURE 4c. *Archispirostreptus dodsoni* (BMNH 1897.11.10.87). **c,** oral view of prefemoral lobe of first pair of male legs.

Description: *Size*: Body length 178–260 mm; maximum body width 15–19 mm.

Number of body rings: 62–70.

Colour: Black.

Collum: Rounded without anterior lobe (Fig. 5c), with 2–3 complete striae and an incomplete stria.

Pre-femoral process of 1st pair of male legs: Proximally wide with laterally deflected apical extension (Fig. 5c).

Gonopod: (Figs 5a, 5b) Sternum broad, short and apically rounded; apex of sternum not reaching level of paracoxite apex; paracoxite rounded and fused tightly to metaplica.

Proximal proplica with raised lateral and medial edges; apically proplicae rounded, overlapping lateral metaplical process proximally and with an apical medial lobe.

Proximal medial edges of oral fold of metaplicae raised.

Proximal half of opposite telocoxites touching medially, further apart distal to lateral metaplical process (Figs 5a, 5b).

Lateral metaplical processes short and broad, crescent-shaped and tapering distally, and may have a small terminal spine. Lateral metaplical process at acute angle with apical metaplical process.

Lateral and medial edges of apical metaplical process convex proximally; apical metaplical process broad and opaque proximally.

Aborally, medial edge of metaplicae raised (Fig. 5b).

Apex of antetorsal process extends past paracoxite apex.

Distribution: Known from Mozambique, South Africa, Zanzibar, Somalia, Tanzania (Krabbe 1982) and Kenya.

Remarks: The opposite telocoxites of the gonopods in *A. gigas* are separated at the level of the lateral metaplical processes as in *A. phillipsii*, *A. lugubris*, *A. syriacus*, *A. tumuliporus*, *A. smithii* and *A. dodsoni*. The convex shapes of the lateral and medial edges of the apical metaplical process of the gonopod are unique to *A. gigas*.

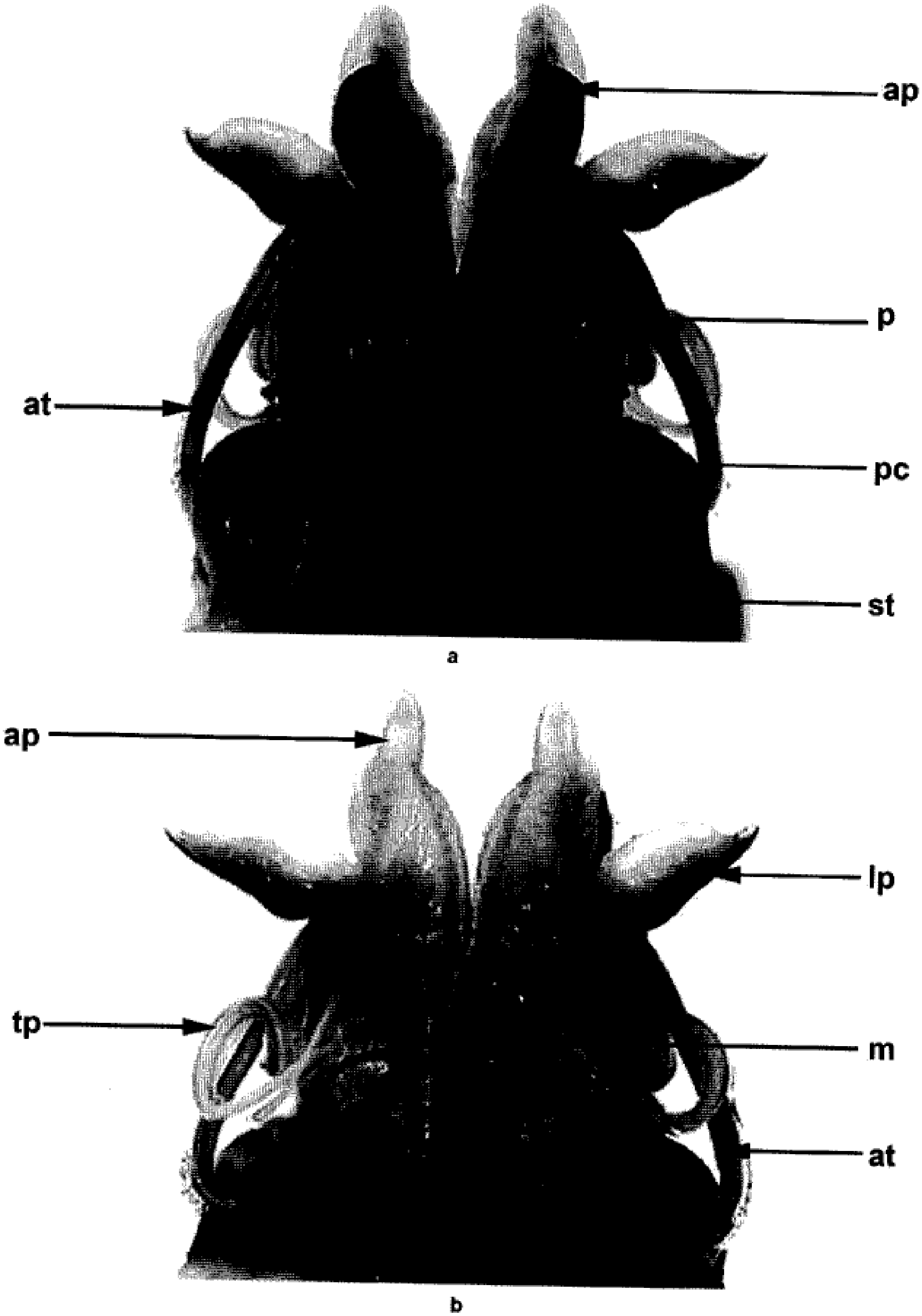

FIGURE 5a, b. *Archispirostreptus gigas* (MRAC 20764). **a,** oral view of gonopods; **b,** aboral view of gonopods.

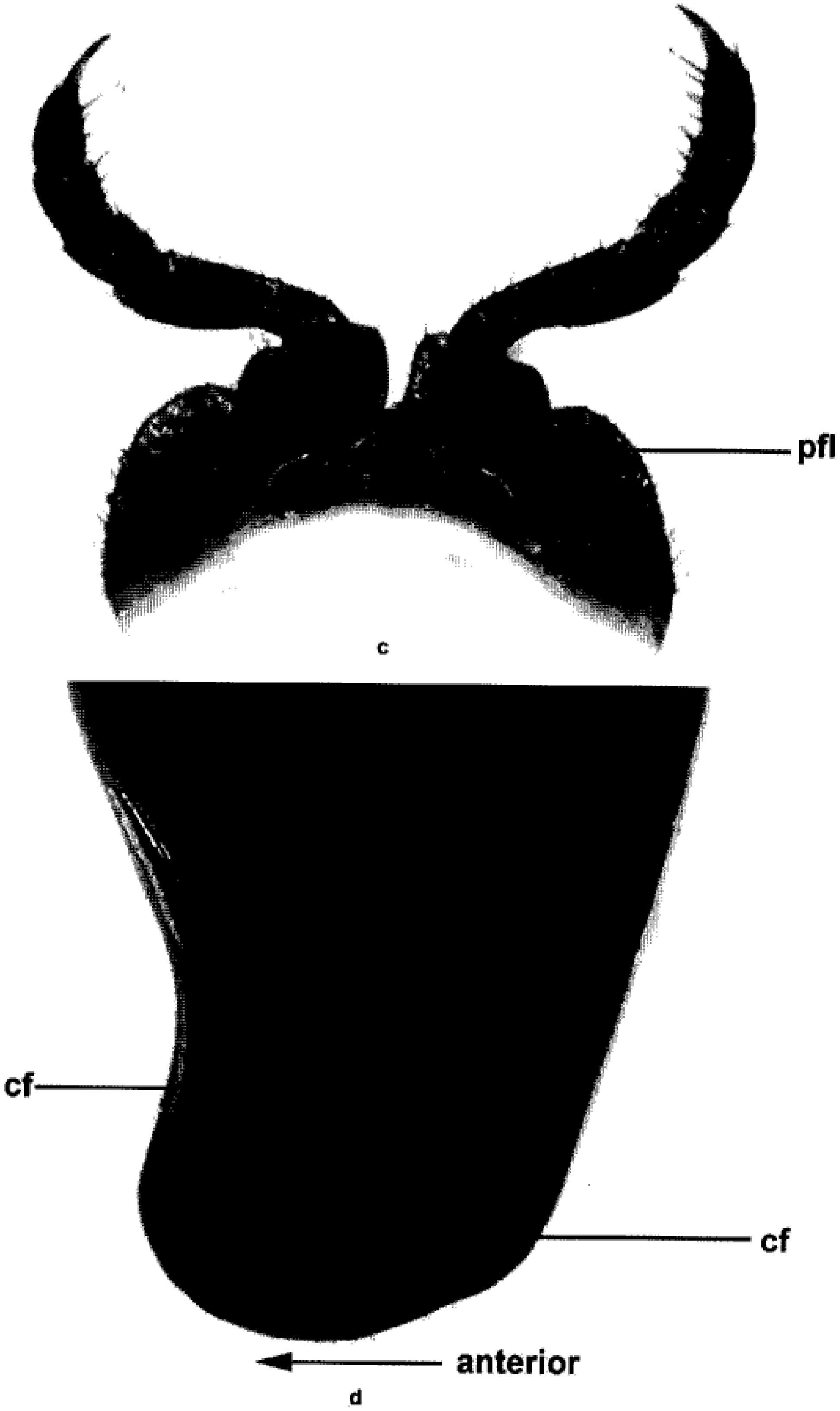

FIGURE 5c, d. *Archispirostreptus gigas* (MRAC 20764). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

Considering where *A. gigas* has been collected and the distance between the localities, the currently known distribution may be a collecting artifact. The known distribution suggests that it is more widespread along the east coast of Africa than further inland.

The type is missing from the ZMH collection where it was said to be housed (Krabbe 1982); this was confirmed by museum curators.

Archispirostreptus lugubris **(Brölemann 1901)**

Fig. 6

Spirostreptus lugubris Brölemann 1901, p. 31–34, figs 8–11.
Graphidostreptus lugubris: Attems 1914
Archispirostreptus lugubris: Schubart 1951; Hoffman 1965; Krabbe 1982

Type material: Holotype: ETHIOPIA: 1 ♂, Sabarguma Allata, 15.iii.1900, P. Magretti (MNHN 1B 106).

Additional material examined: NIGER: 1 ♂, Monts Baguezane, Irrabellaben, 26.viii.1947, L. Chopard & A. Villiers (MNHN 1B 108) (gonopods missing). SENEGAL: 2 ♂, Bambey [14°43'N, 16°14'W], (MRAC 20504); 1 ♂, 1 ♀, Gouloubou [13°27'N, 13°43'W], 2.i.1979, D. Thys (MNHN 1B 224).

Diagnosis: Sternite apex flat; oral fold of metaplicae abruptly narrow at level of telopodite knee (Fig. 6a). Lateral metaplical process slanting gently towards paracoxite (Fig. 6a)

Description: *Size*: Body length 102–155 mm; maximum body width 8–13 mm.

Number of body rings: 55–64.

Colour: Body black or dark brown; legs and antennae brown.

Collum: Anterior produced into lobe, with 2–3 complete striae and 1–2 incomplete striae.

Pre-femoral process of 1st pair of male legs: Basally round with short tapering apical extension.

Gonopod: (Figs 6a, 6b) Sternum broad proximally, apex flat; paracoxite triangular.

Width of proplicae constant.

Metaplicae wide proximally; opposite metaplicae wider apart distal to sternite apex; oral fold of metaplicae narrow at level of telopodite knee.

Lateral metaplical process slanting towards paracoxite and broadly joined to metaplica. Lateral metaplical process at obtuse angle with apical metaplical process (Figs 6a, 6b).

Distally apical metaplical process convex medially and rounded apically.

Origin of antetorsal processes at telopodite knee.

Distribution: Known from Democratic Republic of Congo, Somalia (Krabbe 1982), Niger, Senegal and Ethiopia (Fig. 15).

Remarks: Abrupt narrowing of the oral fold of the metaplicae has only been observed in the gonopods of *lugubris*. The telopodite is similar to those of *A. dodsoni*, *A. tumuliporus*, *A. gigas*, *A. divergens* and *A. smithii*; and the lateral metaplical process resembles that of *A. beccarii*, *A. tumuliporus*, *A. syriacus* and *A. dodsoni* more than *A. gigas*, *A. divergens* or *A. phillipsii*. We have also established that some material of *A. lugubris* (MNHN 1B 224) from Senegal, housed in MNHN had been incorrectly identified as *A. tumuliporus*.

Two subspecies—*Graphidostreptus lugubris maior* Attems 1914, p. 157, figs 155–156 and *Graphidostreptus lugubris villiersi* Schubart 1951, p. 119–124, figs 1–5—from southern Sahara desert have been described. *Archispirostreptus lugubris villiersi* (Schubart 1951) is a smaller variation of the type. Furthermore, the apical metaplical process of the gonopod is shorter and the lateral metaplical process is longer, with a pointed apex, than in *A. lugubris maior* and the other subspecies *A. lugubris lugubris*. Based on gonopod morphology these subspecies represent recognizable forms.

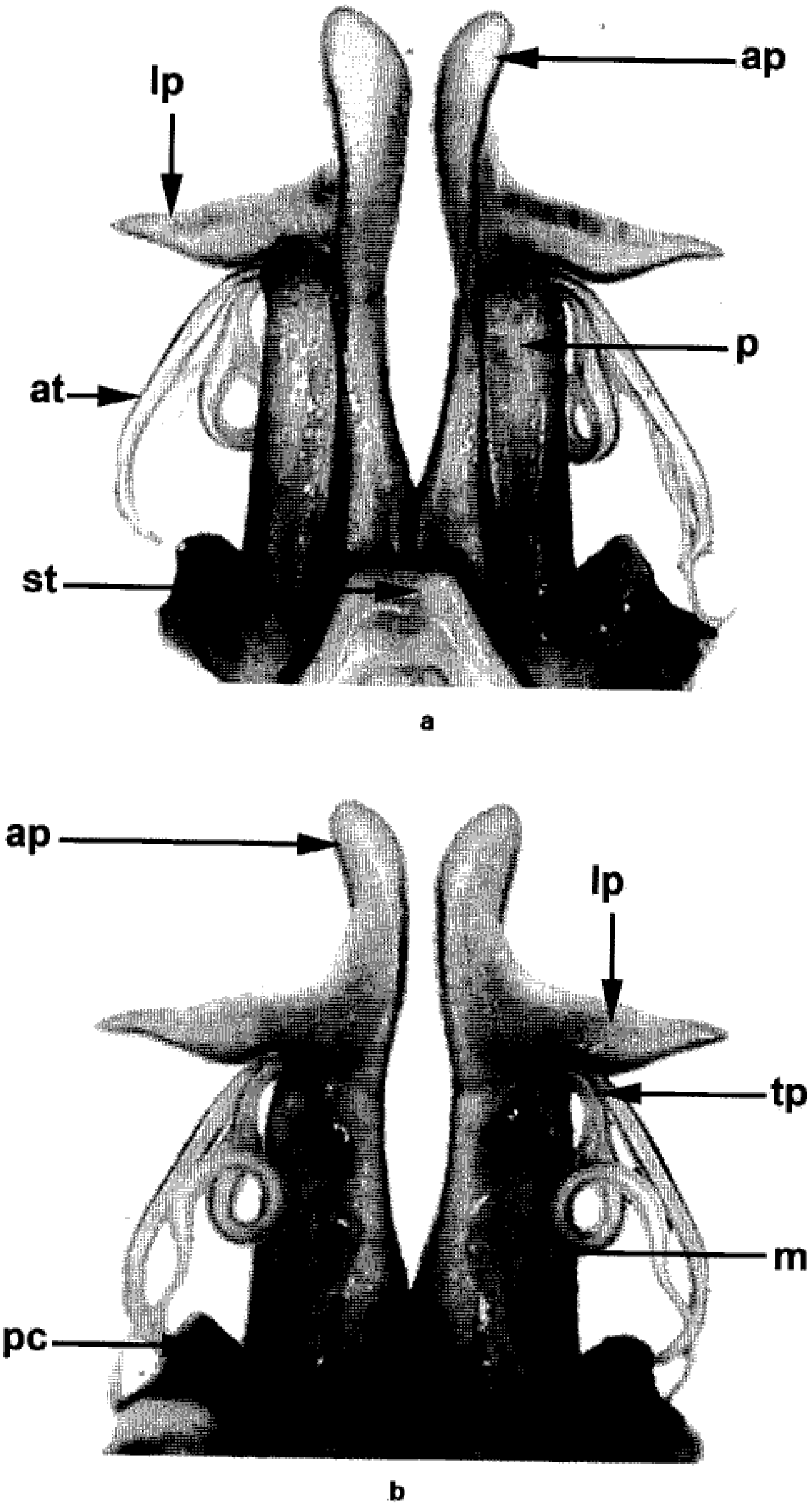

FIGURE 6a, b. *Archispirostreptus lugubris* (MNHN, 1B 106). **a,** oral view of gonopods; **b,** aboral view of gonopods.

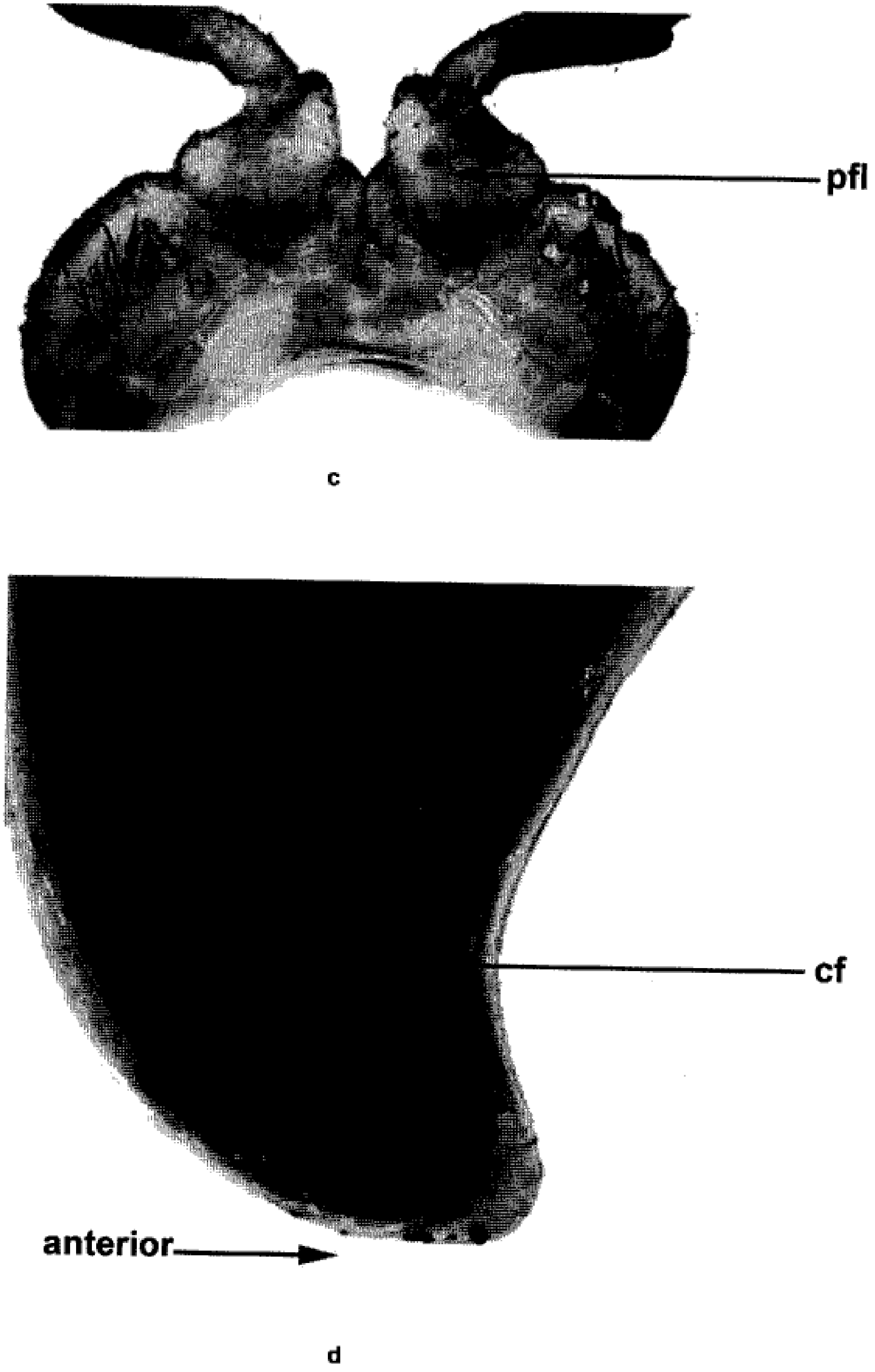

FIGURE 6c, d. *Archispirostreptus lugubris* (MNHN, 1B 106). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

Archispirostreptus phillipsii Pocock 1896

Fig. 7

Archispirostreptus phillipsii Pocock 1896, p. 187, fig. 5.
Graphidostreptus phillipsii: Attems 1914
Archispirostreptus phillipsii: Hoffman 1965; Krabbe 1982
A. Cecchii Silvestri 1897, p. 303–304, fig. 1. **Syn. n.**

Type material: Holotype: SOMALIA: 1 ♂, 1895, (BMNH 1895.6.1).

Diagnosis: Apical metaplical process deflected laterally onto lateral metaplical process. Lateral metaplical process short (as long as metaplica width) and sandwiched between the apical metaplical process and apex of proplica (Figs 7a, 7b).

Description: *Size*: Body length 170–210 mm; maximum body width 14 mm.

Number of body rings: 62–65.

Colour: Black.

Collum: Rounded without anterior lobe, with 3 complete striae.

Pre-femoral process of 1st pair of male legs: Long and parallel, with short apical nipple (Fig. 7c).

Gonopod: (Figs 7a, 7b) Sternum short, wide proximally and flat apically; paracoxite rounded apically.

Proplicae of constant width; rounded apically.

Oral fold of metaplicae wide proximally; opposite metaplicae separate at level of apex of paracoxite. Aboral depression present on metaplicae proximal to lateral metaplical process.

Lateral metaplical process short, as long as apical metaplica width, with a short distal spine. Lateral metaplical process sandwiched between apical metaplical process and apex of proplica.

Apical metaplical process strongly deflected laterally onto lateral metaplical process.

Origin of antetorsal processes distal to telopodite knee. Antetorsal processes with short spikes proximal to a terminal spine (Fig. 7a).

Distribution: Goolis Mountains, Somalia (Krabbe 1982).

Remarks: The laterally deflected apical metaplical processes of the gonopod, a short lateral metaplical process and the wide medial separation of the coxites at the level of the paracoxite apex characterize the gonopod of *A. phillipsii*. *Archispirostreptus phillipsii* is the only species in the genus where the lateral metaplical processes of the gonopod do not extend beyond the lateral margins of the proplicae or metaplicae. The origin of the antetorsal process is distal to the telopodite knee.

The location of the type of *A. Cecchii* is unknown. Therefore, comparisons to *A. phillipsii* were based on description of and gonopod drawing of *A. Cecchii* from Silvestri 1897. Based on the gonopod drawing, *Cecchii* resembles *phillipsii* in that the apical metaplical processes are deflected onto the lateral metaplical processes and the antetorsal process has a distal spine. Both taxa were collected from Somalia. Although the published drawing and description of *A. Cecchii* lack detail they are sufficient to support conspecificity with *A. phillipsii*.

Archispirostreptus smithii Pocock 1899

Fig. 8

Archispirostreptus smithii Pocock 1899, p. 406.
Graphidostreptus smithii: Attems 1914
Archispirostreptus smithii: Hoffman 1965; Krabbe 1982

Type material: Holotype: SOMALIA: 1 ♂, (BMNH 1897.11.10.89).

Additional material examined: SOMALIA: 1 ♀, (BMNH 1897.11.10.90).

Diagnosis: Lateral metaplical process broad and horizontal proximally, distal half bent and tapering towards apical metaplical process (Figs 8a, 8b).

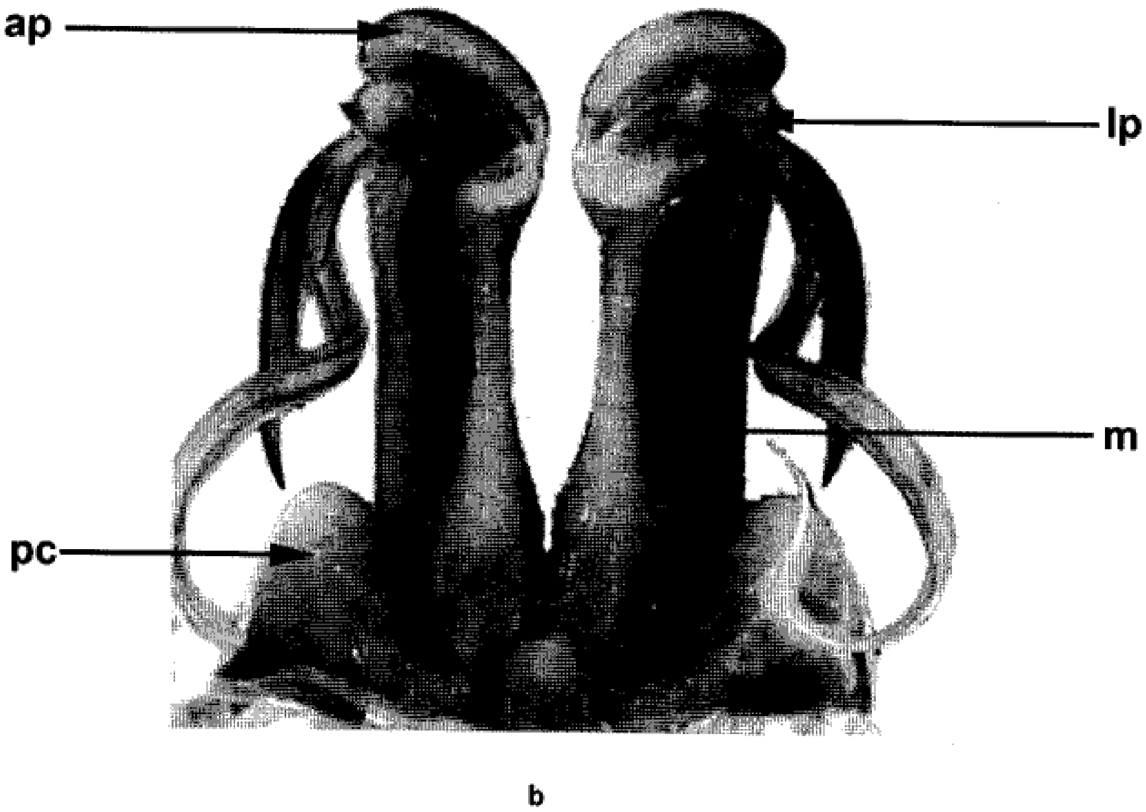

FIGURE 7a, b. *Archispirostreptus phillipsii* (BMNH 1895.6.1). **a,** oral view of gonopods; **b,** aboral view of gonopods.

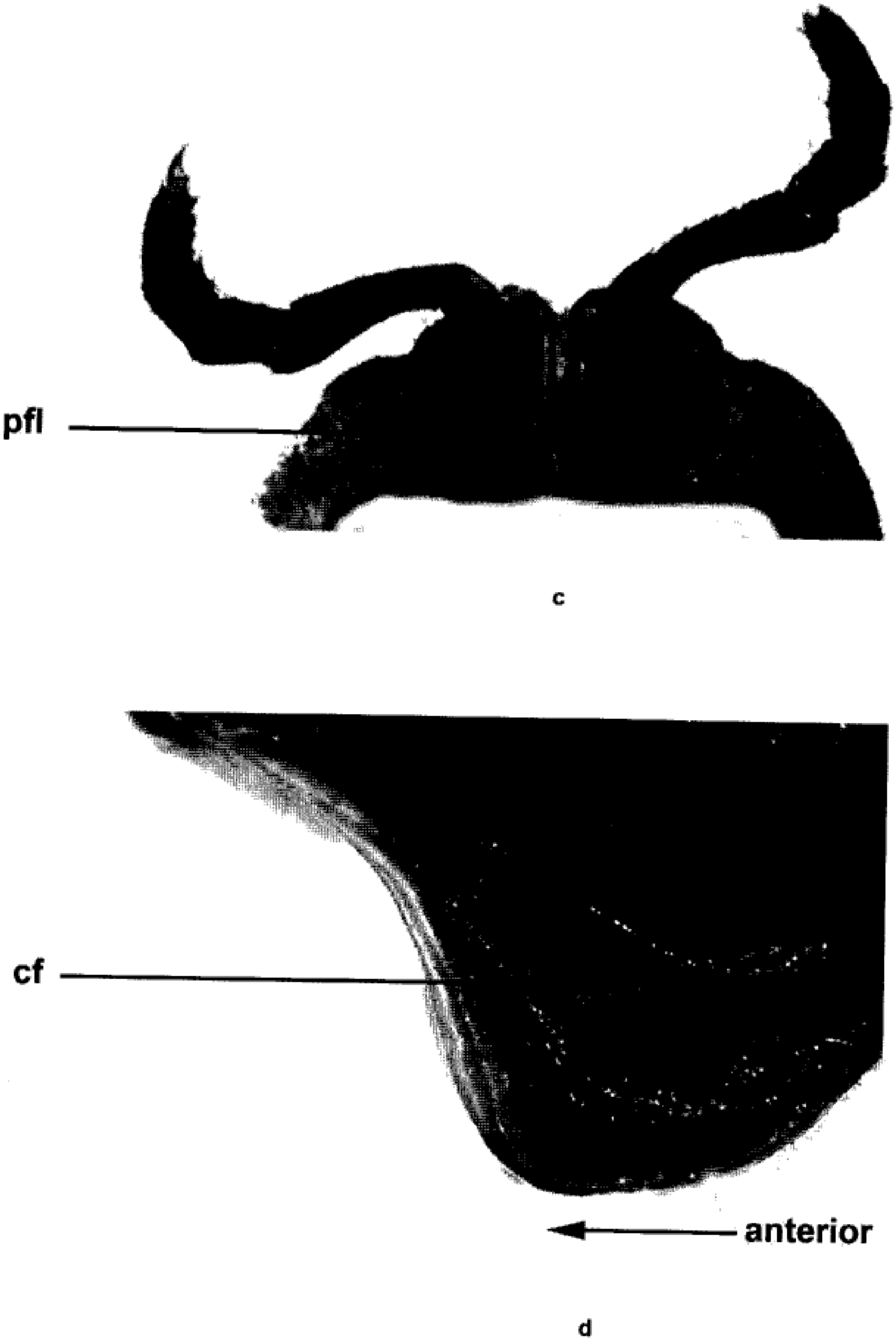

FIGURE 7c, d. *Archispirostreptus phillipsii* (BMNH 1895.6.1). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

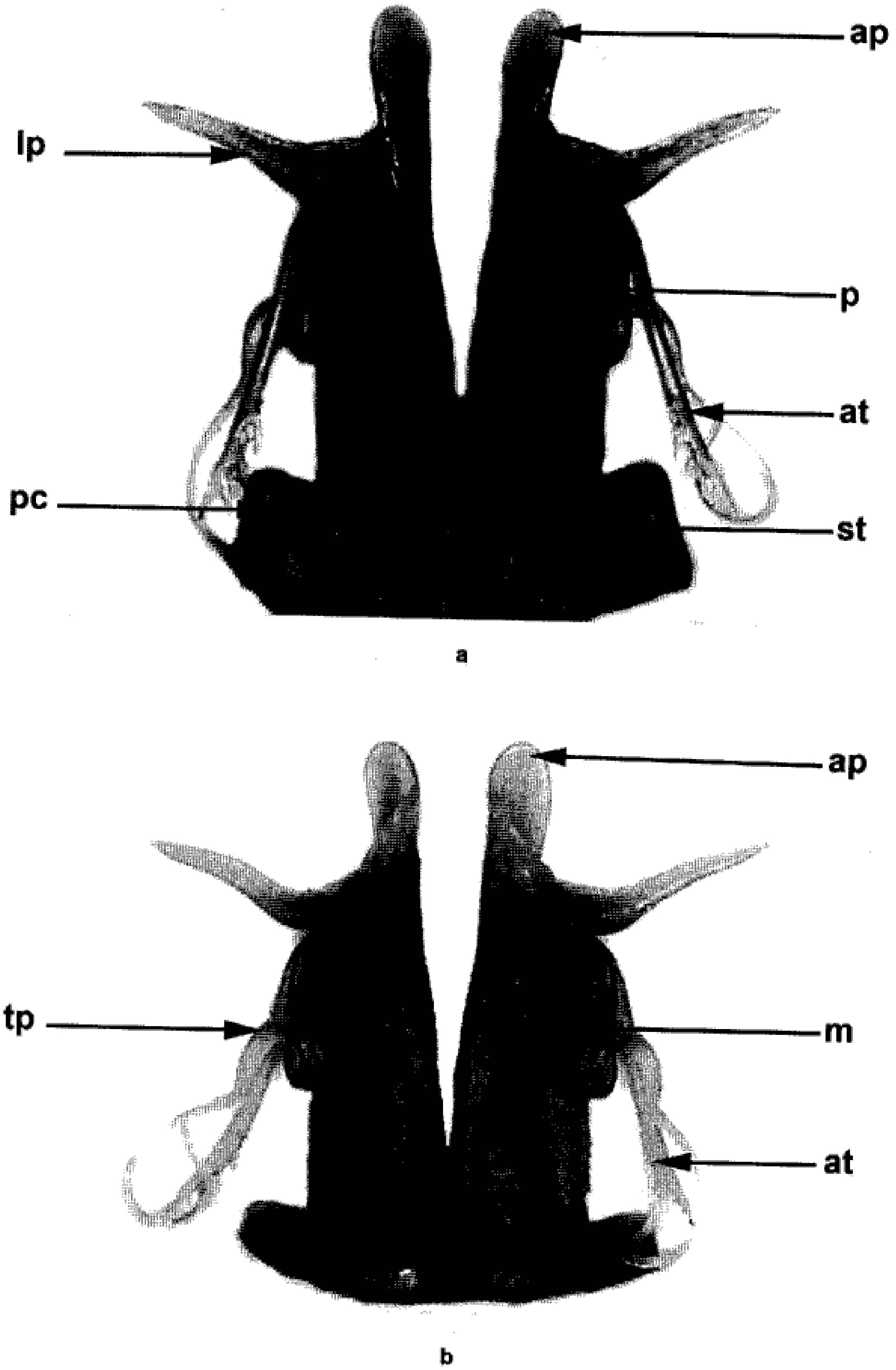

FIGURE 8a, b. *Archispirostreptus smithii* (BMNH 1897.11.10.89). **a,** oral view of gonopods; **b,** aboral view of gonopods.

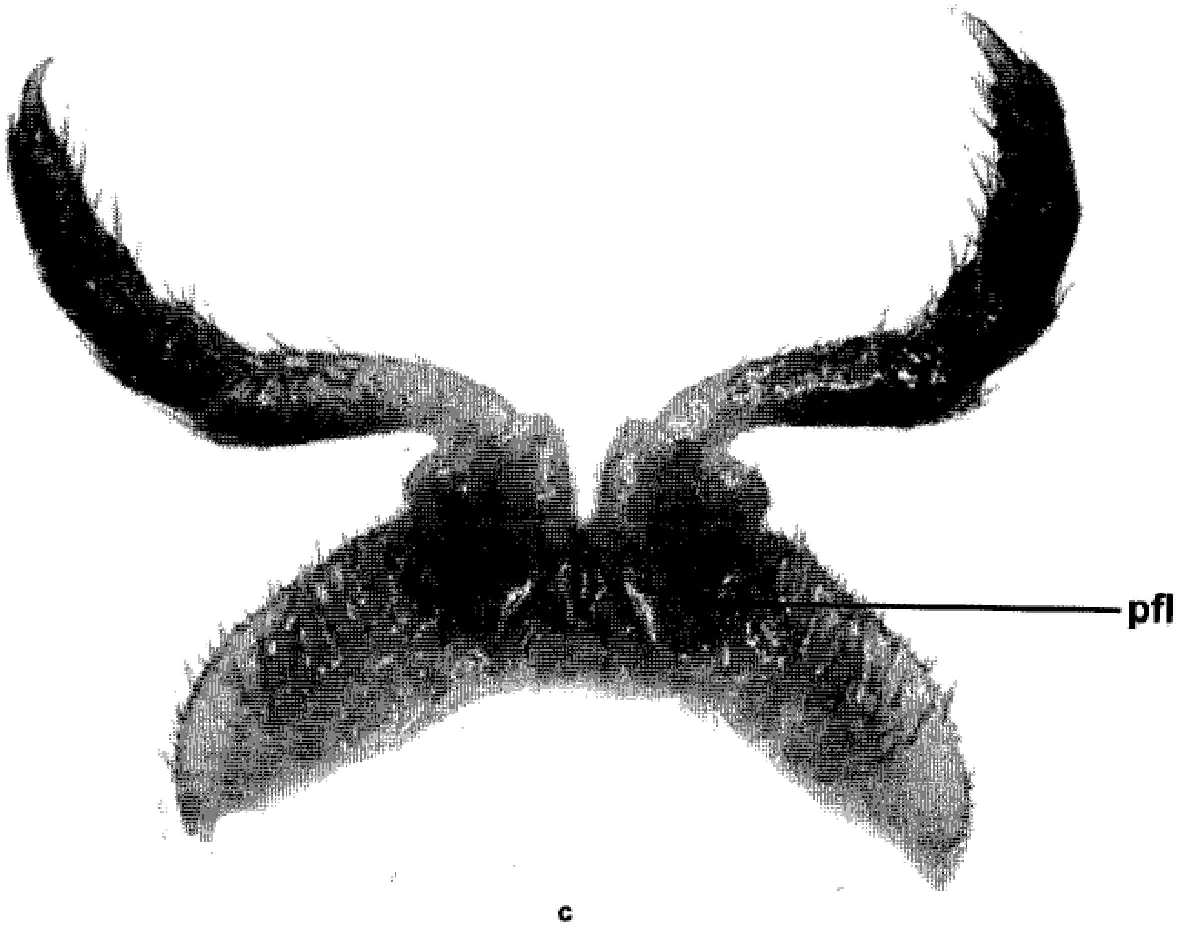

FIGURE 8c. *Archispirostreptus smithii* (BMNH 1897.11.10.89). **c,** oral view of prefemoral lobe of first pair of male legs.

Description: *Size*: Body length ♂ 145–170 mm, ♀ 220 mm; maximum body width 14–18 mm.

Number of body rings: 59–63.

Colour: Body black or brown.

Collum: Produced into anterior lobe, with 2 complete striae. Upper-most stria prominent.

Pre-femoral process of 1st pair of male legs: Triangular with long tapering extension (Fig. 8c).

Gonopod: (Figs 8a, 8b) Apex of sternum broadly rounded, apex not reaching level of paracoxite apex; paracoxite rounded apically and fused tightly to metaplica.

Metaplicae wide apart at level of telopodite spiral.

Proplica width constant; proplica apex overlapping lateral metaplical process proximally.

Lateral metaplical process broad and horizontal proximally, long and tapering distally. Distal half of lateral metaplical process deflected towards apical metaplical process. Apical metaplical process and proximal lateral metaplical process at right angle.

Distribution: Known from Ethiopia (Krabbe 1982) and Somalia.

Remarks: The apical metaplical process of the gonopod is similar to that of *A. lugubris*, *A. bottegi* and *A. dodsoni*, however, the orientation of the lateral metaplical process differs among these species. In *A. smithii* the lateral metaplical process gently bends distally towards the apical metaplical process. Although the position of the antetorsal spikes in relation to the apex is as in the gonopod of *A. tumuliporus*, the orientation of the terminal spike differs between the two species. In addition, the acute and tapering apical metaplical process of *A. tumuliporus* differs from the finger-like apical metaplical process of *A. smithii* and *A. bottegi* (see remarks on *A. lugubris*).

Archispirostreptus syriacus (Saussure 1859)

Fig. 9

Julus syriacus Saussure 1859, p. 329–330. [type locality : Palestine]
Archispirostreptus tumuliporus judaicus (Attems 1926b), p. 225. [type locality : Syria]
Archispirostreptus transmarinus Hoffman 1965, p. 18–23, figs 1–3. **Syn. n.**
Archispirostreptus transmarinus: Krabbe & Enghoff 1978; Krabbe 1982
Archispirostreptus syriacus: Shelley 2009

Type material of *A. transmarinus*: YEMEN: Sanaa, (ZMH 19, 1932).

Material examined: SAUDI ARABIA: 1 ♂, M. Adamson (MNHN 1B 111). JORDAN: 1 ♂, Ajlum, Djerash, 13.iii.1977, Kinzelbach & coll (MNHN 1B 033).

Diagnosis: Apical metaplical process concave proximally, with an angular projection laterally; medial edge of apical metaplical process convex distally (Figs 9a, 9b).

Description: *Size*: Body length 125–140 mm; maximum body width 8–10 mm.

Number of body rings: 59–68.

Colour: Body dark grey or black; legs and antennae brown.

Collum: Rounded ventrally, with 3–4 complete striae and 0–2 incomplete striae.

Pre-femoral process of 1st pair of male legs: Proximally rounded with distal nipple.

Gonopod: (Figs 9a, 9b) Sternum triangular, reaching level of paracoxite apex; paracoxite apex horizontal or broadly rounded and fused tightly to metaplica.

Width of proplicae constant along length; proplica apex covering lateral metaplical process proximally.

Width of metaplicae unchanged along length up to level of lateral metaplical process.

Lateral metaplical process long and tapering, proximal half wider.

Proximal apical metaplical process concave, with an angular projection laterally. Distal apical metaplical process convex medially.

Distribution: Known from Israel, Syria, Yemen, Jordan and Saudi Arabia.

Remarks: *Archispirostreptus syriacus* is the only species from the Middle East. The angular projection on the lateral edge of the apical metaplical process characterizes the gonopod of *A. syriacus*.

Besides having overlapping body size ranges, *A. syriacus* and *transmarinus* have similar gonopods, with a lateral angular projection on the apical metaplical process and a triangular sternite. Therefore, we propose synonymy of *A. transmarinus* with *A. syriacus*. Our conclusions are further supported by the relatively close proximity of the localities from where the material was recorded.

Archispirostreptus tumuliporus (Karsch 1881)

Fig. 10

Spirostreptus tumuliporus Karsch 1881, p. 51–52.
Graphidostreptus tumuliporus: Attems 1914
Archispirostreptus tumuliporus: Schubart 1951; Hoffman 1965; Krabbe & Enghoff 1978; Krabbe 1982; Mwabvu 2005

Type material: Holotype: SUDAN: 1 ♂, Scriba Ghattas, Djur (ZMB 645)

Additional material examined: CHAD: 2 ♂, Tikem Station IRCT [9° 45'N, 15° 00'E], xii.1958, Galichet (MNHN 1B 220). SENEGAL: 1 ♂, 1 ♀, Sine Saloum [13° 55'N, 15° 37'W], 4.ix.1970, M. Mühlenberg & R. Streng (MNHN 1B 223). MALAWI: 1 ♂, (MNHN 1B 251); BENIN: 1 ♂, Dassa Zoumé [7° 47'N, 2° 08'E], 23.xi.1970, Ch. Gasc (MNHN 1B 222). UGANDA: 2 ♂, 1903, Bourg de Bozas (MNHN 1B 224). MALI: 1 ♂, 1 ♀, Toukoto (150 km E. de la Falémé), [14° 35'N, 12° 03'E], vii.1903, Kermorgant (MNHN 1B 225). CAMEROON: 1 ♂, Batouri [4° 27'N, 14° 24'E], 14.i.1993, Jean Dejax, (MNHN 1B 289). ZIMBABWE: 1 ♂, Muzarabani [16° 23'S, 31° 00'E], 1.xii.1998, T. Mwabvu (NMSA 20480); 1 ♂, Mapembe Mountains, Marange [18° 57'S, 32° 27'E], 13.xii.2007, T. Mwabvu (NMSA 21941); 1 ♂, Chipfatsura School, Marange [18° 57'S, 32° 27'E], 20.xii.2005, T. Mwabvu (NMSA 21943).

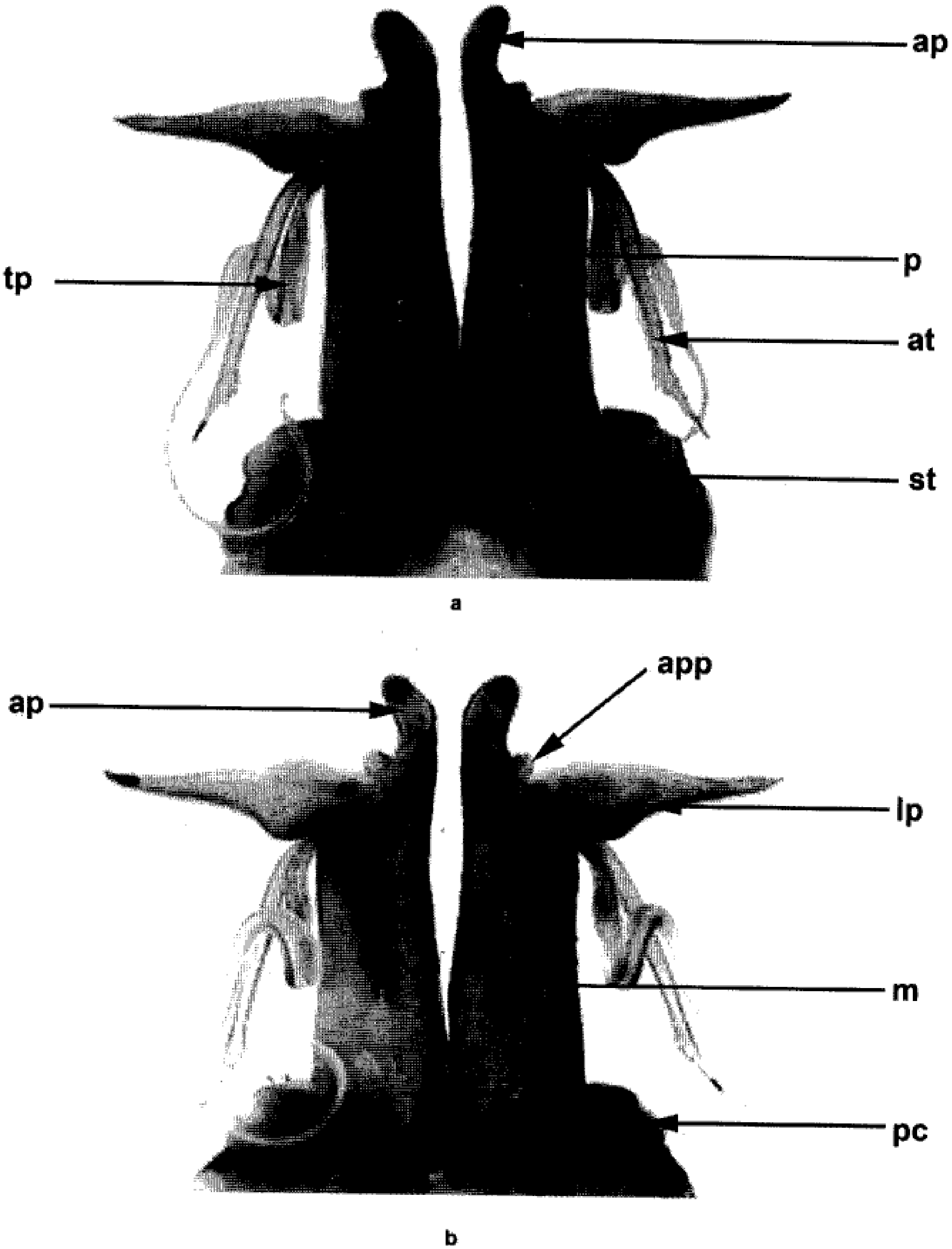

FIGURE 9a, b. *Archispirostreptus syriacus* (ZMH 19, 1932). **a,** oral view of gonopods; **b,** aboral view of gonopods.

FIGURE 9c. *Archispirostreptus syriacus* (ZMH 19, 1932). **c,** oral view of prefemoral lobe of first pair of male legs.

Diagnosis: Apical metaplical process wide and parallel proximally; distal half of apical metaplical process narrow, becoming acute (Figs 10a, 10b).

Description: *Size*: Body length 147–200 mm; maximum body width 12.5–16 mm.

Number of body rings: 59–67.

Colour: Body dark brown or black; legs and antennae brown.

Collum: Laterally square or with a small anterior lobe, with 3–4 complete striae and 2–6 incomplete striae (Fig. 10d).

Pre-femoral process of 1st pair of male legs: Basally round, medial nipple deflected laterally (Fig. 10c).

Gonopod: (Figs 10a, 10b) Sternum rounded apically; paracoxite narrowly rounded and fused tightly to metaplica.

Apical proplica rounded, overlapping lateral metaplical process proximally; medial lobe of apical proplica long and tapering.

Lateral metaplical process wide proximally, tapering distally; lateral metaplical process almost at right angle to apical metaplical process (Fig. 10a).

Apical metaplical process parallel proximally, distal halves wider apart and acute apically.

Distribution: Democratic Republic of Congo, Ghana, Sierra Leone (Krabbe 1982), Chad, Cameroon, Benin, Sudan, Mali, Uganda, Malawi and recently from northern and eastern Zimbabwe.

Remarks: There are significant variations in the form of the gonopods of material identified as *A. tumuliporus* from different parts of Africa. Some of the gonopods are morphologically distinct from the holotype in the shape of the apical and lateral metaplical processes. We have found in the collections some specimens of *A. lugubris* from Senegal which had been incorrectly identified as *A. tumuliporus* (see remarks on *A. lugubris*).

Gonopod variations in *A. tumuliporus* relate to the shape, size and orientation of the lateral and apical metaplical processes. The lateral metaplical processes of specimens from Cameroon are spined distally, specimens from Senegal have a slanting lateral metaplical process, which is at an obtuse angle with the apical metaplical process, and the paracoxites differ in shape and angle at which they are fused to the metaplicae compared with specimens from other localities. The gonopods of specimens from Chad have narrow finger-like apical metaplical processes; distally the apical metaplical processes are similar to those of *A. smithii*, *A. dodsoni* and *A. lugubris*. Based on this evidence, we concluded that *A. tumuliporus* is a species complex and that several specimens of *Archispirostreptus* may have been incorrectly identified or assigned to *A. tumuliporus* because of the broad specific limits that were used.

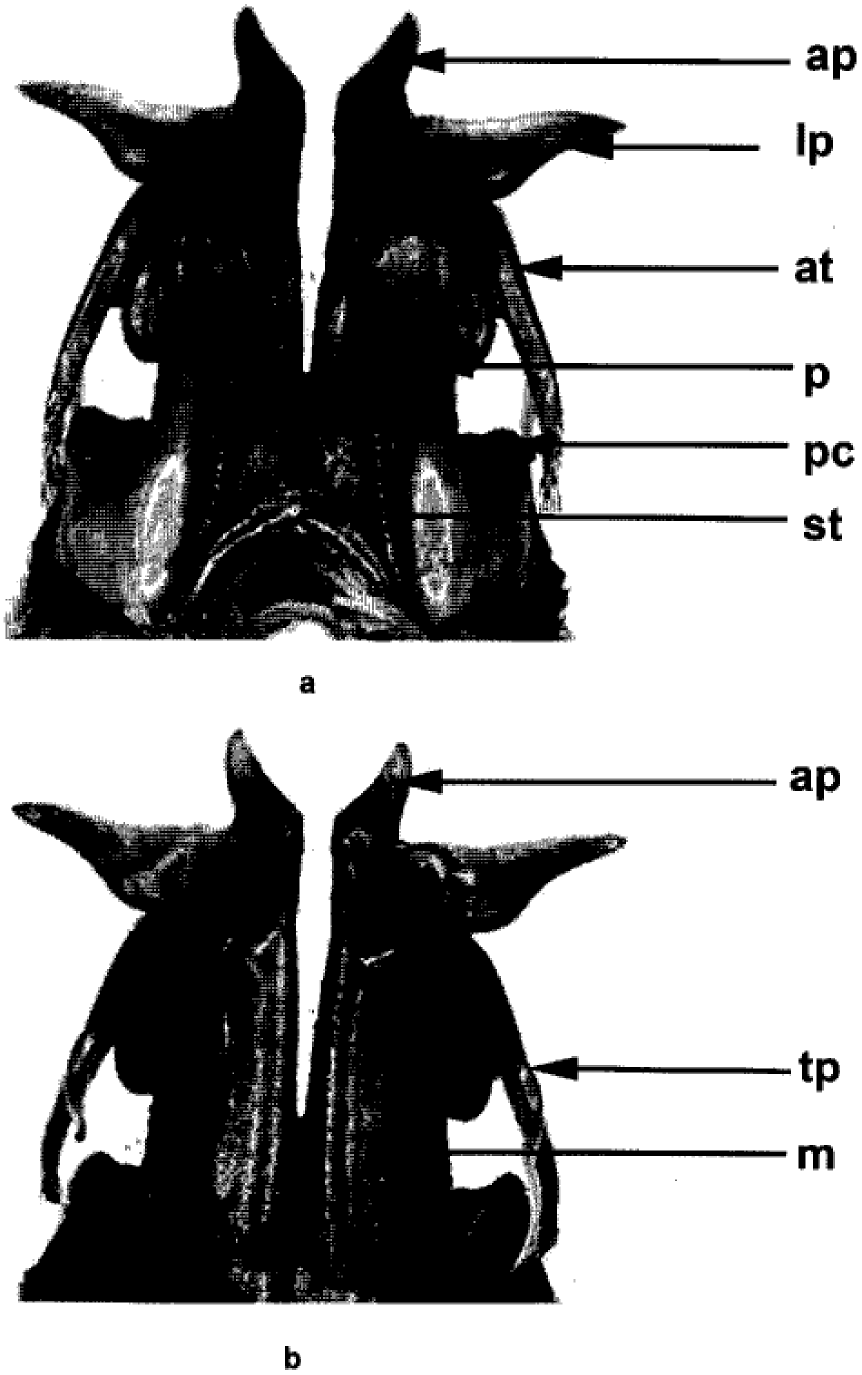

FIGURE 10a, b. *Archispirostreptus tumuliporus* (ZMB 645). **a,** oral view of gonopods; **b,** aboral view of gonopods.

One subspecies *A. t. sudanicus* (Brölemann 1905) (synonymized by Attems 1914, p. 159, fig. 164) from Senegal is recognized here as distinct, based on gonopod shape. The gonopod of the subspecies has a relatively narrow apical metaplical process, which is at an acute angle with a slanting lateral metaplical process. Another geographically distinct form from Chad, which has a very narrow and finger-like apical metaplical process, has been identified.

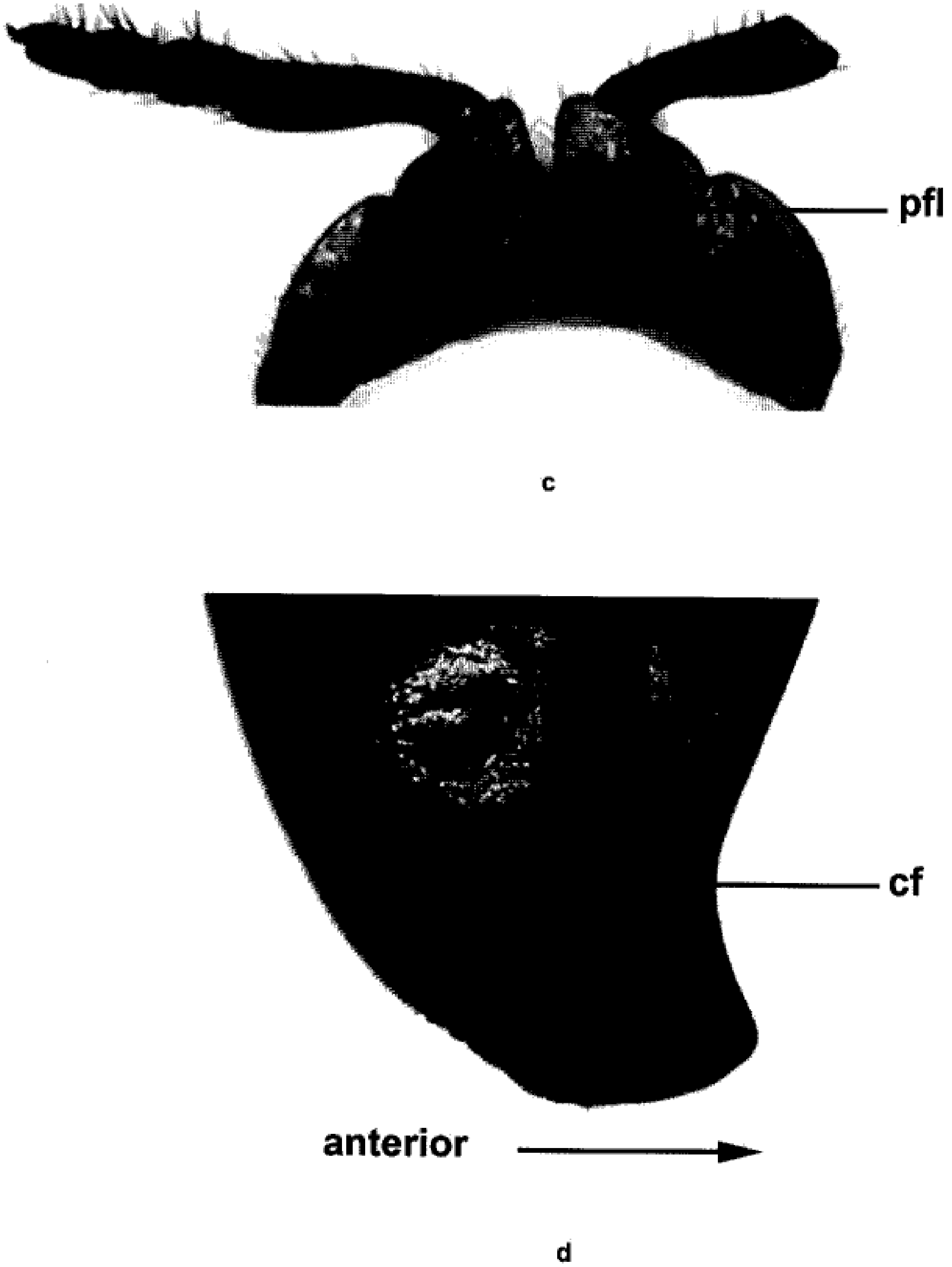

FIGURE 10c, d. *Archispirostreptus tumuliporus* (ZMB 645). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

Key to the species of *Archispirostreptus*, based on male gonopods

1. Apical metaplical process darker proximally than distally; apical metaplical process convex laterally, not finger-like 2
- Apical metaplical process not darker proximally than distally; apical metaplical process not convex laterally, finger-like 3
2. Lateral and medial edges of apical metaplical processes convex proximally (Fig. 5a); apical metaplical processes not deflected or overlapping medially .... *gigas*
- Lateral and medial edges of apical metaplical processes not convex proximally; apical metaplical processes deflected and overlapping medially (Fig. 3a, 3b) .... *divergens*
3. Apical metaplical processes deflected laterally (Figs 7a, 7b) .... *phillipsii*
- Apical metaplical processes not deflected laterally 4
4. Lateral edges of apical metaplical process concave, with an angular projection (Figs 9a, 9b) .... *syriacus*
- Lateral edges of apical metaplical process not concave, without an angular projection 5
5. Distal half of apical metaplical process acute, not rounded apically (Figs 10a, 10b) .... *tumuliporus*
- Distal half of apical metaplical process not acute, rounded apically 6
6. Distal half of lateral metaplical process deflected towards apical metaplical process (Figs 8a, 8b) .... *smithii*
- Distal half of lateral metaplical process not deflected towards apical metaplical process 7
7. Apex of sternum apex flat; metaplica narrow at level of paracoxite apex (Fig. 6a) .... *lugubris*
- Apex of sternum not flat; metaplica not narrow at level of paracoxite apex 8
8. Distal part of lateral metaplical process gently slanting towards paracoxite; proximal lateral metaplical process and proximal apical metaplical process at obtuse angle (Fig. 4a) .... *dodsoni*
- Distal part of lateral metaplical process not slanting towards paracoxite; proximal lateral metaplical process and proximal apical metaplical process at right angle 9
9. Apex of proplica and apical metaplical process not thumb-like; lateral metaplical process wider and horizontal proximally, abruptly tapering distally (Fig. 1) .... *beccarii*
- Apex of proplica and apical metaplical process thumb-like; lateral metaplical process not horizontal proximally or abruptly tapering distally (Fig. 2a) .... *bottegi*

Genus *Cacuminostreptus* gen. n. Mwabvu

Type species: *Cacuminostreptus mazowensis* **sp. n.**

Etymology: Name derived from the Latin word *cacumen* (a point, summit, top, spine) in reference to the spinous antetorsal and lateral metaplical processes of the gonopods.

Diagnosis: Proplicae spathulate (subapically/apically wide); lateral metaplical processes with abrupt narrowing along the length, distally spinous; proximad lobe present on lateral metaplical process; apical metaplical processes short; and antetorsal processes with a distal spine (Figs 11a, 11b, 12a, 12b, 13a, 13b, 14a, 14b).

Description: Large spirostreptid millipedes, body length 130–215 mm; maximum body width 9–15 mm. Body rings 54–67.

Body black; legs and antennae brown.

Prebasilar plate of gnathochilarium reduced, without median sclerite.

Collum black, sometimes with anterior lobe, with 2–6 complete striae and 1–7 incomplete striae.

Pre-femoral process of 1st pair of male legs proximally rounded with laterally deflected apical extension (Figs 11c, 12c, 13c, 14c).

Sternum triangular; paracoxite apex horizontal or broadly rounded.

Proplicae about 2/3 of gonopod length, spathulate and setose apically (Figs 11a, 12a, 13a, 14a); subapical central depression of proplica flanked by raised edges. Medial lobe present on proplica apex, concealed under oral fold of metaplica.

Aborally, medial edges of metaplicae raised.

Apical metaplical processes and lateral metaplical processes short.

Lateral metaplical process arrowhead-shaped with a spine distally (Figs 11a, 12a, 13a, 14a, 11b, 12b, 13b, 14b). Lateral metaplical process may be tilted towards apical metaplical process or crescent-shaped distally.

Telopodite spirals after telopodite knee. Origin of antetorsal processes at telopodite knee. Antetorsal processes crescent-shaped, with a spine at extremity (Figs 11a, 12a, 13a, 14a, 11b, 12b, 13b, 14b). Postfemur of telopodite with three branches at extremity.

Distribution: Known from Mozambique; eastern, south-eastern, western and northern Zimbabwe; Kruger National Park, South Africa.

Remarks: The genus includes *Archispirostreptus conatus* (Attems 1928) and three new species. *Cacuminostreptus* species are smaller than some species of *Archispirostreptus*. The gonopods of *Cacuminostreptus* species differ from *Archispirostreptus* species by having a shorter apical metaplical process, a lateral metaplical process with a constriction and arrowhead-shape, and an antetorsal process without spikes but terminating in a spine. In addition, the proplicae are wider subapically/apically. Unlike *Archispirostreptus* species which have been recorded from East, West and Central Africa, and the Middle East, *Cacuminostreptus* is known only from southern Africa. Based on Hoffman's (2008) definition of the Spirostreptini, *Cacuminostreptus* also belongs to the tribe. A key to the genera of Spirostreptini is given below.

Cacuminostreptus conatus (Attems 1928) comb. n.

Fig. 11

Triaenostreptus conatus Attems 1928, p. 368–369, figs 531–533.
Archispirostreptus conatus: Krabbe 1982; Hamer 1998, 1999; Mwabvu 2005
Spirostreptus conatus: Hoffman 2008

Type material: Syntype: PORTUGESE EAST AFRICA (MOZAMBIQUE): 1 ♂, Zandemela near Chai Chai [24° 16'S, 33° 56'E], (NHMW 2524) (also labelled SAM 6023).

Additional material examined: ZIMBABWE: 1 ♂, Mhlekwane School [2231A2], 17.xii.1996, F. Nyathi (NMZ/D844).

Diagnosis: Apical metaplical process with a narrow, longer and laterally deflected sausage-shaped oral fold of distal metaplica (Fig. 11a); aboral fold of apical metaplical process shorter and wider than oral fold; apex of apical metaplical process conical with raised base.

Description: *Size*: Body length 180 mm; maximum body width 15 mm.

Number of body rings: 54.

Colour: Black.

Collum: Laterally square, with 2–3 complete striae and 1–2 incomplete striae (Fig. 11d).

Pre-femoral process of 1st pair of male legs: Proximally broad and parallel, apical extension long and deflected laterally (Fig. 11c).

Gonopod: (Figs 11a, 11b) Apex of sternum almost reaching level of paracoxite apex; paracoxite apex flat, fused tightly to metaplica.

Proplicae wider and flat apically, and not overlapping lateral metaplical process. Small medial lobe on apical proplica extending distally, concealed under oral fold of metaplica.

Oral fold of apical metaplical process longer and sausage-shaped apically. Aboral fold of metaplica with a diagonal ridge; mesial depression extends distally.

Lateral metaplical process narrowly joined to metaplica, forming acute angle with apical metaplical process (Figs 11a, 11b). Lateral metaplical process triangular mid-length, sharply tapering distally.

Oral fold of apical metaplical process deflected laterally; aboral fold of apical metaplical process shorter and wider than oral fold (Fig. 11a).

Distribution: Known from Chimanimani and Mount Silinda, Zimbabwe; Mozambique, Kruger National Park, South Africa (Krabbe 1982) and Mhlekwane School in south-eastern Zimbabwe.

Remarks: The gonopod of *C. conatus* closely resembles the gonopods of the new species, *C. vumbaensis*, *C. triangulatus* and *C. mazowensis*, by having apically wide proplicae, an arrow-head shape of the distal lateral metaplical process and a crescent-shaped antetorsal process with a distal spine. However, *C. conatus* is distinguished from *vumbaensis* and *mazowensis* by a lateral metaplical process which is narrowly joined to

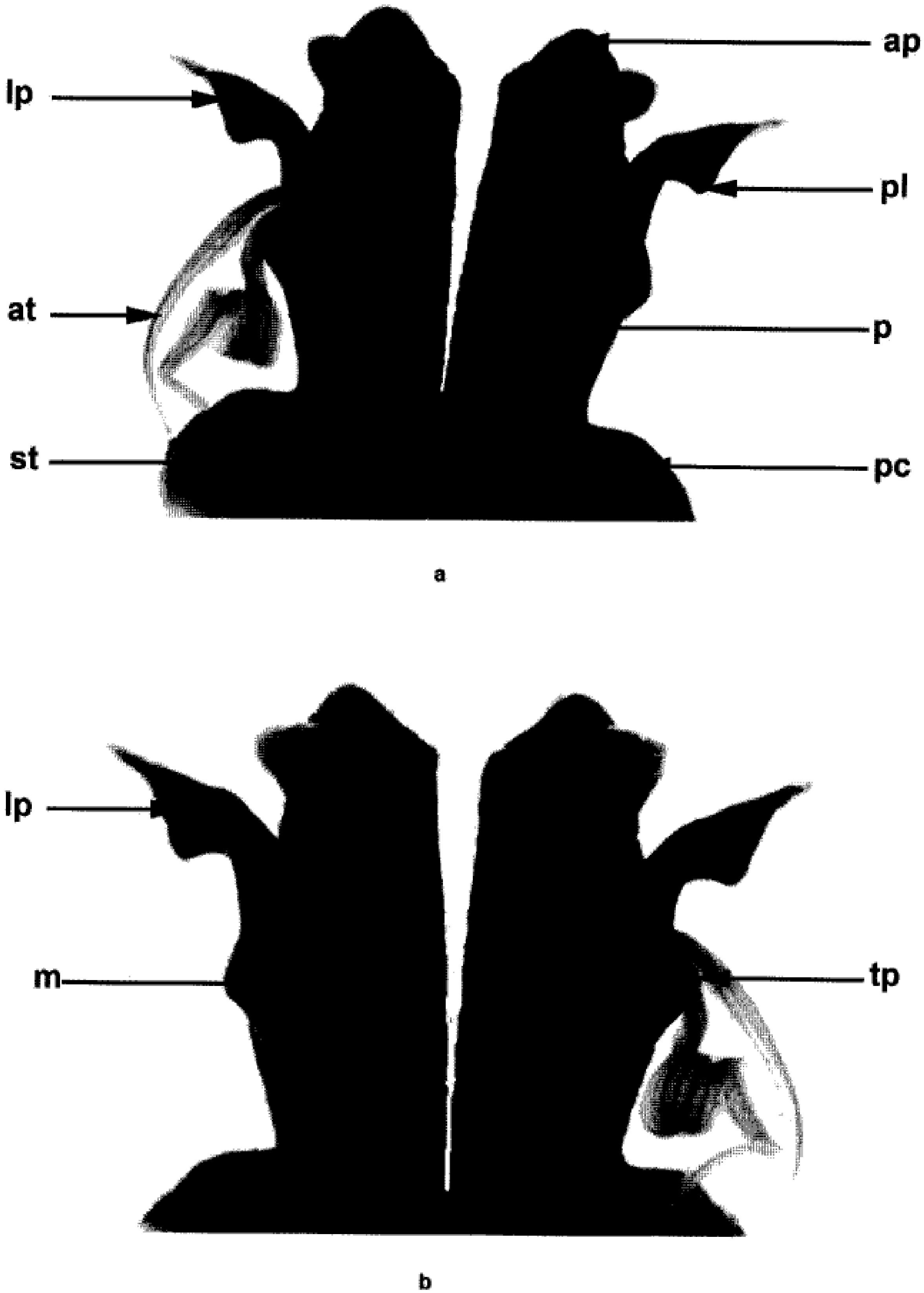

FIGURE 11a, b. *Cacuminostreptus conatus* (NMZ/D844). **a,** oral view of gonopods (without left telopodite); **b,** aboral view of gonopods.

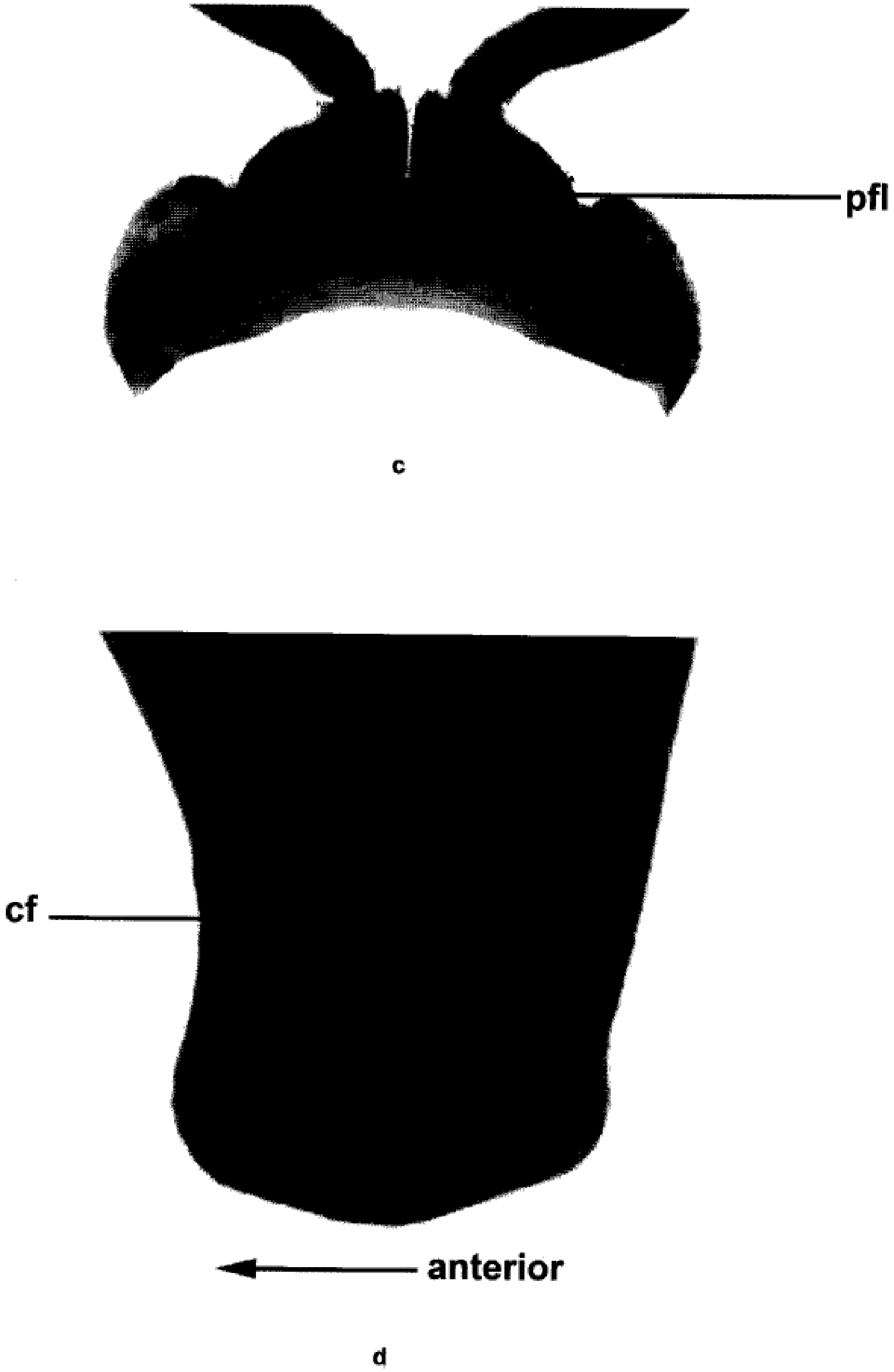

FIGURE 11c, d. *Cacuminostreptus conatus* (NMZ/D844). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

the metaplica and slanting towards the apical metaplical process, a long and laterally deflected oral fold of the apical metaplical process, and the presence of an aboral ridge and depression on the metaplicae. In *C. vumbaensis* and *C. mazowensis* the lateral metaplical process is not deflected towards the apical metaplical process. The triangular shape of the apical metaplical process of the gonopod of *C. triangulatus* is unique in this genus.

***Cacuminostreptus mazowensis* sp. n. Mwabvu**

Fig. 12

Type material: Holotype: ZIMBABWE: 1 ♂, Mazowe Dam [17° 30'S, 30° 58'E], 13.xii.08, T. Mwabvu (NMSA 21945)

Paratypes: ZIMBABWE: 4 ♂, 9 ♀ Mazowe Dam [17° 30'S, 30° 58'E], 13.xii.08, T. Mwabvu (NMSA 21992)

Additional material examined: ZIMBABWE: 1 ♂, Mazowe Dam [17° 30'S, 30° 58'E], T. Mwabvu (NMSA 21970); 1 ♂, Mazowe Dam [17° 30'S, 30° 58'E], 19.xi.1997, T. Mwabvu (NMSA 20529); 1 ♂, Highlands Suburb, Harare [17° 49'S, 31° 02'E], xii.2007, M. Cummings (NMSA 21944).

Etymology: Refers to the type locality, Mazowe Dam, Zimbabwe.

Diagnosis: Lateral margin of metaplicae strongly convex. Apical metaplical process concave apically, with lateral and medial apices produced into short acute horns (Figs 12a, 12b).

Description: *Size*: Body length ♂ 135–150, ♀ 140–160 mm; maximum body width 10–15 mm.

Number of body rings: 59–65.

Colour: Body black; legs and antennae dark brown.

Collum: Produced into a narrow anterior lobe, with 4–6 complete striae and 2–7 incomplete striae (Fig. 12d).

Pre-femoral process of 1st pair of male legs: Proximally wide, medial extension laterally deflected (Fig. 12c).

Gonopod: (Figs 12a, 12b) Apex of sternum not reaching level of paracoxite apex; paracoxite not fused tightly to metaplica, apex flat.

Opposite telocoxites parallel, medial edges in contact (Figs 12a, 12b).

Apical proplica wide and rounded (Fig. 12a), with a triangular medial lobe, and overlaps lateral metaplical process proximally.

Metaplicae convex laterally, distally with a tapering mesial hump.

Lateral metaplical process short; broad proximally with constriction; arrowhead-shaped, crescent-shaped and tapering distally.

Lateral metaplical process and apical metaplical process at right or obtuse angle.

Apex of apical metaplical processes concave, with short horns (Figs 12a, 12b).

Antetorsal processes extend past paracoxite apex.

Distribution: Known from Harare and Mazowe Dam (20 km north of Harare), Zimbabwe.

Remarks: Although the gonopod of *C. mazowensis* closely resembles that of *vumbaensis*, the metaplicae are less convex and the apex of the apical metaplical process is flat in *C. vumbaensis*. In *C. mazowensis* the apex of the apical metaplical process is concave.

***Cacuminostreptus triangulatus* sp. n. Mwabvu**

Fig. 13

Type material: Holotype: ZIMBABWE: 1 ♂, Sahwe River, Mavuradona [1631A3], 8.xi.1989, D. G. Broadley (NMZ/D568)

Etymology: Refers to the triangular shape of the apical metaplical process.

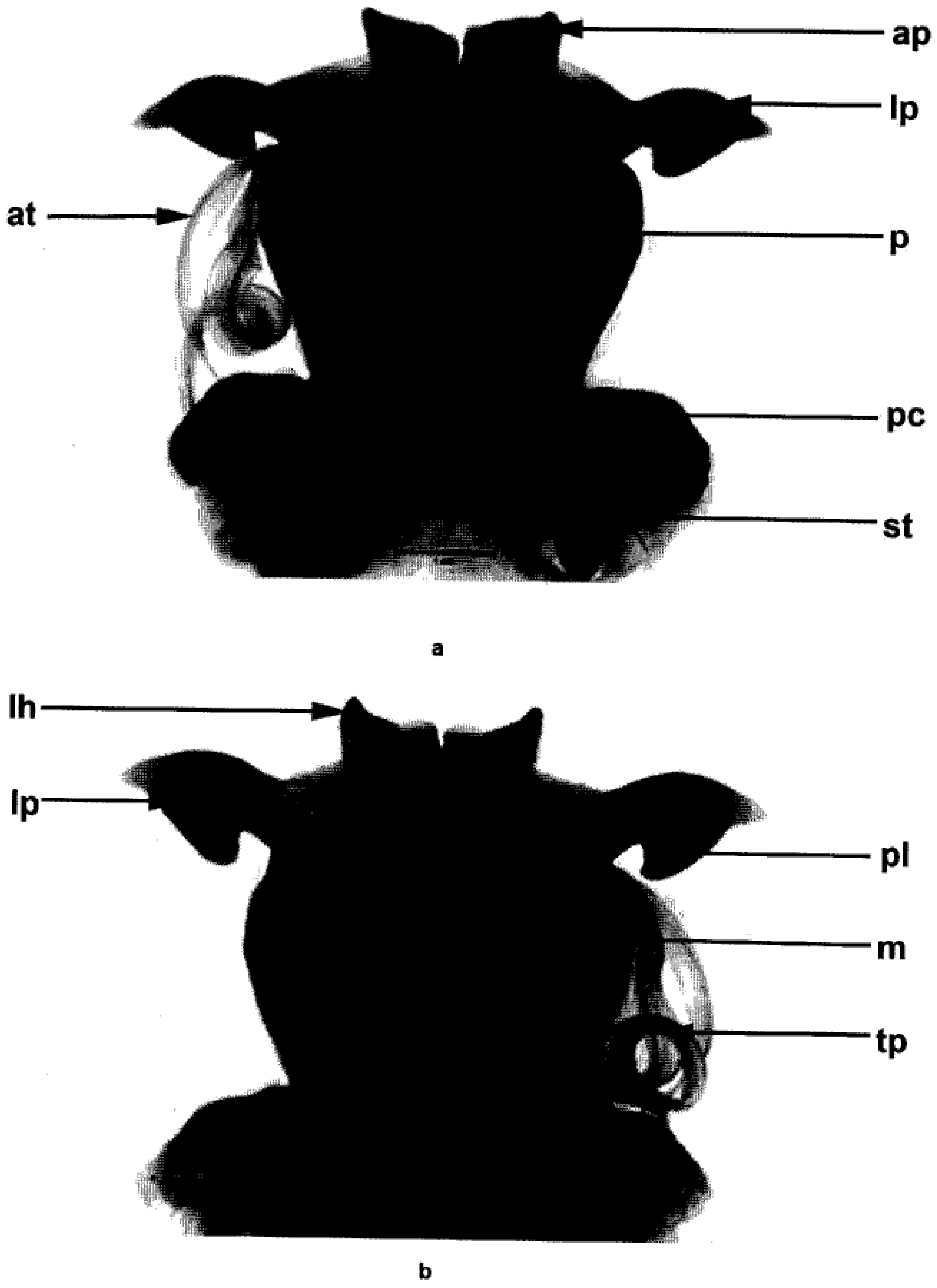

FIGURE 12a, b. *Cacuminostreptus mazowensis* (NMSA 21970). **a,** oral view of gonopods (without left telopodite); **b,** aboral view of gonopods.

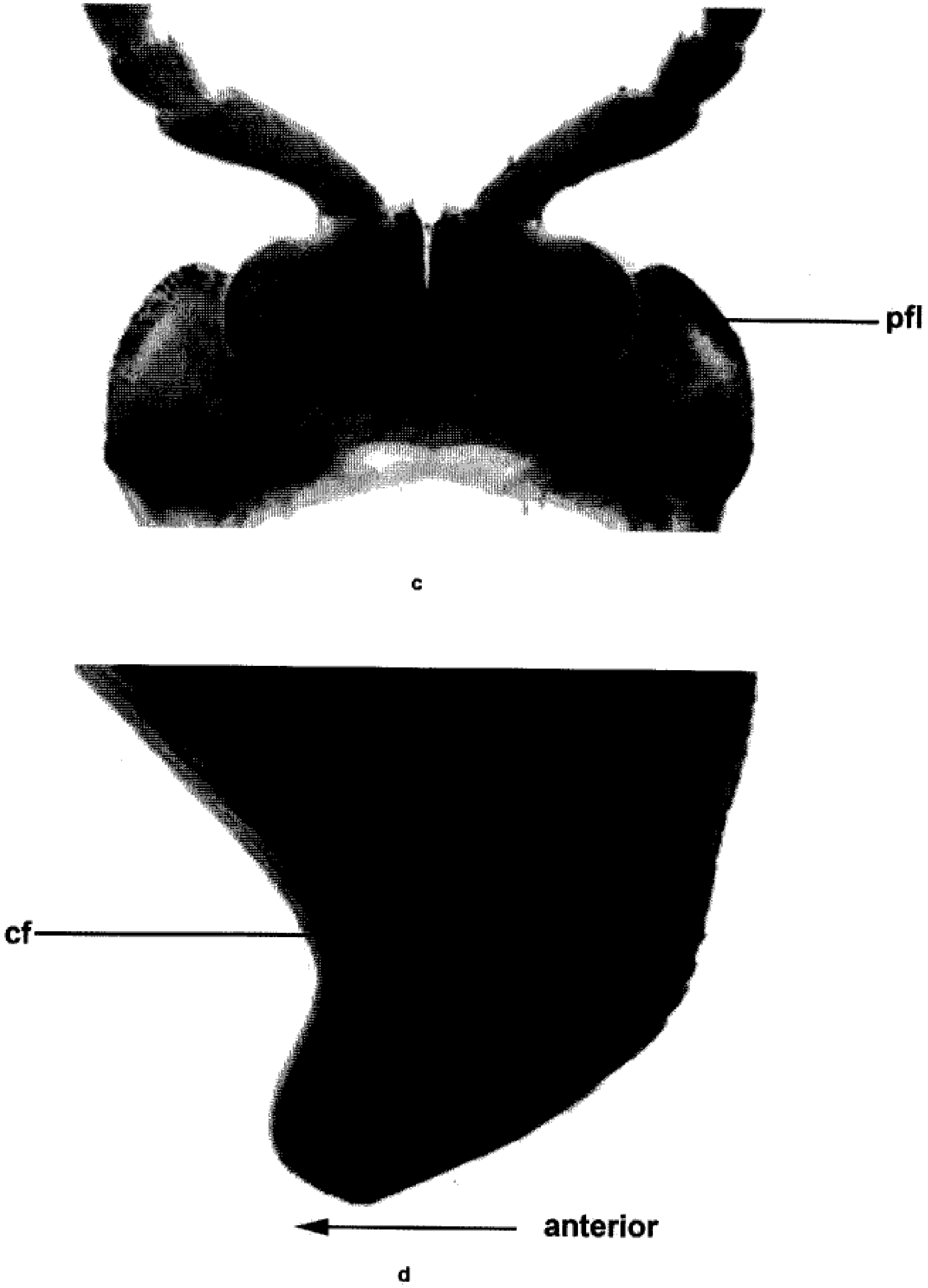

FIGURE 12c, d. *Cacuminostreptus mazowensis* (NMSA 21970). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

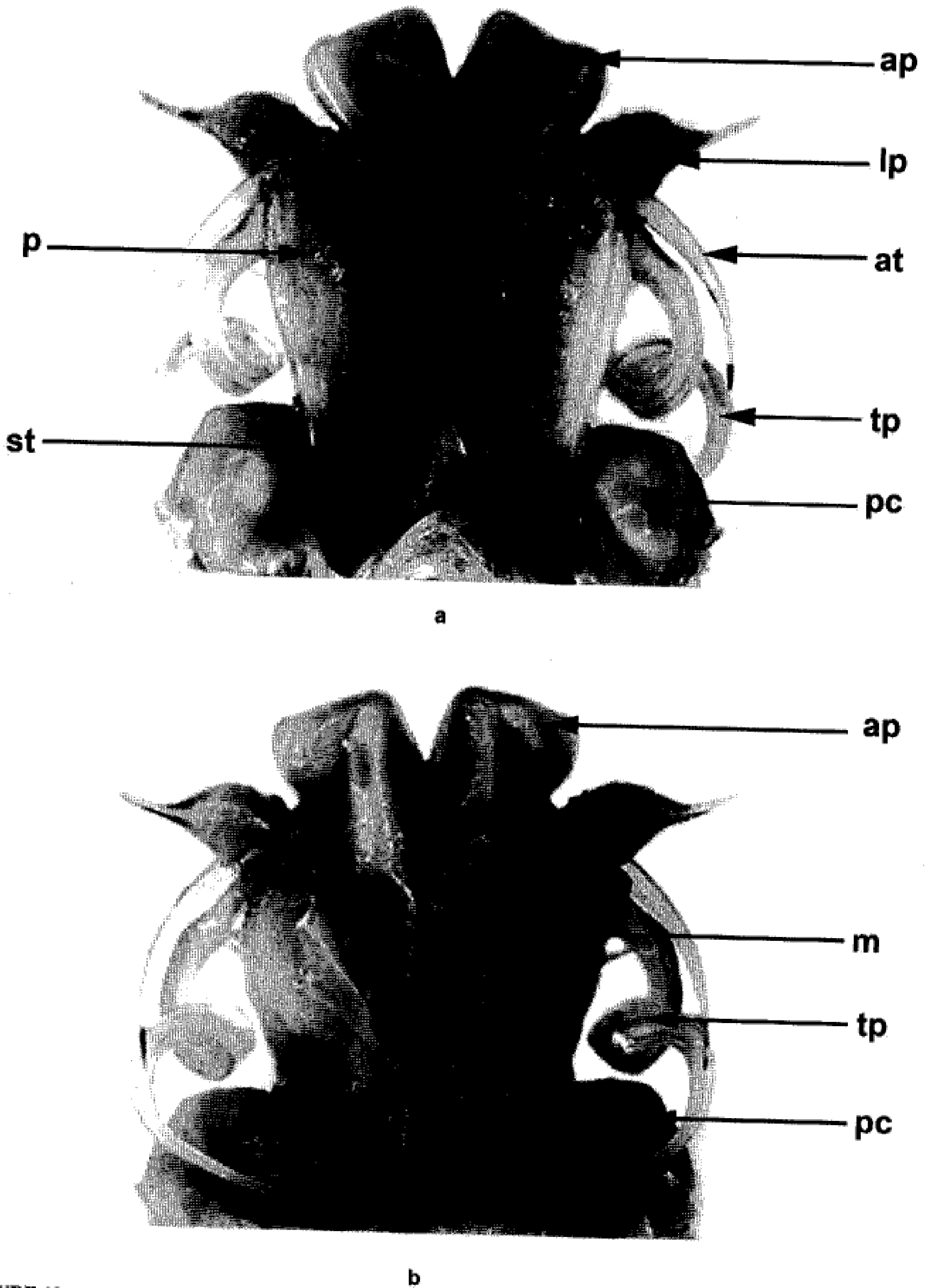

FIGURE 13a, b. *Cacuminostreptus triangulatus* (NMZ/D568). **a,** oral view of gonopods; **b,** aboral view of gonopods.

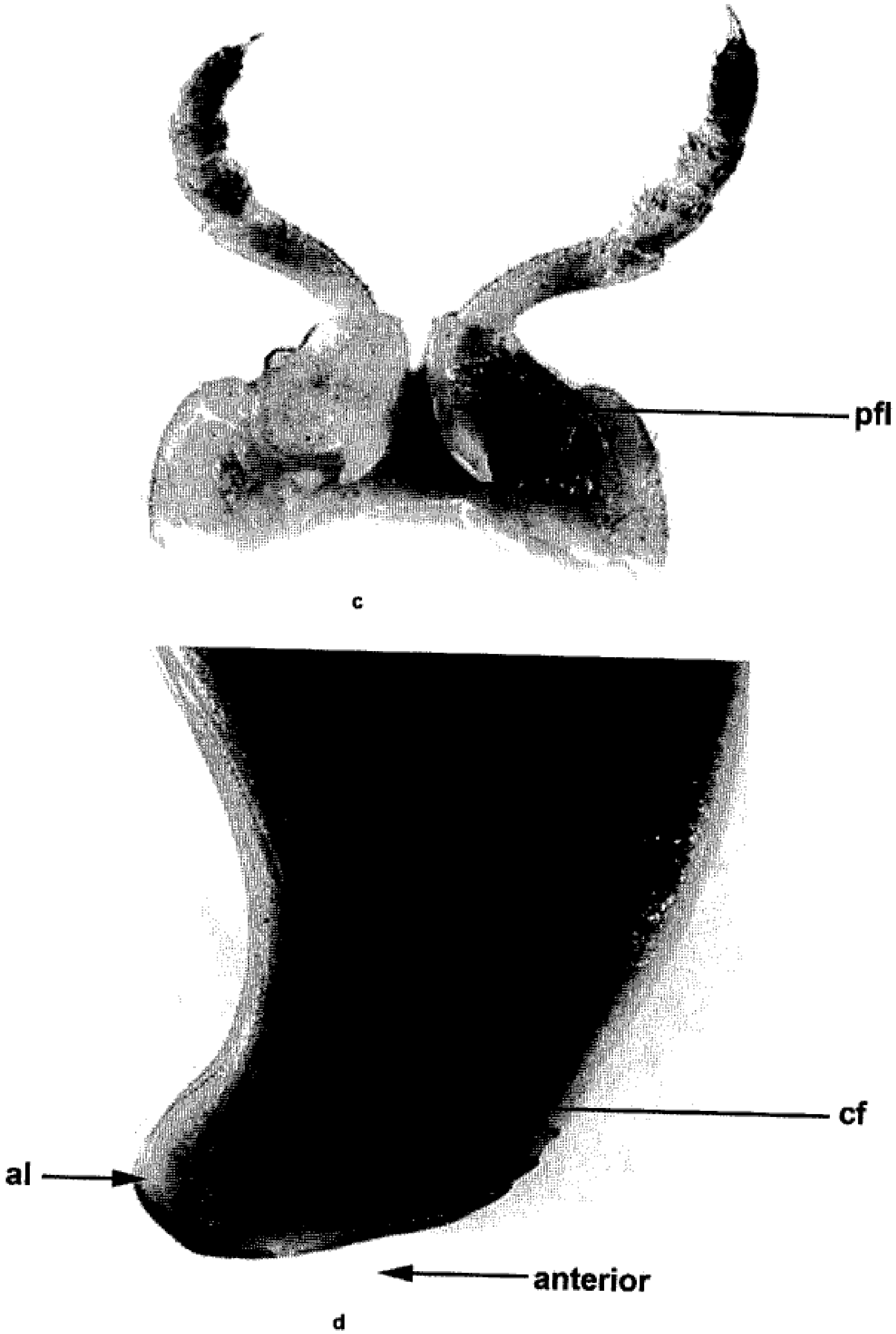

FIGURE 13c, d. *Cacuminostreptus triangulatus* (NMZ/D568). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

Diagnosis: Apical metaplical processes triangular, touching proximally and separate distally forming V-shape (Fig. 13a).

Description: *Size*: Body length 140 mm; maximum body width 11 mm.

Number of body rings: 61.

Colour: Body dark brown; legs and antennae light brown.

Collum: Anterior produced into narrow lobe, with 3 complete striae (Fig. 13d).

Pre-femoral process of 1st pair of male legs: Proximally oval with long laterally deflected mesial extension (Fig. 13c).

Gonopod: (Figs 13a, 13b) Apex of sternum reaching level of paracoxite apex; paracoxite fused tightly to metaplica, apex flat.

Telocoxites touching and parallel up to level of apical metaplical process (Figs 13a, 13b).

Proplicae broadly rounded apically; central groove of proplica flanked by gently raised edges. Medial lobe of distal proplica short and rounded apically.

Opposite metaplicae separate at level of lateral metaplical process. Medial ridge of metaplicae extend from lateral metaplical process to apex of apical metaplical process.

Lateral metaplical process deflected anteriad, and extending beyond lateral margins of paracoxite; lateral metaplical process narrow proximally, widens and tapering distally. Proximad lobe produced from wider part of lateral metaplical process, lobe extending towards telopodite (Fig. 13a).

Lateral metaplical process and apical metaplical process at acute angle (Fig. 13a).

Apical metaplical process triangular, slightly deflected laterally and wider apart distally; apical metaplical process shaped like an inverted triangle (Fig. 13a). Medial edges of opposite apical metaplical processes form a V-shape distally.

Distribution: Known from a single locality at the Sahwe River in Mavuradonha Wilderness Area, in western Zimbabwe

Remarks: The triangular shape of the apical metaplical process of the gonopod distinguishes *C. triangulatus* from congeners. However, the shapes of the lateral metaplical process and antetorsal process do not show significant difference from those of *C. conatus*, *C. mazowensis* and *C. vumbaensis*. The medial edges of the opposite coxites of the gonopod of *C. triangulatus* seem to be fused up to the level of the lateral metaplical process as in the gonopods of *C. mazowensis*.

***Cacuminostreptus vumbaensis* sp. n. Mwabvu**

Fig. 14

Type material: Holotype: ZIMBABWE: 1 ♂, Chimanimani [19°47'S, 32°52'E], 1957, (NMZ/D602)

Additional material examined: SOUTH AFRICA: 1 ♂, Kruger National Park [22°08'S, 31°03'E], (NMSA 9273). ZIMBABWE: 1 ♂, Chimanimani [19°47'S, 32°52'E], 1957, (NMSA 7223); 1 ♂, Chimanimani [19°47'S, 32°52'E], 1963, (NMSA 8949); 1 ♂, Nyanga [18°12'S, 32°43'E],1998, T. Mwabvu (NMSA 21937); 1 ♂, Chirinda Forest [20°40'S, 32°60'E], 1998, T. Mwabvu (NMSA 20507); 1 ♂, Eastern Highlands Tea Estates [18°12'S, 32°43'E], 2008, T. Mwabvu (NMSA 21937); 1 ♂, Mount Silinda [20°40'S, 32°60'E], 1955, (NMSA 6250). 1 ♂, Pungwe River, Honde Valley [18°14'S, 32°40'E], x.1998, T. Mwabvu (NMSA 20492); 1 ♂, Gweru [19°27'S, 29°49'E], 6.xii.2003, T. Mwabvu (NMSA 20494).

Etymology: The specific name refers to the Vumba Mountains (75 km north of Chimanimani) which are part of the eastern highlands of Zimbabwe, where *vumbaensis* is common.

Diagnosis: Apex of apical metaplical process flat; apical metaplical process convex laterally (Fig. 14a).

Description: *Size*: Body length 130–215 mm; maximum body width 7–15 mm.

Number of body rings: 58–67.

Colour: Body black; legs and antennae reddish brown or dark brown.

Collum: Broad with rounded anterior lobe, with 3–5 complete striae and an incomplete stria (Fig. 14d).

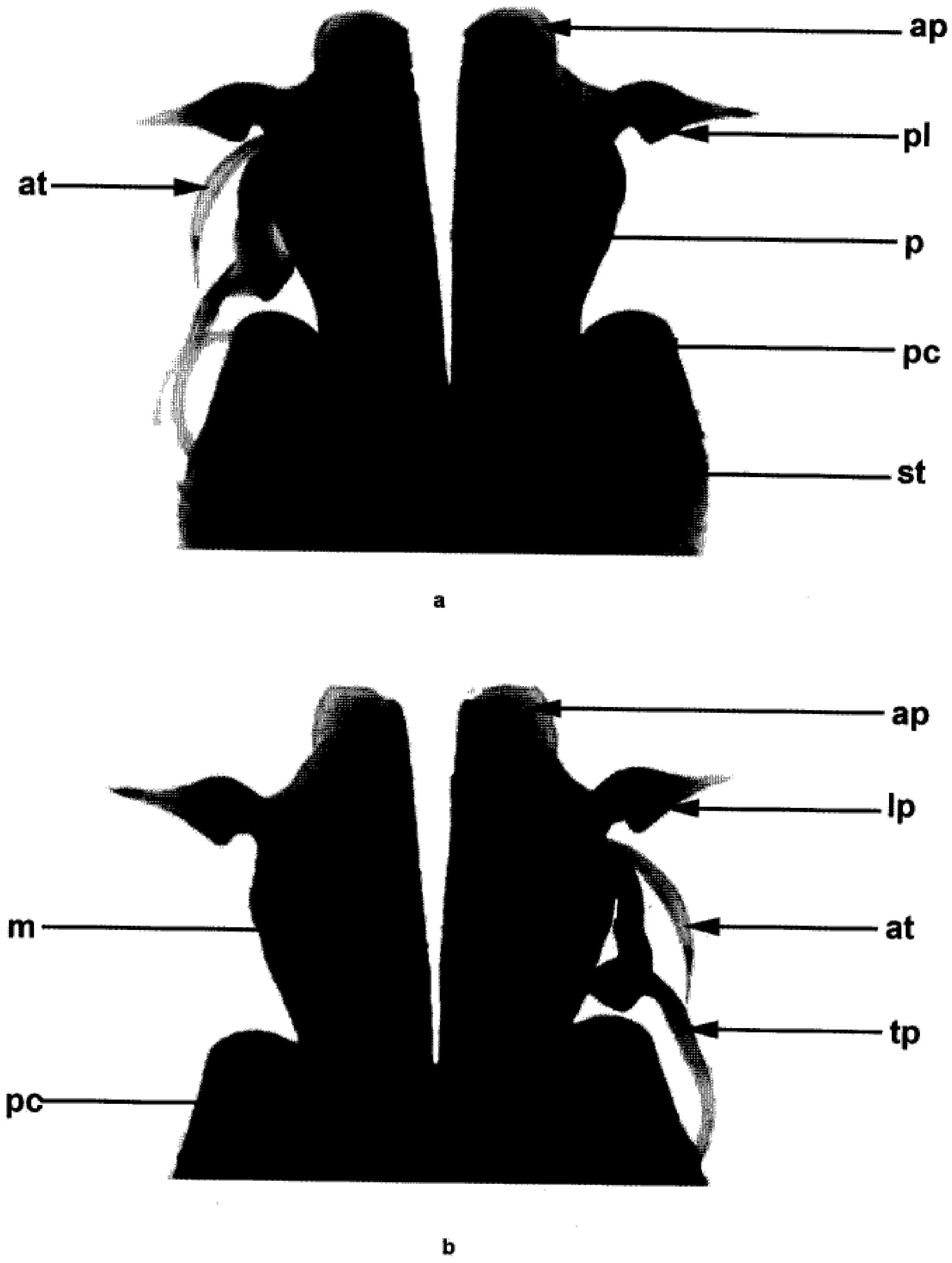

FIGURE 14a, b. *Cacuminostreptus vumbaensis* (NMZ/D602). **a,** oral view of gonopods (without left telopodite); **b,** aboral view of gonopods.

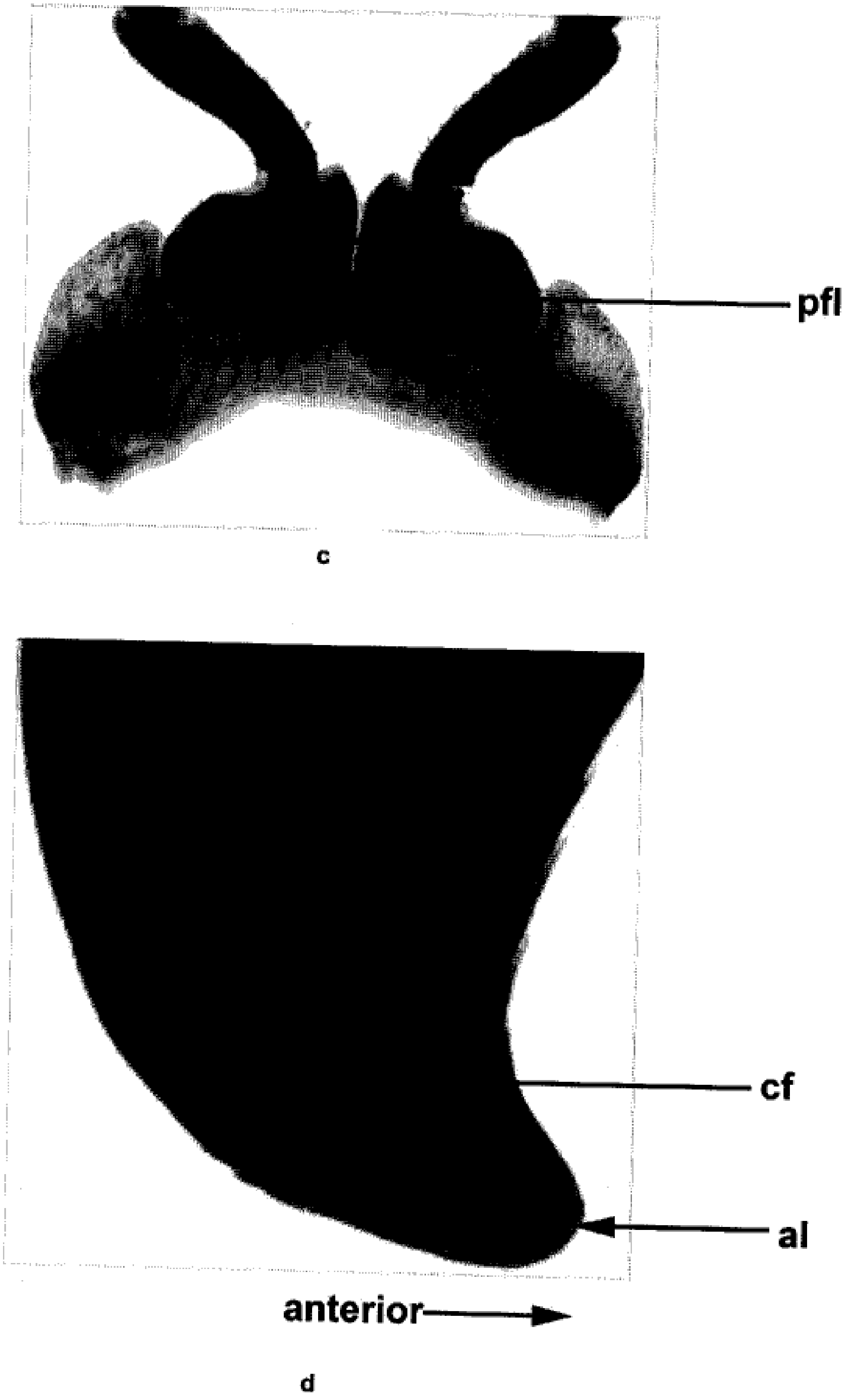

FIGURE 14c, d. *Cacuminostreptus vumbaensis* (NMZ/D602). **c,** oral view of prefemoral lobe of first pair of male legs; **d,** lateral view of collum.

Pre-femoral process of 1^{st} *pair of male legs*: Proximally wide and parallel, mesial apical extension nipple-shaped and deflected laterally (Fig. 14c).

Gonopod: (Figs 14a, 14b) Apex of sternum not extending to level of paracoxite apex; paracoxite rounded apically (Figs 14a, 14b).

Apex of proplica wide; medial lobe of apical proplica long and extends distally. Subapical groove present on proplicae.

Metaplicae narrow proximally.

Lateral metaplical process narrow proximally leading to crescent-shaped arrowhead apex; distally tapering.

Proximal lobe of arrowhead short, extending towards telopodite (Figs 14a, 14b).

Oral fold of apical metaplical process overlaps proximal part of lateral metaplical process.

Distribution: Known from the eastern highlands of Zimbabwe; Kruger National Park, South Africa and western Mozambique.

Remarks: There are variations in the size of the gonopods and the orientation of the lateral metaplical process within and between populations. The gonopod of *C. vumbaensis* resembles closely that of *C. mazowensis*. The two species differ in the convexity of the lateral edges of the metaplicae, the shape of the apex of the apical metaplical process and the shape of the lateral metaplical process. The longer lateral metaplical process of *C. vumbaensis* closely resembles that of *C. conatus* and *C. triangulatus* than *C. mazowensis*.

C. vumbaensis has been recorded from a wide range of vegetation types and altitudes. In Zimbabwe the species is found in miombo woodland and montane vegetation at altitude greater than 1 000 m above sea level. Further south *C. vumbaensis* occurs in dry savanna at altitude below 500 m above sea level, in southern Zimbabwe and Kruger National Park, South Africa.

Key to the species of *Cacuminostreptus* based on male gonopods

1\. Apical metaplical process triangular (Fig. 13a).. *triangulatus* **sp. n.**
\- Apical metaplical process not triangular 2
2\. Oral fold of apical metaplical process longer and narrower than aboral fold; distally oral fold deflected laterally (Fig. 11a).. *conatus*
\- Oral fold of apical metaplical process not longer than aboral fold; distally oral fold not deflected laterally 3
3\. Lateral margins of metaplicae strongly convex; apex of apical metaplical process concave and straight laterally, with small lateral and medial horns apically (Figs 12a, 12b) .... *mazowensis* **sp. n.**
\- Lateral margins of metaplicae not strongly convex; apex of apical metaplical process flat and convex laterally, without lateral and medial horns apically (Figs 14a, 14b)... *vumbaensis* **sp. n.**

Species incertae sedis

S. arabs Pocock 1895, p. 298–299.

This species was described from Hadramaut, Yemen. Although Krabbe (1982) listed this species under *Archispirostreptus* she doubted this placement. We concur that *arabs* should be assigned to a different genus, however, without the type material or new material any placement would be tentative. The type material is missing from the BMNH collection; this was confirmed by the curator, Janet Beccaloni. According to Hoffman (2008) the Spirostreptini are characterised by a bifid or trifid prostatic groove with each branch ending in a small process. Although the distal trifurcate ending of the telopodite in *arabs* is consistent with the Spirostreptini it is unclear from the drawing whether the prostatic groove also has three distal branches. The antetorsal process of the gonopods of *arabs* is very short and does not extend beyond the knee bend of the telopodite. The antetorsal process of *arabs* also lacks the distal spikes which characterise *Archispirostreptus*. In addition, the proximal half of the free telopodite is broad with a side spine and the prefemoral process of the first pair of male legs is rectangular without distal tapering as in *Archispirostreptus* species.

Nomen dubium

A. sumptuosus Silvestri 1896b, p. 60–61, fig. 3.

The species description was based on a female specimen from Somalia. The location of the type material is unknown.

Taxonomy and species relationships

As currently defined, *Archispirostreptus* is heterogeneous and can be divided into two groups: the east African species and the southern African species. There are two distinct forms of gonopods in the species currently assigned to *Archispirostreptus*. The shapes of the proplicae, metaplicae, lateral and apical metaplical processes, the orientation of the apical metaplical processes, and the presence/absence of a spine or spikes on the antetorsal process characterise the gonopods of each group.

The gonopods of the mainly east African species (*tumuliporus*, *divergens*, *smithii*, *bottegi*, *becarrii*, *phillipsii*, *dodsoni*, *lugubris* and *gigas*) have a long and finger-like apical metaplical process, a tapering lateral metaplical process without abrupt narrowing and distal spikes on the antetorsal process; the proplica is tongue-shaped. We have erected a new genus, *Cacuminostreptus*, to accommodate the southern African species—*C. conatus* and three new species, *mazowensis*, *vumbaensis* and *triangulatus*. Although the two genera are closely related, the gonopods of *Cacuminostreptus* species differ from *Archispirostreptus* by having spathulate proplicae, shorter apical metaplical processes, lateral metaplical processes with abrupt narrowing and antetorsal processes which have a spine at the extremity.

Distribution

Archispirostreptus and *Cacuminostreptus* occur mainly in the eastern half of Africa (Fig. 15). Although both genera have been recorded in the savanna woodland, forests and at high altitude, they are allopatric.
Most *Archispirostreptus* species were recorded from Kenya, Somalia, Ethiopia and Eritrea. However, *A. tumuliporus* and *A. gigas* spread to the south into Malawi and Zimbabwe, and Mozambique, respectively. Unlike *A. divergens*, *A. dodsoni*, *A. phillipsii*, *A. bottegi* and *A. beccarii*, which have restricted ranges and are known from single localities, *A. tumuliporus* and *A. gigas* are widely distributed (Fig. 15). *C. vumbaensis* occurs in the montane forests of the eastern highlands of Zimbabwe, as well as in the miombo woodland in central Zimbabwe and the dry savanna in Kruger National Park, South Africa. All the *Cacuminostreptus* species are restricted to the eastern half of southern Africa. *Cacuminostreptus conatus* and *C. vumbaensis* are the most widely distributed (Fig. 15).

Key to the genera of Spirostreptini

1. Apical metaplical process long and finger-like; antetorsal process of telopodite with laciniate edges distally .... *Archispirostreptus* Silvestri 1895
\- Apical metaplical process short and not finger-like; antetorsal process of telopodite without laciniate edges distally 2
2. Metaplicae rounded and flattened distally, without lateral metaplical process .... *Choristostreptus* Hoffman 2008
\- Metaplicae not rounded or flattened distally, with lateral metaplical process 3
3. Metaplicae with large convex lateral lobe at level of proplica apex and with short distal lateral lobe .... *Namibostreptus* Mwabvu 2009
\- Metaplicae without large convex lateral lobe at level of proplica apex or short distal lateral lobe 4
4. Metaplicae with apical cavity on mesial side .... *Limnostreptus* Hoffman 2008
\- Metaplicae without apical cavity on mesial side 5

5. Distal metaplica with median hump; apical metaplical process lying on proplica apex and medially convex; telopodite with tongue-like lobe distal to origin of antetorsal process .... *Plagiotaphrus* Attems 1914
- Distal metaplica without median hump; apical metaplical process not lying on proplica apex or medially convex; telopodite without tongue-like lobe distal to origin of antetorsal process 6
6. Metaplicae golf-club shaped; apical metaplical process produced laterally into rounded lobe; lateral metaplical process not arrowhead-shaped, and without proximad lobe or abrupt narrowing .... *Spirostreptus* Brandt 1833
- Metaplicae not golf-club shaped; apical metaplical process not produced laterally into rounded lobe; lateral metaplical process arrowhead-shaped, with proximad lobe and abrupt narrowing .... *Cacuminostreptus* **gen. n.**

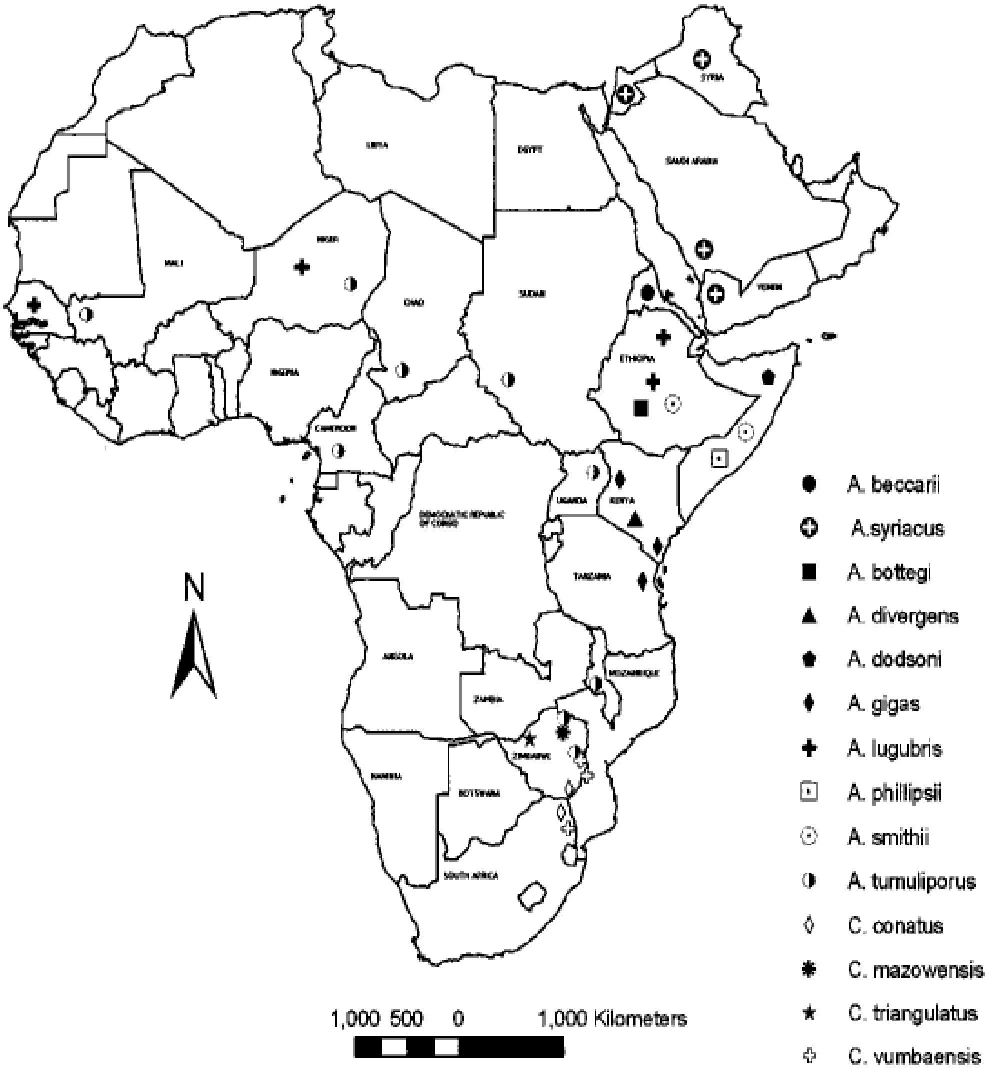

FIGURE 15. Distribution of *Archispirostreptus* and *Cacuminostreptus* species.

Discussion

The descriptions of a new genus and three new species support Hamer's (1997; 2000) observations that millipede genera in Africa require revision because several genera are poorly defined, and because some taxa have not been described. These observations are corroborated by new genera and new species of spirostreptids that have been discovered following surveys, or after studying material in various collections (see Hamer

2000; Vandenspiegel 2001; Vandenspiegel 2004; Mwabvu & Vandenspiegel 2005; Mwabvu *et al.* 2007; Mwabvu & Vandenspiegel 2009; Hoffman 2008; Mwabvu *et al.* 2009a; Mwabvu *et al.* 2009b).

Non-gonopod characteristics are unreliable indicators of taxon validity in the Spirostreptini because they overlap among taxa and do not differentiate species in neither *Archispirostreptus,* nor the new genus, *Cacuminostreptus.* However, the shapes of the apical metaplical processes, lateral metaplical processes and apical proplicae, and the form of the distal antetorsal processes of the gonopods differentiate the genera and the species.

The present records of *Archispirostreptus* species suggest a wide distribution in Africa, particularly in the savanna biome. However, some species have been collected in the forests of the east African mountain system only. The present distribution of *Archispirostreptus* suggests that it was widely distributed in the past before parts of Africa became drier in the late Pliocene or early Pleistocene. This is supported by the isolated occurrence of *A. lugubris villiersi* (whose body size and gonopod are smaller than in conspecifics) in the Air Mountains, Niger (Schubart 1951); the presence of the genus in localities immediately south of the Sahara desert, in western Sudan, Mali, Chad and Senegal; and the occurrence of *A. syriacus* in Syria, Yemen, Israel, Jordan and Saudi Arabia. Until more localities in central Africa and the western half of Africa have been surveyed we can not establish whether the known distributions of the species are real or a collecting artifact. However, the absence of *A.divergens, A. dodsoni, A. phillipsii, A. bottegi* and *A. beccarii* from areas south of their type localities (Fig. 15) is unlikely to be a collecting artifact because several areas in the highlands of East Africa have been surveyed without yielding any of these species.

The absence of *Archispirostreptus* species in South Africa despite the occurrence of *A. tumuliporus* in Zimbabwe is probably explained by the different vegetation types and climatic conditions south of the Limpopo River. Although the tree species which dominate miombo woodland (*Brachystegia spiciformis* and *Julbernardia globoflora*) have a wide distribution they do not extend into South Africa probably because of their apparent intolerance to frost conditions which are common south of the Limpopo River (Werger & Coetzee 1978). We infer that the lack of suitable food litter and suitable habitats, and the unfavourable climatic conditions account for the absence of *Archispirostreptus* species in South Africa.

Cacuminostreptus is endemic to southern Africa, south of the Zambezi River (Fig. 15). The area between the Zambezi and Limpopo Rivers seems to be the centre of endemism of the genus. Assuming that the radiation of the genus is relatively recent, *Cacuminostreptus* may not have had adequate time to disperse widely into diverse biomes. Although the genus mainly occurs in the miombo woodland, *C. vumbaensis* has also been recorded in montane forests in eastern Zimbabwe. That *Archispirostreptus* and *Cacuminostreptus* are allopatric, with the former occurring north of the latter (Fig. 15), suggests differences in vegetation preferences or tolerance to climatic conditions. Because *C. vumbaensis* and *C. conatus* occur in the dry savanna on either side of the Limpopo River we infer that the two species have greater tolerance to diverse environmental conditions and may have catholic habitat preferences. That *C. vumbaensis* also occurs in montane forest in the Chimanimani mountain system further supports our hypothesis that the genus is tolerant of a wide range of conditions.

The occurrence of *C. conatus* and *vumbaensis* in south-eastern Zimbabwe and Kruger National Park, South Africa, mirrors the distributions of *Bicoxidens brincki* Schubart 1966 (the largest *Bicoxidens* species) (see Mwabvu *et al.* 2007) as well as the large-bodied *Spirostreptus unciger* Attems 1928, *S. heros* Porat 1872 and *S. kruegeri* (Attems 1928) (see Mwabvu *et al.* 2009b). Despite the relatively small body size of *C. vumbaensis* and *C. conatus*, their distributions suggest that the dry savanna is not necessarily a barrier to smaller species. This is contrary to Enghoff's (1992) observations that specimens of *A. tumuliporus judaicus* from arid localities were larger than specimens from less arid environments. Although we suggested body size-habitat correlations for *Spirostreptus* species in southern Africa (see Mwabvu *et al.* 2009b), these correlations may not hold for all spirostreptid genera. For example, the small body sizes of *Archispirostreptus* and *Cacuminostreptus* species, relative to *Spirostreptus*, may not be correlated to some of their habitats. This is unlike *S. unciger, S. heros* and *S. kruegeri*, which occur in the hot and dry savanna, and are bigger (longer, wider and with more body rings) than species which are found in wetter areas. Generally, these species of *Spirostreptus* have 4–6 more body rings, their maximum body diameter is 4–5 mm greater and they are up to 40 mm longer than the species of

Cacuminostreptus which occur in similar localities (see Mwabvu *et al.* 2009b). With respect to *Archispirostreptus*, the wide body size ranges among the species are probably explained by their occurence in different vegetation types and disjunct localities, unlike the regional endemic genera, *Spirostreptus* (see Mwabvu, *et al.* 2009b), *Bicoxidens* (see Mwabvu, *et al.* 2007) and *Cacuminostreptus*, that seem to occur in relatively fewer vegetation types and in similar climatic belts.

Because the distributions of spirostreptid millipedes seem to be influenced by climatic factors and associated vegetation type, it is not surprising that similar patterns of distribution occur in different genera. Based on the similar distribution patterns and the coexistence of genera, we infer that more species belonging to different genera can be found in a single locality than previously estimated. Therefore, areas of overlapping distributions and coexistence of species should be identified when biodiversity conservation is intended. Additionally, if these areas do not have high human populations, such as in dry savanna, they could be targeted for conservation without facing resistance from communities and politicians.

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CHAPTER 5

A REVISION OF THE TAXONOMY AND DISTRIBUTION OF *Archispirostreptus* Silvestri 1895 (DIPLOPODA, SPIROSTREPTIDA, SPIROSTREPTIDAE), AND DESCRIPTION OF A NEW SPIROSTREPTID GENUS WITH THREE NEW SPECIES.

LIST OF ERRATA

Chapter 5: **A revision of the taxonomy and distribution of *Archispirostreptus* Silvestri 1895 (Diplopoda, Spirostreptida, Spirostreptidae), and description of a new spirostreptid genus with three new species.**

1. **What is the type species of *Graphidostreptus*? Who placed it in synonymy? Why?**

The type species of *Graphidostreptus* is *Spirostreptus gigas* Peters 1855. The synonymisation was based on similar gonopod morphology; the gonopods are characterized by spikes on the antetorsal process.

2. **Type material of the subspecies of *A. lugubris* should be included.**

The location of the type of the subspecies of *A. lugubris maior* is unknown, therefore it was not examined. The gonopod of *A. lugubris villiersi* was missing, although the specimen was available. As a result, original descriptions were used in the study to study most subspecies. Although the subspecies represent recognizable forms, they do not appear sufficiently different to justify species rank.

3. **The subspecies of *A. tumuliporus* should be included.**

The location of the type of the subspecies *A. tumuliporus sudanicus* is unknown. It could be that the type was lost or the type was designated. Drawings of the gonopods in the original were used in the study.

4. **Page 13, *A. dodsoni* locality.**

The locality information is based on the specimen label.

5. **Phylogenetic Analysis of *Archispirostreptus* and *Cacuminostreptus* species**

Materials and Methods

Character and data matrices were constructed using male gonopod characters. A phylogenetic analysis was performed using PARS 3.6 and CONSENSE 3.6 (both in the phylogeny inference program, PHYLIP) to produce an extended majority rule consensus tree. The reliability of the tree was tested using bootstrap analysis with the use of 1000 replicates. *Orthoporoides pyrhocephalus* (C. L. Koch 1865) was selected as the outgroup because it has a gonopod structure similar to the ingroup.

Results and Discussion

The phylogenetic analysis separates the ingroup into two groups, all the *Archispirostreptus* species and *Cacuminostreptus triangulatus* (Group A), and a strongly supported group of *C. mazowensis*, *C. vumbaensis* and *C. conatus* (Group B) (Fig. 16). Although Group A contains all the *Archispirostreptus* species, the group is poorly supported. *Archispirostreptus smithii, A. dodsoni and A. lugubris*, form a polytomy; the relationships within the clade are unresolved.

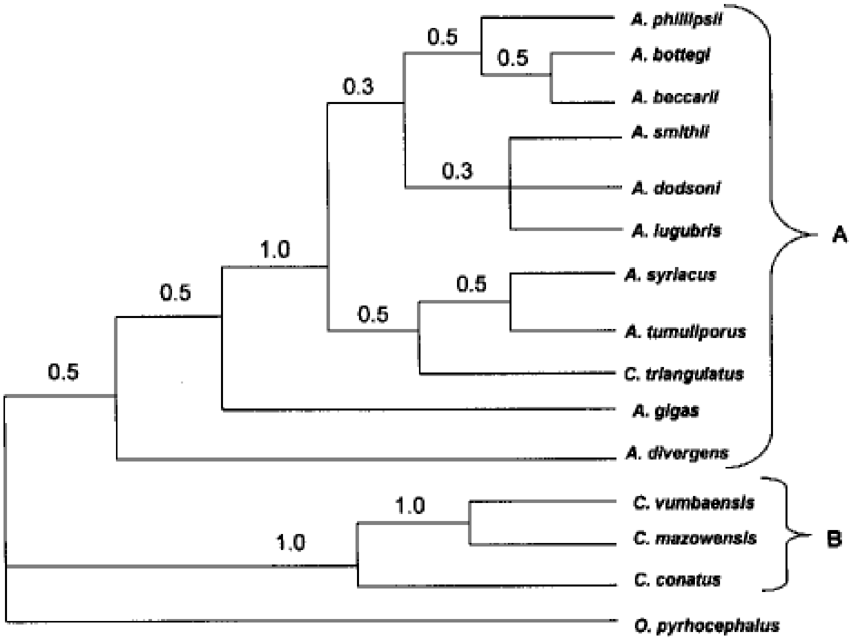

Figure 16. A consensus tree of *Archispirostreptus* and *Cacuminostreptus* species using *Orthoporoides pyrhocephalus* as an outgroup. The numbers indicate the number of times the groups to the right of each fork occur among the trees out of 1.00.

The early separation of *C. mazowensis*, *C. vumbaensis* and *C. conatus* to form a strongly supported clade corroborates our observation that the taxa are closely related and support the erection of the genus. Group B is paraphyletic. The presence of *C. triangulatus* in the *Archispirostreptus* species clade is not consistent with generic diagnosis. This inconsistency and the polytomy in the phylogeny could have been a result of the small number of unambiguous gonopod characters (relative to the number of taxa) available (Scotland *et al.* 2003). Hamer and Slotow (2000) also reported many unresolved relationships among *Doratogonus* species and attributed this to characters that do not provide phylogenetic information. In future, non-gonopod characters and characters from females should be included in analyses. In addition, DNA sequences should be explored further to compliment morphological evidence (Bond, 2004).

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Appendix 1: Character matrix for cladistic analysis of *Archispirostreptus* and *Cacuminostreptus*

1. Apical proplica: 0—not tongue-shaped or spathulate; 1—tongue-shaped; 2—spathulate
2. Sternite apex: 0—triangular; 1—horizontal
3. Oral fold of metaplica: 0—not longer than aboral fold; 1—longer than aboral fold
4. Lateral margins of metaplica: 0—straight; 1—convex
5. Proximal metaplica: 0—without abrupt narrowing; 1—with abrupt narrowing
6. Lateral process: 0—tapering uniformly; 1—not tapering uniformly; 2—not tapering
7. Lateral process shape: 0— without arrowhead shape; 1—with arrowhead shape
8. End process shape: 0—conical; 1—finger-like; 2—triangular
9. Apical end process: 0—rounded; 1—acute; 2—horizontal
10. End process: 0—not deflected; 1—deflected laterally; 2—deflected medially
11. Lateral angular projection on end process: 0—absent; 1—present
12. Proximal lateral and medial edges of end processes: 0—straight; 1—convex
13. End processes: 0—do not overlap; 1—overlap
14. End and lateral process: 0—uniformly opaque; 1—not uniformly opaque
15. Antetorsal process origin: 0—at knee; 1—distal to knee
16. Apical antetorsal process: 0—with spikes; 1—with spine

Appendix 2: Data matrix for cladistic analysis of *Archispirostreptus* and *Cacuminostreptus*

Taxon	**Character states**
15	16
O. pyrhocephalus	0000000000000000
beccarii	1000022100000010
bottegi	0000022100000010
gigas	1000010000010100
lugubris	1100122100000000
divergens	1000000012001100
phillipsii	1000100101000010
syriacus	1000022100100000
tumuliporus	1000022010000000
dodsoni	1000022100000000
smithii	1000022100000000
mazowensis	2001011020000001
conatus	2011011000000001
vumbaensis	2001011020000001
triangulatus	2001011220000001

6. Distribution map of *Archispirostreptus* species

The distribution map of *Archispirostreptus* species (below) is an improved version of Figure 15 in the published taxonomic revision of *Archispirostreptus* (Chapter 5 in the thesis). The recent map has included all the records that had been omitted in the earlier version. Records of *Cacuminostreptus* species have been excluded.

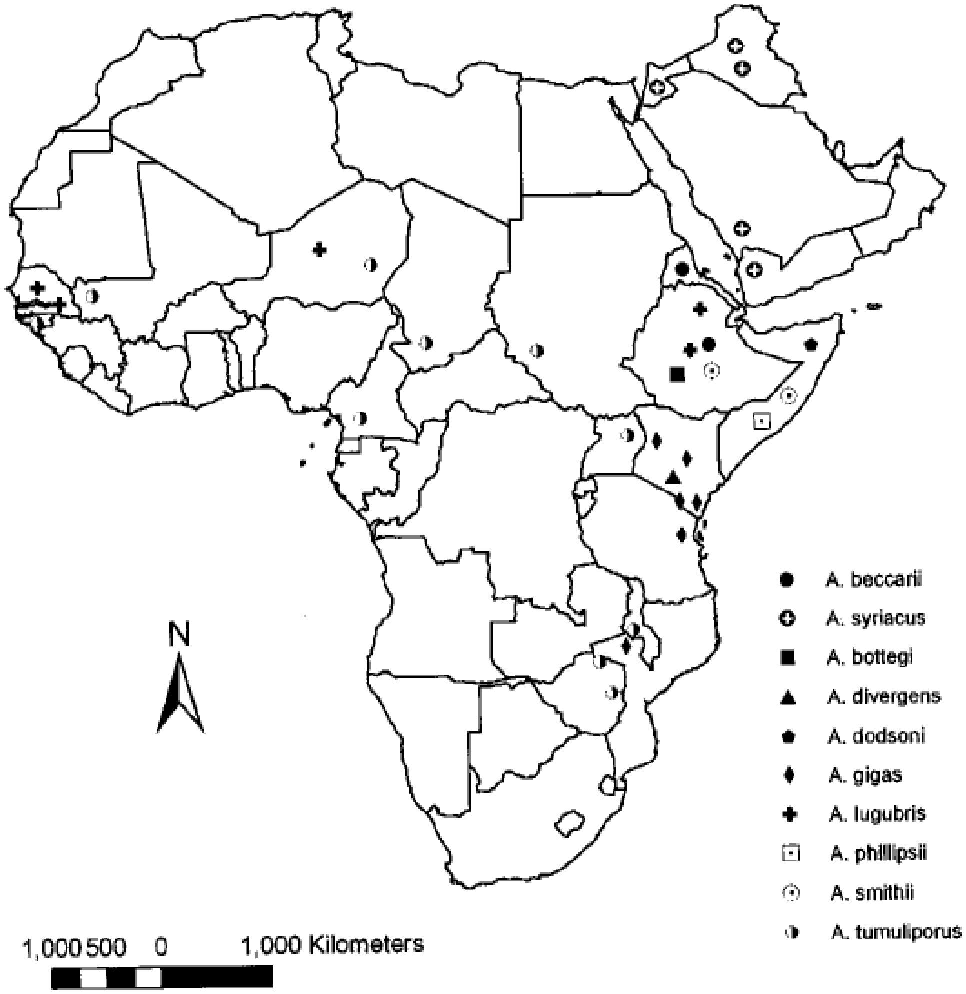

FIGURE 15. Distribution of *Archispirostreptus* species.

7. Distribution map of *Cacuminostreptus* species

The distribution map of *Cacuminostreptus* species (below) is an addition to the published taxonomic revision of *Archispirostreptus* (Chapter 5 in the thesis). The map includes all the known localities from which the species have been recorded.

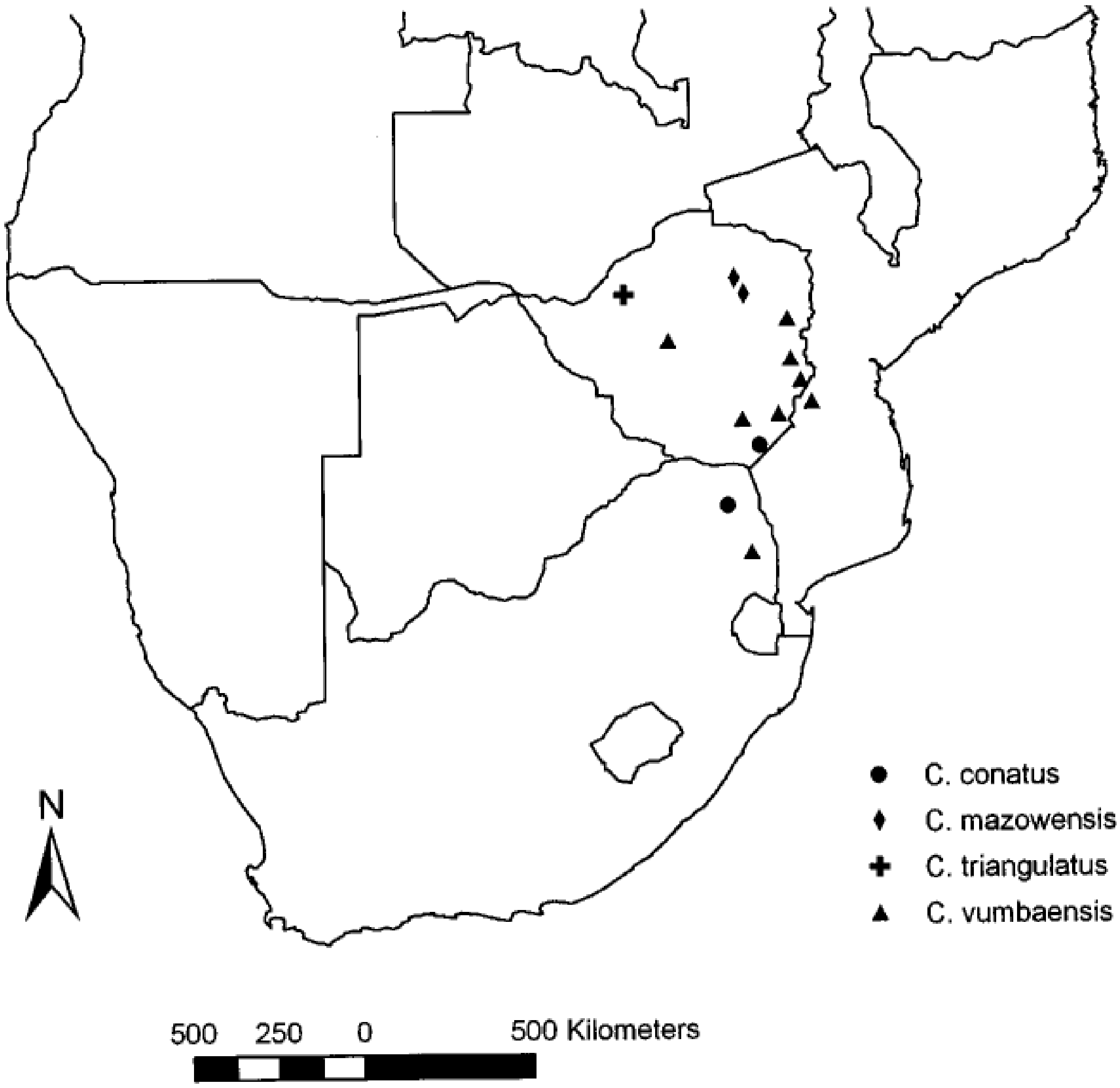

FIGURE 16. Distribution of *Cacuminostreptus* species

CHAPTER 6

SPIROSTREPTID MILLIPEDES (MYRIAPODA: DIPLOPODA) OF THE TAITA HILLS, KENYA, INCLUDING DESCRIPTIONS OF THREE NEW SPECIES.

Spirostreptid Millipedes (Myriapoda: Diplopoda) of the Taita Hills, Kenya, Including Descriptions of Three New Species

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Abstract

We present a checklist and distributional analysis of spirostreptid millipedes in the Taita Hills region of Kenya. We recorded a total of nine species in this area, of which three in the genera *Bucinogonus*, *Lophostreptus*, and *Tibiozus*? are new to science and described herein. No species was collected from all 12 isolated forest fragments in the Taita Hills. The most common and widely distributed species were *Tibiozus*? *vulgaris* and *Lophostreptus ptilostreptoides*, which were collected in eight and five localities, respectively. Three species – *Archispirostreptus gigas*, *Lophostreptus armatus*, and *Lophostreptus minimus* – were collected from only one locality outside of the forest, in grassland. Our observations suggest that most of the millipede species in this region were probably widely distributed in the Taita Hills prior to fragmentation of the forest.

Key words: East Africa, millipedes, Spirostreptidae, taxonomy.

Introduction

The Eastern Arc Mountains contain most of the moist, montane tropical forest in Tanzania and Kenya and are the biologically richest areas, for their size, in East Africa. They harbor an unusually high proportion of rare and endemic animals and plants, and have been classified as one of the 17 most threatened tropical hotspots worldwide (Myers 1988, Myers et al. 2000, Burgess et al. 2007). The only range found within Kenyan boundaries are the Taita Hills. Unfortunately, human encroachment and over-exploitation have dramatically reduced the forest cover of this region. The remaining forest fragments in the Taita Hills are very small and becoming more fragmented and degraded over time (some are less than one hectare).

The Taita Hills Biodiversity Project (THBP), a collaboration between a number of Belgian and Kenyan institutions (Bytebier 2001), has demonstrated that the Taita forest fragments form a unique ecosystem in Kenya, with an unusually high number of plants and animals that can be found nowhere else in the world. Among the invertebrates, Myriapoda (including spirostreptid millipedes) constitute a large proportion of the endemic species found in this region. Although not all of the available material has yet been fully studied, 60% of the species collected appear to be new to science.

The present study gives an account of the spirostreptid fauna of the Taita Hills (Table 1) and is mainly based upon material collected during the THBP from 1999 to 2003. During this period, intensive sampling in the remaining forest fragments of the Taita Hills resulted in the collection of 315 samples of diplopods, 36 of which contained spirostreptids. Although we are aware of the fact that descriptive taxonomy should preferably not be based on a local faunal survey, it is inevitable that new species are collected when comprehensive surveys like the THBP are conducted in tropical countries. In this paper we describe the three new species of spirostreptid millipedes found during our surveys, and compare them with previously described species. What is of great

Pp. 195-207, *in* S. M. Roble and J. C. Mitchell (eds.). 2009. A Lifetime of Contributions to Myriapodology and the Natural History of Virginia: A Festschrift in Honor of Richard L. Hoffman's 80th Birthday. Virginia Museum of Natural History Special Publication No. 16, Martinsville, VA.

interest in the present study is that it is probably the first African collection programme aimed at Diplopoda that has been conducted over several years, and has most species represented by large samples.

Study Area and Methods

Study Area

The Taita Hills are about 25 km west of Voi in southeastern Kenya. The hills rise abruptly from the surrounding Tsavo plains to an elevation of 600-700 m asl., ascending to a series of ridges with Vuria, the highest point, at 2208 m. The Taita Hills comprise four main hills: Dabida, Kasigau, Mbololo, and Sagala. Forest fragments remain on all four hills but the Dabida complex is the most fragmented and consists of several small forests: Chawia, Fururu, Macha, Mwachora, Ngangao, Vuria, and Yale (Wilder et al. 1998; Fig. 1).

Methods

Millipedes were collected primarily by hand, during day and night, and by using pitfall traps. Specimens were preserved in 70% ethanol. The habitat and substrate on which each specimen was found were noted.

Descriptive terminology: The taxonomy of spirostreptid millipedes is based chiefly on gonopod structure (modified legs) found on the seventh body ring

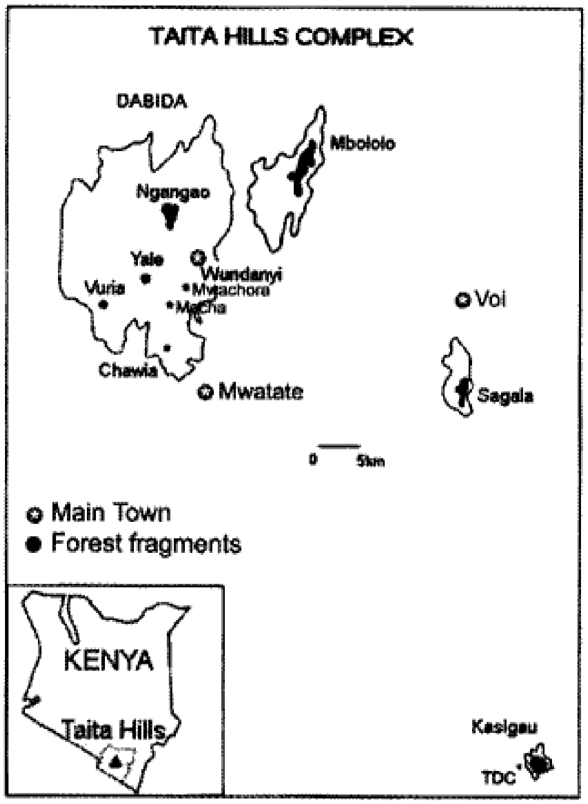

Fig. 1. Map of the Taita Hills, Kenya.

Table 1. Local distribution of spirostreptids recorded in Taita Hills, Kenya. Names in bold are new to science and the species underlined are endemic to the Taita Hills.

Locality	Dabida							Kasigau	Mbololo	Sagala	TDC	Wundanyi
Species	Chawia	Fururu	Ngangao	Macha	Mwachora	Vuria	Yale					
Anastreptus scalatus								*			*	
Archispirostreptus gigas											*	
Bucinogonus aviceps			*		*				*			
Calostreptus chelys								*			*	
Lophostreptus armatus											*	
L. minimus											*	
L. ptilostreptoides	*		*				*		*			*
Taitastreptus flavipes			*					*	*			
Tibiozus? vulgaris	*	*	*		*	*	*		*	*		

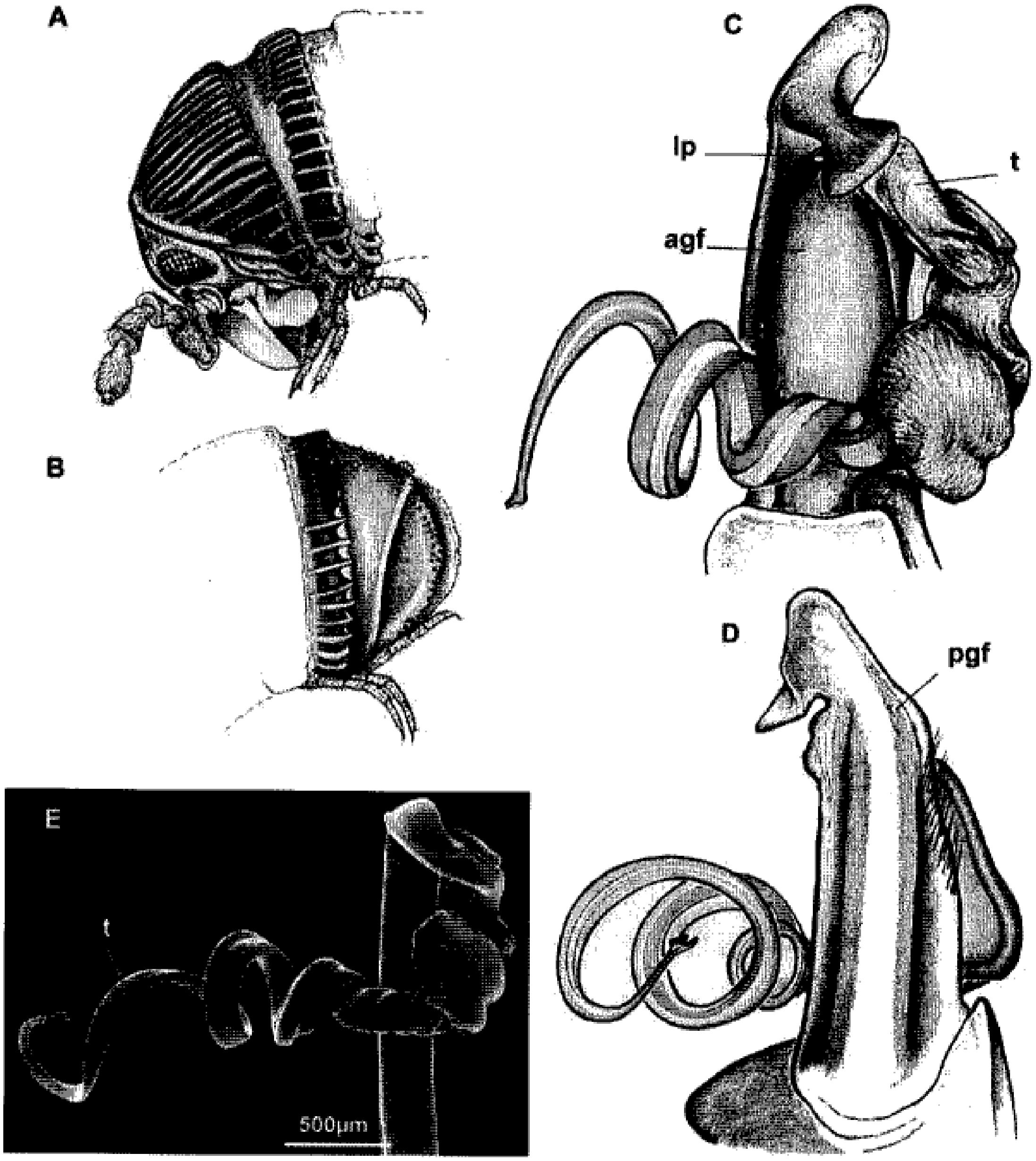

Fig. 2. *Anastreptus scalatus* male. A. Lateral view of head, collum, and first body ring of adult; B. Lateral view of last body ring, preanal, and anal ring; C. Anterior view of right gonopod; D. Posterior view of right gonopod; E. Anterior view of right telopodite. Abbreviations: agf, anterior gonocoxal fold; lp, lateral process; pgf, posterior gonocoxal fold; t, telopodite.

of mature males. Most of the terms used in this paper for describing the gonopods of Taita species are adapted from Hamer (1999). In addition, discrimination of taxa also depends on the structure of peripheral characters such as the general shape of the collum and telson, presence or absence of spines on the anal valves, structure of the first pair of legs, and the distribution of adhesive pads on locomotory legs. For each species, the number of body rings including apodous ring and preanal ring is given, as well as a short diagnosis allowing differentiation between the species known from the Taita Hills.

For scanning electron microscopy (SEM), samples were air dried and mounted on aluminium stubs, coated with gold in a sputter coater and observed with a JEOL JSM-6480LV scanning electron microscope. After observation, dry SEM material was removed from stubs and returned to alcohol.

Abbreviations: MRAC, Musée royal de l'Afrique centrale, Tervuren, Belgium; NMK, National Museum of Kenya, Nairobi, Kenya; TDC, Taita Discovery Centre; VMNH, Virginia Museum of Natural History, Martinsville, Virginia, U.S.A.

Synonymy: Taxonomy and nomenclature follow Krabbe (1982) where synonymies of described species can be found.

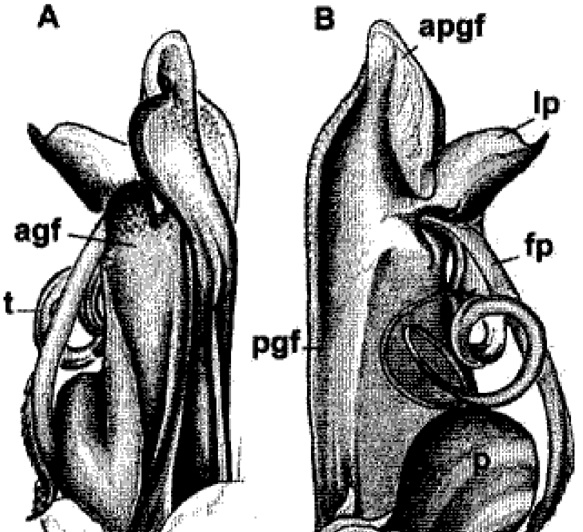

Fig. 3. *Archispirostreptus gigas* male. A. Anterior view of left gonopod; B. Posterior view of left gonopod. Abbreviations: agf, anterior gonocoxal fold; apgf, apical posterior gonocoxal fold; fp, femoral process; lp, lateral process; p, paracoxite; pgf, posterior gonocoxal fold; t, telopodite.

Taxonomic Account

Order Spirostreptida

Family Spirostreptidae

Anastreptus scalatus (Karsch, 1881)

Fig. 2

Material examined: **KENYA**: 1♀: Tsavo West, TDC, S 03°25′ E 38°46′, 5.XII.2000, VandenSpiegel D. (MRAC 20070); 1♂: Tsavo West, Kasigau Forest, 6.XII.2000, VandenSpiegel D. (MRAC 19460); 1♂: Taveta district, Taita, 6.XII.2000 Selempo Edwin (MRAC 20560); 1♂: Mt. Kasigau, XII.2001, Selempo E. (MRAC 21036); 1♂: Mt. Kasigau, XII.2001, Selempo E. (MRAC 21041).

Diagnosis: Medium-sized spirostreptid millipede characterized by the posterior half of each body ring distinctly wider than the anterior half; each body ring ornamented with numerous strongly raised, short longitudinal ridges (Figs. 2A-B). Gonopod telopodite with a particularly long and helicoidal distal part (Figs. 2C-E).

Remarks: In Kenya, the species has been collected at Mombasa and in the Taita Hills, as well as in Sokoke forest ca. 20 km south of Malindi, Ngong Hills, Bushwackers near Kibwezi. In Tanzania, it is known from the Pwani region, Kisarawe District, Ruvu South Forest Reserve. All det. H. Enghoff, Zoological Museum, University of Copenhagen, Denmark (unpubl. data). In the Taita Hills, specimens of *Anastreptus scalatus* have been collected at night primarily after rain. No specimens were collected within the forest, but rather always in localities where herb cover was dominant. The body surface texture is similar to that of *Calostreptus chelys* Cook but the longitudinal ridges are more pronounced in *A. scalatus* (Table 2; Fig. 2A).

Archispirostreptus gigas (Peters, 1855)

Fig. 3

Material examined: **KENYA**: 1♂, 2♀: Tsavo, TDC, S 03°25′ E 38°46′, 6.XII.2000, VandenSpiegel D. (MRAC 20254).

Diagnosis: A very large species and certainly the biggest Kenyan spirostreptid millipede. Females can reach 30 cm total length but males are shorter, up to 24 cm. Gonopod telopodite characterized by a spinous or tasselled femoral process (Fig. 3).

Remarks: This species has a wide distribution and is known from South Africa (Transvaal), Mozambique, Tanzania, Kenya, to Somalia (Mogadiscio). Within Kenya it is common along the coast, at Meru National Park, Taita Discovery Center, and Samburu National Park.

Bucinogonus aviceps sp. n.

Figs. 4-5

Material examined: **KENYA** (Taita Hills): Holotype ♂, Mwachora forest, S 03°24′ E 38°22′, III.IV.1999, pitfall traps, Rogo Lucy (MRAC 18052). Paratypes: 1♂: Mbololo Forest, S 03°19′ E 38°27′, 3VII-2VIII.1999, 1800-1900 m, pitfall traps, Mwakos R. (MRAC 18484). 1♂, 1♀: Ngangao Forest, S 03°22′ E 38°20′, 17-18. VI.1999, 1820-1900 m, pitfall traps, VandenSpiegel D. (MRAC 18482).

Diagnosis: Apically, posterior gonocoxal fold bird head-shaped with a short lateral beak; posterior gonocoxal fold with a subapical extension facing the gonocoel; telopodite forms a single incomplete loop close to the coxite just above the depression of paracoxite; apically, anterior coxal fold with a short median spine.

Etymology: So named to highlight the bird head-shape of the apical posterior coxal fold.

Description: Number of body rings including preanal ring: ♂ 54-57, ♀ 63; length, ♂ 63-66 mm, ♀ 65 mm; maximum diameter ♂ 3-4 mm, ♀ 4 mm. Body colour dark brown (preserved), antennae and legs brown. Antennae extend to 4th body ring in males, 2nd body ring in females. Collum narrow ventrally, slightly produced posteriorly and with 2 submarginal folds. First ozopore on 6th body ring; longitudinal striae on all rings except preanal ring, more prominent anteriorly. First pair of male legs with long, sausage-shaped prefemoral processes (Fig. 5A). Gonopod with a conical sternite (Fig. 5B); paracoxite tightly fused to coxite and with a central depression. Posterior coxal fold apically rounded with a short, tapering horizontal lateral process, length approximately half the coxite width (Fig. 4A). Subapically, posterior fold with an ear-shaped median extension directed towards the gonocoel, almost level with the apical lateral process (Fig. 4B). The width of coxite remains the same except subapically at the lateral process. Anterior coxal fold rounded apically, with a straight spine adjacent to the gonocoel (Figs. 4B, 5B). Telopodite forming a broad incomplete loop resting in the depression of the paracoxite just below the level of sternite tip, apically with two branches that cross each other (Figs. 4B, 5D). Solenomerite with a sub-terminal hyaline lamella (Figs. 4B, 5D)

Affinities: The genus *Bucinogonus* contains two species – *B. kandti* (Carl, 1909) and *B. silvestrii* Demange et Mauries (1975) – which differ mainly by the structure of the telopodite. The gonopod of the new species is similar to that of *B. kandti* (both have a lateral coxal process, a straight spine on the anterior coxal fold, and a telopodite with a sub-terminal lamella) and supports our assertion that these two species are congeneric. The major differences appear to be in body size and the shape of the telocoxite. Additionally, in *B. kandti* the body surface is keeled, the anterior coxal fold tapers distally (thus coxite is broader proximally), the telopodite forms a complete loop, and the prefemoral processes of the 1st pair of male legs are spade-shaped and wider apart apically, unlike in the new species.

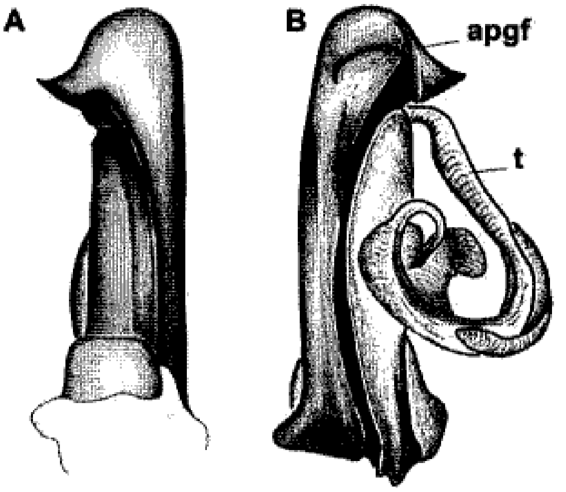

Fig. 4. *Bucinogonus aviceps* sp. n. male. A. Posterior view (without telopodite) of right gonopod; B. Anterior view of left gonopod. Abbreviations: apgf, apical posterior gonocoxal fold; t, telopodite.

Remarks: Known only from Taita Hills, Kenya, where the species was collected from Dabida complex, as well as in Mbololo. Specimens were caught inside the forest using pitfall traps.

Calostreptus chelys Cook, 1896

Fig. 6

Material examined: **KENYA**: 1♂: Taita Hills, Kasigau, 6.XII.2000, VandenSpiegel, D. (MRAC 21380); 1♂: Taveta district, Taita, 10.IIV.2001, Selempo E. (MRAC 20560).

Diagnosis: Anterior part of the posterior section of each body ring slightly raised and with longitudinal ridges. Preanal ring (telson) dorsally with a distinct granular keel in the middle. Apex of posterior gonocoxal fold hammer-shaped; most of post knee telopodite loops close to the coxite, distal part is in the loop (Fig. 6).

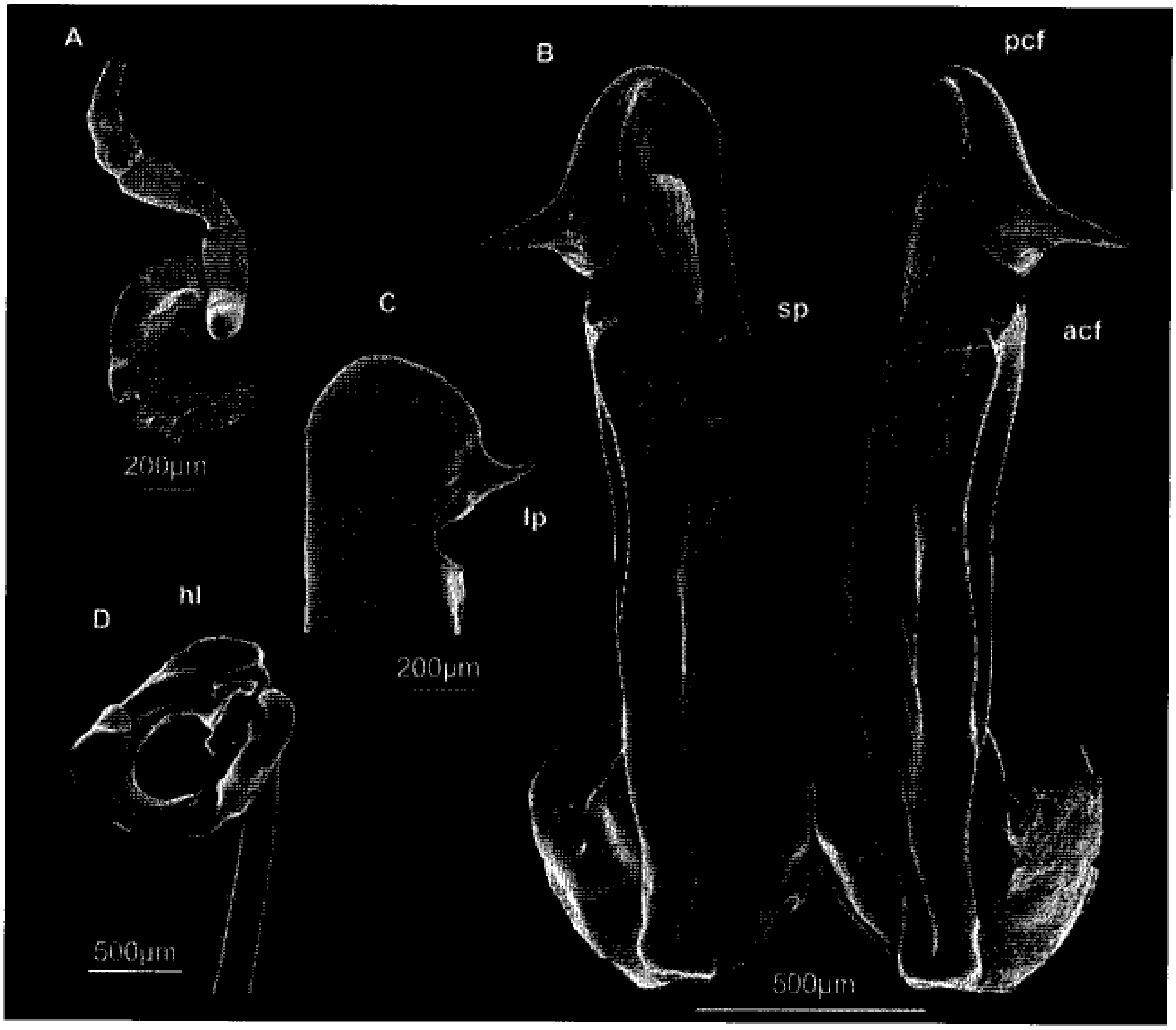

Fig. 5. *Bucinogonus aviceps* sp. n. male (SEM). A. Anterior view of first left leg; B. Anterior view of gonopods (without telopodites); C. Posterior view of apical posterior gonopod; D. Lateral view of left telopodite. Abbreviations: acf, anterior coxal fold; hl, hyaline lamella; lp, lateral process; p, paracoxite; pcf, posterior coxal fold; sp, straight spine; st, sternite.

Remarks: This species is new for the Kenyan fauna, having been reported previously only from Mpapua, Tanzania, and Upemba, DR Congo (Krabbe 1982). General body texture is very similar to *Anastreptus scalatus*, which has more prominent longitudinal ridges. *Calostreptus chelys* was also found in a biotope very similar to that of *A. scalatus* (Table 2).

Lophostreptus armatus Pocock, 1896

Fig. 7

Material examined: **KENYA**: 3♂, 3♀:, Tsavo West, TDC, S 03°25′ E 38°46′, 5.XII.2000, night catch, VandenSpiegel D. (MRAC 19445); 10: same data, water tank, night catch (MRAC 19451).

Diagnosis: Apically, posterior coxal fold bends laterally, with a lateral process proximally curving away from the coxite and paracoxite (Fig. 7).

Remarks: Mature specimens of both sexes were found in the wet season at night always in localities where herb cover was dominant; specimens were never caught in the Taita forest. This species is also known from Mount Kenya and Upemba, DR Congo.

Lophostreptus minimus sp. n.

Fig. 8

Material examined: **KENYA**: Holotype ♂, Tsavo West, TDC, S 03°25′ E 38°46′, 5.XII.2000, in grassland, VandenSpiegel D. (MRAC 21784).

Diagnosis: Apically, posterior coxal fold constricted/narrow, with a tapering crescent-shaped lateral process pointing towards paracoxite; paracoxite not raised, almost at right angle with coxite.

Etymology: from Latin, referring to the fact that this species is, up to now, the smallest species of the genus.

Description: Number of rings 42; length 34 mm; maximum diameter 2 mm. Body colour black, antennae black, legs brown. Head with markings above level of eyes on either side of a vertical line that extends to the collum but not below the level of the eyes. Two spots present at the front of the head between the antennae, just below the vertical line. Collum ventrally square-shaped with 3 submarginal folds. First ozopore on 6th body ring. Posterior section of each body ring raised, with longitudinal ridges. Prefemoral processes of first legs of males close together, each producing a proximal lateral extension before sharply narrowing distally. Apically posterior coxal fold not enlarged, but produces a crescent-shaped tapering lateral process directed towards the paracoxite (Fig. 8). Telopodite twists upwards towards the knee just above the paracoxite forming a complete loop; femoral process foliated.

Affinities: The posterior part of each body ring is slightly raised as in *Anastreptus scalatus* and *Calostreptus chelys*, but the gonopod of this species is clearly that of a *Lophostreptus*. At first glance, the new species seems to be a small specimen of *L. armatus*, but a close examination shows that the apical posterior coxal fold of the gonopod is significantly more reduced in *L. minimus*. The lateral process in *L. armatus* curves away from the coxite and paracoxite unlike in *L. minimus*. The broader and lobed part of the telopodite is directed medially in *L. minimus* as opposed to laterally in *L. armatus*.

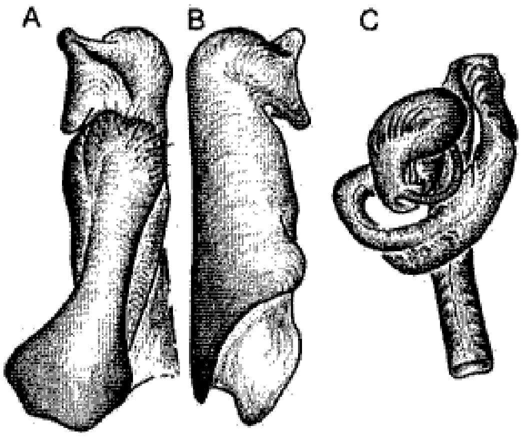

Fig. 6. *Calostreptus chelys* male. A. Anterior view of left gonopod; B. Posterior view of left gonopod; C. Lateral view of the left telopodite.

Remarks: Known only from the type locality. The species seems to prefer the upper part of the grassland and may have been overlooked during the THBP survey.

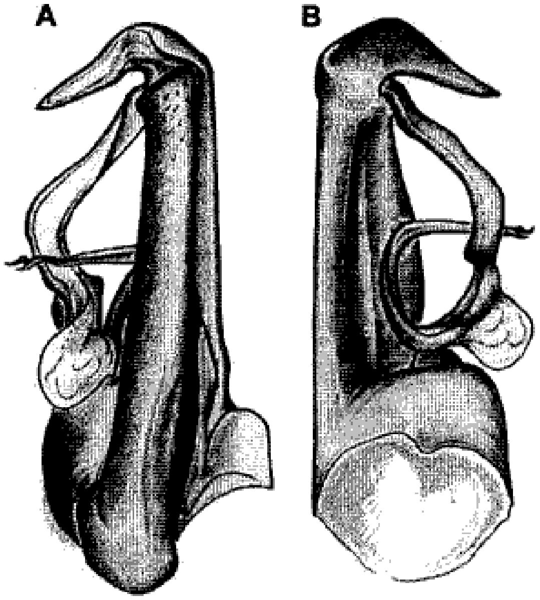

Fig. 7. *Lophostreptus armatus* male. A. Anterior view of left gonopod; B. Posterior view of left gonopod.

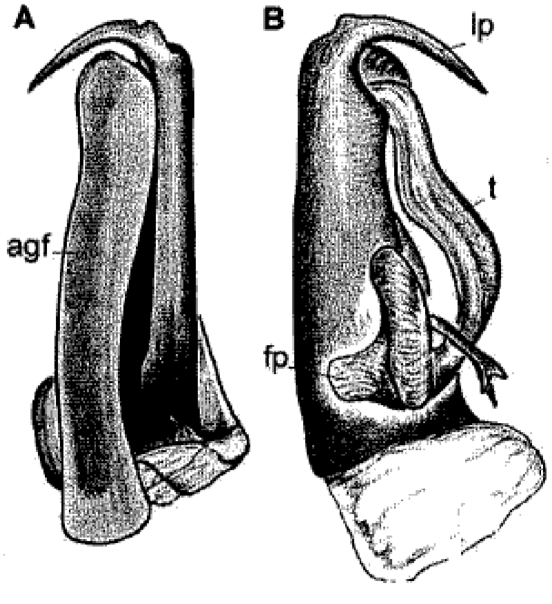

Fig. 8. *Lophostreptus minimus* sp. n. A. Anterior view of left gonopod (without telopodite); B. Posterior view of left gonopod. Abbreviations: agf, anterior gonocoxal fold; fp, femoral process; lp; lateral process; t, telopodite.

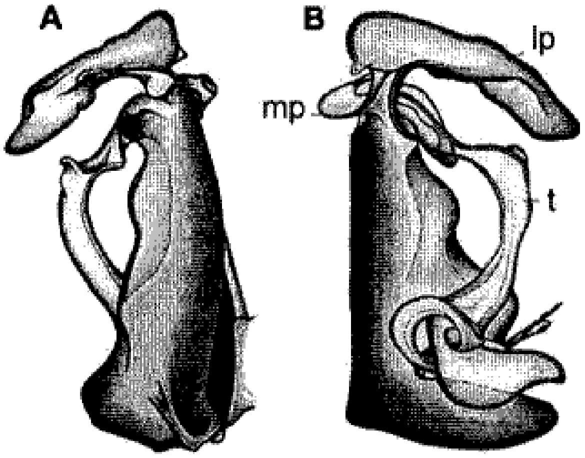

Fig. 9. *Lophostreptus ptilostreptoides* male. A. Posterior view of right gonopod; B. Anterior view of right gonopod. Abbreviations: lp, lateral process; mp, median process; t, telopodite.

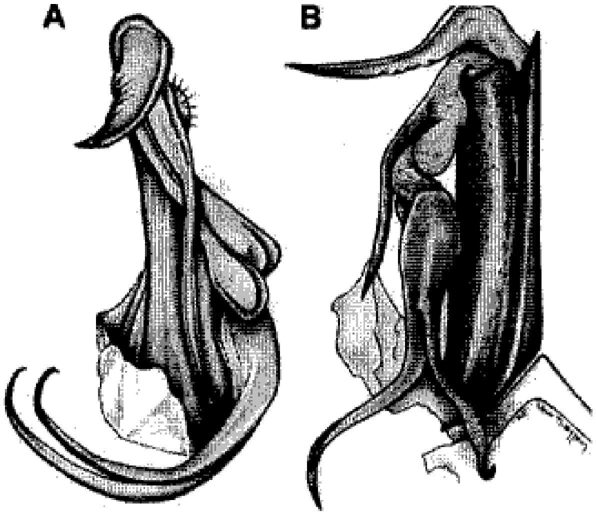

Fig. 10. *Taitastreptus flavipes* male. A. Lateral view of right gonopod; B. Anterior view of left gonopod.

Lophostreptus ptilostreptoides Carl, 1909

Fig. 9

Material examined: **KENYA** (Taita Hills): 1♂, 1♀: Mbololo forest, S 03°19′ E 38°27′, 3.VII-2.VIII.1999, 1800-1900 m, pitfall traps, Mwakos R. (MRAC 18027); 1♂: same locality, 22.VI.1999, VandenSpiegel D. (MRAC 18481); 1♂: Chawia forest, S 03°29′ E 38°20′, 1-20.VI.1999, 1500 m, pitfall traps, Mwakos R. (MRAC 18068); 2♂, 1♀: same locality, 25.VI.1999, Mwakos R. (MRAC 18483); 2♂, 1♀: same locality, 7.XII.1999, VandenSpiegel D. & Michiels J.P. (MRAC 18429); 1♂, 1♀: Yale forest, S 03°39′ E 38°33′, 16.IV-16.V.1999, 1840 m, Mwakos R. (MRAC 18213); 1♂, 3♀: Ngangao forest, S 03°22′ E 38°20′, 23-28.XI.1999, Mwakos R. (MRAC 18438); 7: Wundanyi lodge, 3.XII.1999 night catch, VandenSpiegel D. & Michiels J.P. (MRAC 18400); 1♀: Wundanyi, 3.XII.1999 around houses, VandenSpiegel D. & Michiels J.P. (MRAC 18439); 1♂: Wundanyi, 3.XII.1999 night catch, (2100-2200 h), VandenSpiegel D. & Michiels J.P. (MRAC 18492).

Diagnosis: Apically, posterior coxal fold with a lateral process slanting towards paracoxite, just above the apex of anterior coxal fold a median process overlaps the opposite process (Fig. 9).

Remarks: This species was previously known from Kenya (Voi), Rwanda (Kagera), and Tanzania (Kilimandjaro, Usambara). In the Taita Hills, it occurs in all Dabida forest fragments, as well as in Mbololo Forest. This millipede is most frequently observed within the forest but also occurs in grassland.

Taitastreptus flavipes VandenSpiegel, 2001

Fig. 10

Material examined: **KENYA**: 1♀: Taita Hills, Mbololo Forest, S 03°19′ E 38°27′, 21.VI.1999, 1800-1900 m, Vanden Spiegel D. (MRAC 17978); 1♂: same locality, 8.XII.1999, VandenSpiegel D. & Michiels J.P. (MRAC 18416); 4♂,1♀: Taita Hills, Ngangao Forest, S 03°22′ E 38°20′, 16-22.IV.1999, 1820 m, Mwakodi R. (MRAC 18056); 2♀: same locality, 23-28.XI.1999, Mwakos R. (MRAC 18437); 1♂,1♀: Tsavo West, Kasigau, S 03°49′ E 38°40′, 6.XII.2000, 1000 m, forest, in trees, VandenSpiegel D. (MRAC 19563).

Diagnosis: Apically, gonopod telopodite deeply forked with equally-sized branches; the femoral process is long and straight (Fig. 10).

Remarks: Known only from the type locality. This species with yellow legs is notable for its arboreal tendencies (VandenSpiegel 2001).

Tibiozus? vulgaris sp. n.

Figs. 11-12

Material examined: **KENYA**: Holotype ♂, Taita Hills, Ngangao Forest, 4.XII.1999, VandenSpiegel D. & Michiels J. P. (MRAC 018478). Paratypes (same data as holotype): 1♂, 1♀ (VMNH); 2♂ (NMK); 2♂, 10♀, 2 juveniles (MRAC 18478).

Other material: **KENYA** (Taita Hills): 2♀: Mbololo forest, S 03°19′ E 38°27′, 21.VI.1999, 1800-1900 m, VandenSpiegel D. (MRAC 17975); 3♂, 1♀: same data except 22.VI.1999 (MRAC 17985); 4♀: same locality, 8.XII.1999, VandenSpiegel D. & Michiels J.P. (MRAC 18417); 3♀: Chawia forest, S 03°29′ E 38°20′, 25.VI.1999, VandenSpiegel D. (MRAC 17997); 1♀: same locality, 1-20.VI.1999, pitfall traps, Mwakos R. (MRAC 18067); 1♀: same data as preceding (MRAC 18070); 1♀: same data as preceding except 10-26. VI.1999 (MRAC 18018); 1♂: same locality, III-IV.1999, pitfall traps, Rogo Lucy (MRAC 18091); 2♂, 2♀: same locality, 7.XII.1999, VandenSpiegel D. & Michiels J.P. (MRAC 18427); 20: Ngangao forest, S 03°22′ E 38°20′, 19.VI.1999, 1820 m, VandenSpiegel D. (MRAC 18006); 18: same data except 18.VI.1999, hand collecting (MRAC 18112); 1♀: same locality, 17.VIII.1999, Mwakodi R. (MRAC 18044); 1♂, 1♀: same locality, 20.XI.1999, Mwakos R. (MRAC 18407); 1♂: Ngangao forest, S 03°22′ E 38°20′, 4.XII.1999, VandenSpiegel D. & Michiels J.P. (MRAC 21785); 2♂: same data. (MRAC 21786); 1♂, 1♀: same data. (MRAC 21787); 2♀: Vuria forest, S 03°24′ E 38°17′, 26.VI.1999, 2200 m, VandenSpiegel D. (MRAC 18082); 1♂: Mwachora forest, S 03°24′ E 38°22′, 20.VI.1999, VandenSpiegel D. (MRAC 21788); 5♀: same data, pitfall (MRAC 21789). 3♂, 22♀: Yale forest, S 03°39′ E 38°33′, 19.VI.1999, 1840 m, VandenSpiegel D. (MRAC 18121); 3♂: same data, pitfall traps (MRAC 18047); 3♂, 7♀: Fururu forest, VandenSpiegel D. & Michiels J.P. (MRAC 18447); 2♀: Sagala forest, S 03°50′ E 38°58′, 5.XII.1999, VandenSpiegel D. & Michiels J.P. (MRAC 18453);

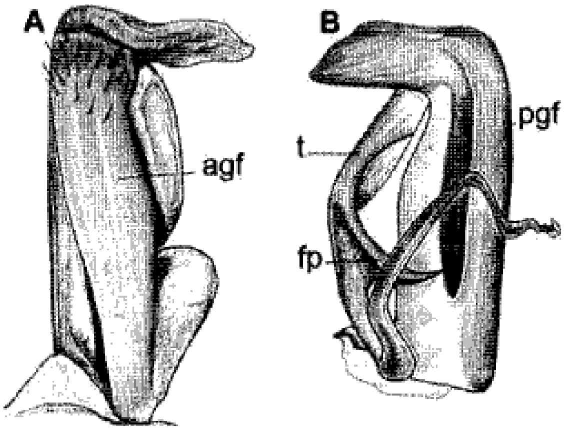

Fig. 11. *Tibiozus vulgaris* sp. n. A. Anterior view of right gonopod (without telopodite); B. Posterior view of right gonopod. Abbreviations: agf, anterior gonocoxal fold; fp, femoral process; pgf, posterior gonocoxal fold; t, telopodite.

Diagnosis: Medium-sized spirostreptid with the apical part of the posterior gonocoxal fold extended laterally, giving gonopod an inverted L shape (Fig. 11). Telopodite with a small spine just before the knee, proximal half of telopodite much broader than distal half. Origin of femoral process distal to exit-point of telopodite from gonocoxite, femoral process laterally attached to the telopodite by a thin membrane.

Etymology: Specific name referring to the fact that the species is common ("vulgaris" in Latin) in most of the Taita Hills forest fragments.

Description: Number of body rings: ♂, 47-48; ♀, 47-49 (including preanal ring); length: ♂, 55 mm, ♀ 80 mm; maximum diameter: ♂ 4 mm, ♀ 5 mm. Body colour dominantly blackish, posterior part of metazonite darker, antennae blackish, legs light brown to red brown. Head smooth, eyes widely separated (shortest distance between eyes 2 mm), each with ca. 52 ocelli in 9 rows, antenna extending to the 2nd body ring. No frontal setae, 4 supralabral setae in a transverse row, a row of labral setae, labrum tridentate. Gnathochilarium stipes with proximal field of prominent setulae, prementum modified, its lateral ends isoplanar with adjoining sclerite but median two-thirds strongly and abruptly depressed to a much lower level (Fig. 12A). Odontomere of mandible partly fused with psectromere, sectile edge of latter with four lobes; pectinate lamellate in eight to ten rows (see Hoffman and Howell 1996 for terminology). Collum: anterior corner protrudes slightly ventrad, and with 3-5 submarginal groves (Fig. 12B). First ozopore: 6th body ring, usually up to one-half of metazonite length behind suture on midbody segments. Body rings almost circular; no legless body rings in front of telson. Prozonite smooth, suture between pro- and metazonite straight; metazonite rugose, metazonital striae present throughout entire perimeter of pleuroterga. Paraproct convex, distal margins set off by well-marked submarginal groove. Hypoproct not fused with preceding segment. First pair of legs as shown in Figure 12C, coxae touching medially, with lateral setae, prefemoral process wider than long with small basal projection on anterior side and short setose tubercles laterally. Walking legs relatively long with a small ventral pad on tibia and post femur. Tarsal claws long and almost straight.

Gonopods with a small, conical sternite; paracoxite rounded, largely not fused to coxite except basally. Apical

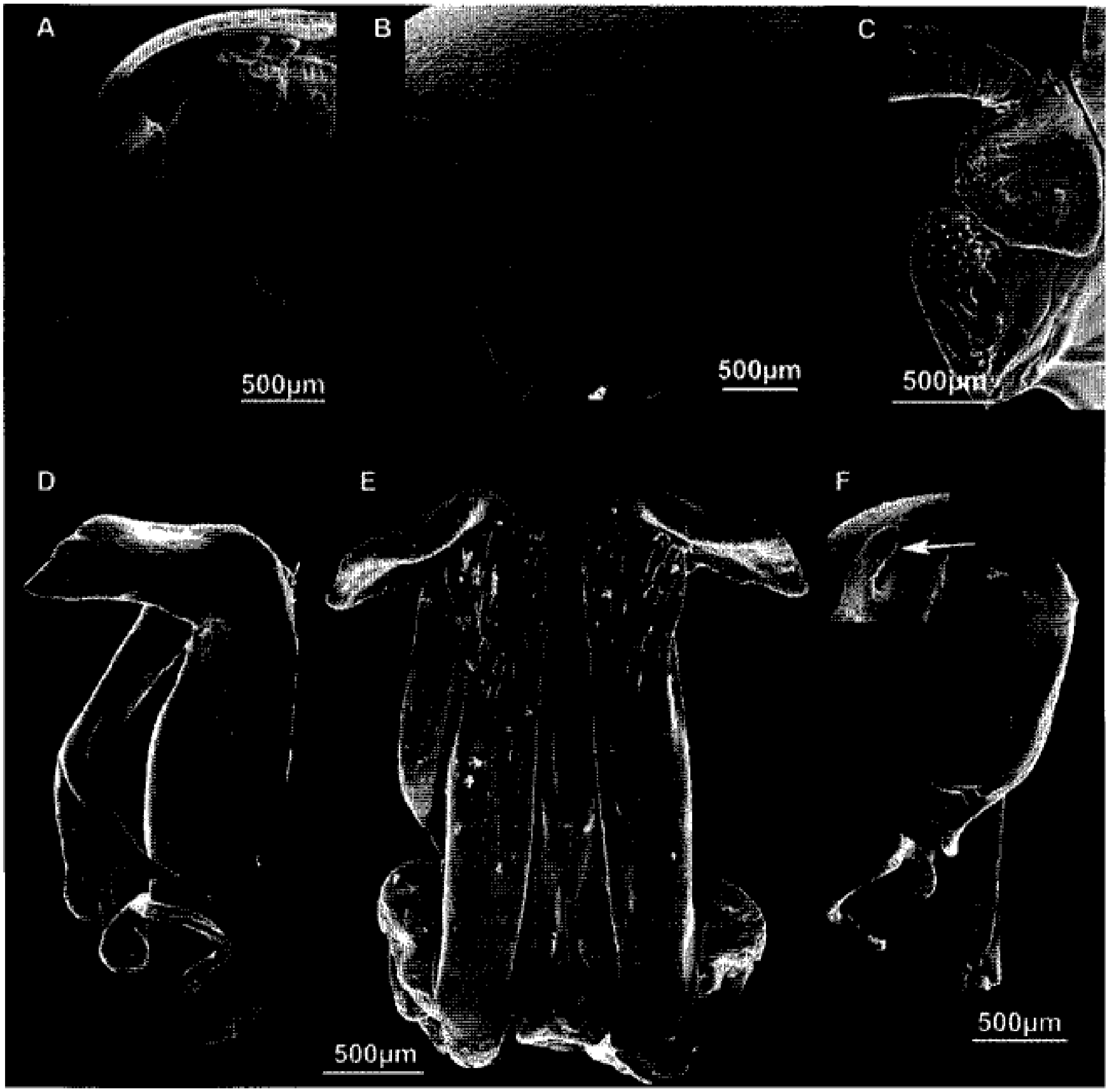

Fig. 12. *Tibiozus vulgaris* sp. n. A. Gnathochilarium; B. Lateral view of collum; C. Anterior view of first left leg; D. Posterior view of right gonopod; E. Anterior view of gonopods; F. Lateral view of telopodite showing the spine at the knee (upper inset: detail of the telopodite showing the prefemoral spine).

part of the posterior coxal fold extended laterally into a horizontal process projecting outside the body when at rest (Figs. 12D, 12F). Proximal half of telopodite much broader than distal half, a short spine lying flat against the telopodite is present just before the knee (arrow in Fig. 12F); origin of femoral process distal to exit-point of telopodite from gonocoxite.

Affinities: At first glance, the new species seems to be referable either to the genus *Brevitibius*, which is known to be represented in the Usambara Mountains (Krabbe 1982), or to *Tibiozus*, which is known from Uganda (Demange 1975). Close observations show that the telopodite of *vulgaris* has a short prefemoral telopodite spine (before the knee), lacks abrupt narrowing, and has no significant inflation after the femur. These characters suggest that this species is more closely related to *Tibiozus* than *Brevitibius*. Among the two species of the genus *Tibiozus*, *T. robustus* Attems, 1950 and *T. sixi* Demange, 1975, the new species seems to be closest to *T. sixi* from Uganda. The two species have a similar telopodite with a small prefemoral spine (before the knee in *vulgaris*, at the knee in *sixi*), and one femoral

Table 2. Characters allowing differentiation between the spirostreptids recorded in Taita Hills, Kenya.

Species	Max. body length (mm)	Max. body diameter (mm)	Max. no. of body rings	Body ring sculpture	Color when alive	Habitat
Anastreptus scalatus	♂66; ♀71	♂4; ♀5	♂47; ♀49	Metazonite with high ridges	Brown with darker metazonite	Grassland
Archispirostreptus gigas	♂240; ♀300	♀20	♀69	smooth	Dark brown to black	Grassland
Bucinogonus aviceps	♂66; ♀65	♂4; ♀4	♂57; ♀63	Metazonite striae	Dark brown	Forest
Calostreptus chelys	♂62; ♀?	♂5; ♀?	♂47; ♀?	Metazonite with ridges; telson with granular keel	Brown with darker metazonite	Grassland
Lophostreptus armatus	♂70; ♀75	♂5; ♀5	♂47; ♀48	Metazonite with low ridges	Brown with darker metazonite	Grassland
L. minimus	♂34	♂2	♂42	Metazonite with low ridges	Brown with darker metazonite	Grassland
L. ptilostreptoides	♂80; ♀90	♂4; ♀5	♂58; ♀58	Metazonite with low ridges	Brown	Forest & Grassland
Taitastreptus flavipes	♂45; ♀50	♂3; ♀4	♂47; ♀46	Metazonite striae	Black; legs yellowish	Forest (arboreal)
Tibiozus? vulgaris	♂55; ♀80	♂4; ♀5	♂48; ♀49	Metazonite rugose	Blackish; legs brown	Forest

process distal to the exit-point of the telopodite from the gonocoxite. Similarities also exist with *T. robustus*, but this species has an additional lateral process at the level where the telopodite makes a loop.

Remarks: *Tibiozus* is one of the poorly defined genera of the family Spirostreptidae and the generic status of *T. vulgaris* would need to be investigated further once other African spirostreptid genera have been revised; the present placement is therefore tentative. The species is widespread within the Taita Hills and was always caught in the forest.

Discussion

The new material collected in the Taita Hills contains seven genera and nine species of spirostreptid millipedes, three of which are new to science. Collecting was performed twice a year during four years using various collecting techniques such as pitfall traps, day and night hand collecting, and Winkler extraction. A major difficulty remains in deciding which species are really confined to the Taita Hills or simply have been overlooked at lower elevations and different biotopes. Among the spirostreptid millipedes collected in the Taita Hills three species – *Bucinogonus aviceps*, *Tibiozus? vulgaris*, and *Taitastreptus flavipes* – can be considered endemic to this region of Kenya. They are also the only species restricted to forest fragments; the other species are distributed over forest and grassland (*Lophostreptus ptilostreptoides*) or where herb cover is dominant (*Anastreptus scalatus*, *Archispirostreptus gigas*, *Lophostreptus armatus*, and *L. minimus*).

Similarities of the Taita Hills spirostreptid diversity with that in other Eastern Arc montane forests is not very clear because many places were only superficially sampled and many of the small spirostreptids are still undescribed. In so far as diplopods are concerned, only three areas, all in Tanzania, can be considered as reasonably well known: the east Usambaras around Amani, the northern Ulugurus, and the easternmost end of the Uzungwas at Mwanihana (Hoffman 1993). None of the spirostreptid species found in those regions were found in the Taita Hills. In other families like Harpagophoridae (VandenSpiegel and Hoffman 2001) and Ammodesmidae (VandenSpiegel and Golovatch 2003), links with the Usambara Mountain forest occur but only at the generic level.

Male-Based Identification Key to the Spirostreptidae of the Taita Hills, Kenya

1 -Large millipedes (length > 170 mm, maximum diameter > 8 mm); more than 64 body rings; apically posterior coxal fold with a short slanting lateral process; femoral process spined/tasselled.. *Archispirostreptus gigas*

-Small- to medium-sized millipedes (length <170 mm, maximum diameter <8 mm); less than 64 body rings; apically posterior coxal fold not as above; femoral process not spined/tasselled 2

2 -Telopodite apically deeply forked with equally-sized branches........................... *Taitastreptus flavipes*

-Telopodite apically not forked........................... 3

3 -Telopodite with a short spine just before the knee; femoral process laterally attached to telopodite by a thin membrane .... *Tibiozus? vulgaris* sp. n.

-Telopodite without a short spine just before the knee; femoral process not attached to telopodite...... 4

4 -Apically posterior coxal fold bird head-shaped with a short pointed lateral beak, subapically with an ear-shaped projection above the knee; apically anterior coxal fold with a median spine; paracoxite with a depression in the middle.. *Bucinogonus aviceps* sp. n.

-Apically posterior coxal fold bird head-shaped without a short pointed lateral beak, subapically without an ear-shaped projection above the knee; apically anterior coxal fold without a median spine; paracoxite without a depression in the middle 5

5 -Posterior half of body rings with raised longitudinal ridges 6

-Posterior half of body rings without raised longitudinal ridges 7

6 -Preanal ring with a keel in middle; apically posterior coxal fold hammer-shaped; telopodite without a long and helicoidal distal part .... *Calostreptus chelys*

-Preanal ring without a keel; apically posterior coxal fold not hammer-shaped; telopodite with a long and helicoidal distal part............ *Anastreptus scalatus*

7 -Apically posterior coxal fold with a median process that overlaps the opposite process .... *Lophostreptus ptilostreptoides*

-Apically posterior coxal fold without a median process... 8

8 -Maximum body diameter 2 mm; apically posterior coxal fold with a tapering crescent-shaped lateral process pointing towards paracoxite.. *Lophostreptus minimus* sp. n.

-Maximum body diameter 5 mm; apically posterior coxal fold lateral process not crescent-shaped, distal end turned away from paracoxite ......*Lophostreptus armatus*

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CHAPTER 7

Genetic divergence and relationships among selected African millipede genera (Diplopoda: Spirostreptida: Spirostreptidae).

7.1 Abstract

The taxonomy of spirostreptid millipedes is based on male genital morphology; these taxonomies have not been re-assessed using non-morphological characters. The taxonomic validity of the genera *Archispirostreptus* Silvestri 1895, *Bicoxidens* Attems 1928, *Orthoporoides* Krabbe 1982, *Doratogonus* Attems 1914, *Plagiotaphrus* Attems 1914, *Cacuminostreptus* Mwabvu 2010 and *Spirostreptus* Brandt 1833, and intra-specific variation in the widely-distributed *Bicoxidens flavicollis* Attems 1928 were assessed, and relationships among the genera were inferred by analysis of sequences of the mitochondrial 16S rRNA and cytochrome *c* oxidase 1 genes. Bayesian, maximum parsimony and neighbour-joining analyses were performed on each dataset to determine genetic distances and phylogenetic relationships among the taxa. The three analyses (of the same dataset) produced trees that were congruent in structure. Based on these genera, the order Spirostreptida is monophyletic (Bayesian posterior probability 1.00). The high genetic distances among genera (> 20 %) supported taxonomic validity of the genera, including the recently described *Cacuminostreptus*. Although sequence data appear congruent with taxonomies that are based on genitalic morphology, the high mean CO1 inter-generic genetic distance suggests inappropriate taxonomic assignments. In addition, the high sequence divergence also suggests slow genitalic evolution relative to molecular evolution. This further supports the notion that millipede gonopod morphology underestimates species richness. Within the colour-polymorphic *B. flavicollis,* high sequence divergence among populations (16S = 6 %; CO1 = 19.1 %) suggests the presence of cryptic species. Although taxon sampling was limited, these results are largely concordant with morphologic evidence at genus level, indicating that the two types of data could complement each other in application to millipede taxonomy.

7.2 Introduction

Morphology-based taxonomy is extensively used to delimit taxa (Schlick-Steiner *et al.*, 2007), particularly in groups that are poorly known and difficult to identify, such as millipedes (Hamer, 1999; 2000). Despite increasing use of DNA sequence data in invertebrate taxonomy (e.g. Carapelli *et al.*, 2000; Pfenninger *et al.*, 2007; Burns *et al.*, 2008; Hebert *et al.*, 2004), genital/gonopod morphology is still central to spirostreptid millipede taxonomy (e.g. Hoffman, 2008; Hamer, 2009; Mwabvu *et al.*, 2009a; Mwabvu & Van den Spiegel, 2009; Mwabvu *et al.*, 2010) because the divergent male genitalia suggest reproductive isolation (Bond *et al.*, 2003). Therefore, most millipede species are defined on the basis of their genitalic morphology. Although gonopod morphology supports monophyly of genera in the Spirostreptidae (see Hamer, 1999; 2000; Van den Spiegel, 2001; 2004; Mwabvu *et al.*, 2007; 2009b; 2010), morphology may fail to identify cryptic diversity (see Bond & Sierwald, 2002). For example, Bond *et al.* (2003) reported speciation without gonopod divergence in a spirobolid millipede, *Anadenobolus* Karsch. Based on this evidence, morphology-based classifications are being re-evaluated against other character sources because morphology alone could underestimate diversity (see Hebert *et al.*, 2003). For example, DNA sequences identified cryptic species in Lepidoptera genera *Cymothoe* Hüber (van Velzen *et al.*, 2007) and *Perichares* Scudder (Burns *et al.*, 2008), in an ant *Tetramorium* Mayr (Schlick-Steiner *et al.*, 2006), and in a Diptera genus *Chironomus* Meigen (Pfenninger *et al.*, 2007).

Given that morphology fails to separate genetically-distinct species (see Bond & Sierwald, 2002; Bickford *et al.*, 2006, Adams *et al.*, 2009), the use of DNA sequence data to distinguish taxa, identify new species and estimate phylogeny is becoming prominent in systematics (Hebert *et al.*, 2004). However, that DNA may not always reveal cryptic species, particularly those that diverged recently (Pfenninger *et al.*, 2007), lends support to arguments for using more than one type of data in systematics (Dayrat, 2005; Padial *et al.*, 2010). As molecular sequencing techniques become advanced and increasingly available, DNA sequence data (see Tautz *et al.*, 2003; Will *et al.*, 2005) are used increasingly to complement morphology in order to speed up identification (Hajibabaei *et al.*, 2007), improve taxonomic resolution, identify cryptic diversity (Wiemers & Fiedler, 2007; Bond, 2004) and facilitate species delimitation (Lefébure *et al.*, 2006).

Inter-generic, inter-specific and intra-specific genetic variations, and sequence divergence, have not been assessed in African spirostreptid millipedes. However, analysis of the mitochondrial genome, which has relatively fast-evolving molecular markers, has facilitated the study of evolutionary relationships in other taxa (Funk, 1999). Based on the concept that each taxon has a unique and diagnostic sequence, sequences of mitochondrial *cytochrome c oxidase* 1, 16S rRNA and 18S rRNA genes have been used to assess genetic divergence in many taxa. For example, mitochondrial 16S rRNA gene sequences were used in taxonomic studies of the Chilopoda (Edgecombe & Giribet, 2004), the Polydesmida (Marek & Bond, 2007), the Hymenoptera (Dowton & Austin, 1994), the Australian elapid snakes (Keogh *et al.*, 2000), the *Anadenobolus excisus* Karsch millipede species complex (Bond & Sierwald, 2002), the North African toad (Froufe *et al.*, 2009), Madagascan frogs (Vences *et al.*, 2005) and the cichlid fish (Farias *et al.*, 2000).

The present study is a first attempt to use genetics in taxonomic studies of African spirostreptid millipedes. Given that generic and specific boundaries of some taxa are ambiguous, DNA sequences could clarify their taxonomic validity. Although sequence divergence threshold values of 2–3 % have been assigned for insects and mammals (Rubinoff *et al.*, 2006), the levels of sequence divergence and threshold values for designating millipede species need to be determined. Given that systematic data would have implications for conservation decisions (Funk & Richardson, 2002; Bickford *et al.*, 2006) assigning divergence threshold values for millipedes is imperative. Furthermore, using DNA sequences to complement morphological data could lead to better phylogenetic hypotheses, produce stable classifications and resolved phylogenies. Such a combined evidence approach is widely supported (e.g. Page *et al.*, 2005; Dayrat, 2005; Padial *et al.*, 2010), and has been used in taxonomic revisions of other taxa (see Schlick-Steiner *et al.*, 2006).

Given the importance of accurate identification of taxa and reliable phylogenetic hypotheses in biodiversity conservation and the implications for other disciplines, the objective was to determine the extent of genetic differences among selected millipede genera, and to establish whether qualitative morphology-based taxonomic groups are supported by DNA sequence data. Furthermore, I seek to establish whether the order Spirostreptida (represented by the selected genera) is monophyletic and determine the extent of genetic variation in the colour-polymorphic and widely-distributed millipede *B. flavicollis* Attems 1928.

7.3 Materials and Methods

Total genomic DNA was extracted from fresh specimens, frozen specimens and millipedes preserved in 70 % or 100 % ethanol. Fresh specimens of *B. flavicollis*, *B. aridis* Mwabvu 2009, *S. kruegeri* (Attems 1928), *S. sebae* Brandt 1833, *Doratogonus uncinatus* (Attems 1914), *Doratogonus* sp. 1, *Archispirostreptus tumuliporus* (Karsch 1881), *Plagiotaphrus sulcifer* Attems 1914 and *C. mazowensis* Mwabvu 2010 were collected from Zimbabwe; *S. sebae* was collected from Zambia and *S. kruegeri*, *D. cristulatus* (Porat 1872) and *Orthoporoides pyrhocephalus* (Lock 1865) were collected from South Africa (Appendix 2). All specimens were collected by hand, after which the material was preserved in ethanol or frozen at -20° C. Specimens that were collected from Zambia and South Africa are housed in the Natal Museum, Pietermaritzburg, South Africa, and those collected from Zimbabwe are in the Natural History Museum, Bulawayo, Zimbabwe.

Legs removed from the midbody rings of individual specimens were ground using a pestle and mortar. DNA was then extracted following the manufacturer's instructions using the Qiagen DNeasy Blood and Tissue Kit (Qiagen). DNA concentrations were determined using a spectrophotometer (Nanodrop, ND-1000), after which the quality and purity of DNA was inferred from the ratio of absorbance at 260 nm and 280 nm. Good quality DNA was indicated by a ratio in the region of 1.8 (NanoDrop Technical Support Bulletin T009, 2007). Agarose gel electrophoresis was carried out to assess the purity and integrity of DNA which was used as template in polymerase chain reactions (PCR); high quality DNA was indicated by a single high-molecular weight band per sample on the gel, with little smearing. After electrophoresis in 0.5 X TBE (tris-borate-EDTA) as running buffer at 15 V for 16 hours, the 1.5 % (w/v) agarose gel (containing 200 µl of 0.05 mg/ml ethidium bromide) was examined by transillumination with UV light.

Polymerase chain reactions targeting part of the mitochondrial 16S rRNA gene were performed in 25 µl reactions. The reaction mixture was made up of 9 µl DNA solution, 0.8 µl PCR water, 2.5 µl 10 X reaction buffer (Super-Therm), 4 µl magnesium chloride (25 mM) (Super-Therm), 4 µl primer 1 (6 µM), 4 µl primer 2 (6 µM), 0.5 µl of 10 mM deoxyribonucleic triphosphates (dNTP's) (Roche Diagnostics) and 0.2 µl *Taq* polymerase (5 U/µl) (Super-Therm). Optimal PCR conditions were determined by gradient PCR using four different primer sets, two temperature profiles and four DNA: PCR water dilutions of 1:0; 1:1; 1:2 and 1:3. The thermal cycling profile included: [denaturation at 94 ° C for 5 minutes], followed by 36 cycles of [denaturation at 96 ° C for 30 seconds; annealing at 50 ° C to 60 ° C for 1 minute; extension at 72 ° C for 30 seconds] and a final extension at 72 ° C for 7 minutes. Primers for the amplification of 16S rRNA gene were: F1 5'AGGACGTCAAGTCAAGGTGCAGC3' and R1 5'AATCCACCTTCATGATGCACTTC3' (Lavrov *et al.*, 2002); Rhino 16SJB 5'CCATGTATTTGATAAACAGGCA3' and Rhino 16SNC 5'GTGGGGGTATTGGAAAATGTTC3' (Bond & Sierwald, 2002); and Rhino16SJA 5'TTAATCCAACATCGAGGTCG3' and Rhino16SND 5'ATATTGAGATATCTGGTTCTTT3' (Bond & Sierwald, 2002).

A second thermal cycling profile comprised [denaturation at 95 ° C for 5 minutes] followed by 25 cycles of [denaturation at 94° C for 30 seconds; annealing at 50 ° C to 60 ° C for 30 seconds; extension at 72 ° C for 1 minute], with a final extension at 72 ° C for 10 minutes. Primer sets used in conjunction with this profile were: FW-Primer TM-56 5'GATTTAATCCAACATCGAGG3' and RW-Primer TM-55 5'TAATCCAACATCGAGGTC3' (Inqaba Biotechnical Industries (Pty) Ltd, Pretoria, South Africa); Rhino 16SJB 5'CCATGTATTTGATAAACAGGCA3' and Rhino 16SNC 5'GTGGGGGTATTGGAAAATGTTC3' (Bond & Sierwald, 2002); and Rhino16SJA 5'TTAATCCAACATCGAGGTCG3' and Rhino16SND 5'ATATTGAGATATCTGGTTCTTT3' (Bond & Sierwald, 2002).

PCR products were electrophoresed in 1.5 % agarose gels containing 200 µl ethidium bromide (0.05 mg/ml) using 0.5 X TBE buffer at 15 V for 16 hours. The PCR products were viewed with a UV transilluminator (Unitec, BTS-15.M) and DNA bands excised from the gel were preserved at – 20° C. Purification of excised DNA fragments was carried out using a Zymoclean™ Gel Recovery Kit (Zymo Research, USA). Products were sequenced on an ABI 3730 capillary sequencer at Inqaba Biotechnical Industries Pty. Ltd., Hatfield, Pretoria, South Africa. DNA samples that did not amplify after PCR were cloned and sequenced for *cytochrome oxidase* 1 at Inqaba Biotechnical Industries Pty. Ltd., Hatfield, Pretoria, South Africa.

Raw sequences were edited in BioEdit version 7 (Hall, 1999), and aligned using the Clustal W algorithm in BioEdit, and by inspection. The alignments were trimmed to 684 nucleotides of mitochondrial 16S rRNA gene and 520 nucleotides of the mitochondrial *cytochrome oxidase* 1 gene, respectively. Saturation analyses were carried out in Dambe (Xia & Xie, 2001) to evaluate the levels of homoplasy and to establish the reliability of the datasets as indicators of phylogenies. Saturation results in an underestimation of the true number of substitutions in a sequence and is caused by the occurrence of multiple substitutions (among other factors) at the same site (Xia & Xie, 2001). A default model (F84) was used by DAMBE to correct for underestimation of substitutions. Bayesian, maximum parsimony and neighbor-joining analyses were performed to determine genetic distances and phylogenetic relationships among the taxa. Modeltest (Posada & Crandall, 1998) was used to select the model of nucleotide substitution which best fitted each sequence dataset. The general time-reversible (GTR) model was selected using the Akaike Information Criterion (AIC) for both the 16S rRNA and *cytochrome oxidase* 1 datasets, and was used subsequently in Bayesian and neighbour-joining analyses. Neighbour-joining and maximum parsimony analyses were implemented in PAUP (Swofford, 2002). Genetic distances are presented as distance matrices and as neighbour-joining trees trees, which were bootstrapped using 1000 pseudo-replicates. For parsimony analysis, the random additions sequence option (n = 100) for discrete, unordered characters was used. The shortest tree was obtained using the heuristic search option under the tree bisection-reconnection (TBR) branch swapping option. The degree of support for each node of the resulting tree was estimated using bootstrap re-sampling analysis (1000 pseudoreplicates; Felsenstein, 1985). Bayesian analysis was implemented in Mr Bayes 3.0 (Hulsenbeck & Ronquist, 2001) using flat priors. For all analyses, four Markov chains were run for 5 million generations each, and the first 500,000 trees discarded as burn-in. A preliminary run was carried out in order to determine that the burn-in value was sufficiently high to discard all less-likely trees generated before the likelihoods had stabilised. Outgroup sequences of taxa belonging to the Orders Spirobolida (*Narceus* sp. and *Anadenobolus excisus*), Callipodida, Julida, Polyxenida (*Unixenus* sp.) and Spirostreptida (Harpagophoridae: *Thyropygus* sp.) were obtained from the NCBI GenBank database.

7.4 Results

Extracted DNA concentrations differed among species and ranged from 2.81 to 105.17 ng/ µl (Appendix 1). DNA of good quality was obtained only from fresh specimens and from material which had been preserved for less than 5 years.

The ideal annealing temperature range was between 53 and 55 ° C for the samples that amplified. Where amplification was successful, the best PCR results were obtained using a 1: 1 dilution of isolated DNA and PCR water, and the following temperature profile: [5 minutes denaturation at 95 ° C], of 25 cycles of [30 seconds denaturation at 94° C, 30 seconds annealing at 55 ° C, 1 minute extension at 72 ° C], and [a final extension at 72°C for 10 minutes]. The primers used were: Rhino 16SJB-CCATGTATTTGATAAACAGGCA and Rhino 16SNC-GTGGGGGTATTGGAAAATGTTC (Bond & Sierwald, 2002) and FW-Primer: 5-GATTTAATCCAACATCGAGG-3TM-56 and RW-Primer: TAATCCAACATCGAGGTC TM-55 (Inqaba Biotechnical Industries (Pty) Ltd).

Most DNA samples did not amplify despite repeated attempts. Some samples which amplified proved difficult to sequence, even when these fragments were cloned prior to sequencing. Samples of only three species (*B. flavicollis*, *C. mazowensis* and *A. tumuliporus*) were successfully amplified and sequenced for 16S rRNA region. Samples of 12 species (*B. flavicollis, B. aridis, D. cristulatus, Doratogonus* sp. 1, *D. uncinatus, O. pyrhocephalus, P. sulcifer, C. mazowensis, S. sebae, S. kruegeri, A. tumuliporus* and *A. gigas*) were cloned and sequenced for CO1.

Although there was some saturation in transitions, but no saturation in transversions, the test of Xia *et al.* (2003) for substitution saturation indicated little saturation in the CO1 dataset

(Fig. 1), and that it was useful for phylogenetic analysis. With respect to the 16S dataset, there appeared to be little saturation in the ingroup (Spirostreptida) dataset (F84 distance < 0.41), although there was some saturation associated with the outgroups which are separated by higher genetic distances (> 55 %) (Fig. 2).The test of Xia *et al.* (2003) for substitution saturation indicated little saturation in the dataset, which makes 16S a useful gene for phylogenetic analysis of this dataset.

All the sequences were very divergent and the genetic distances were high (Table 1 & 2). The mean CO1 intra-specific genetic distance for *Bicoxidens* species was 17.64 % and the mean inter-specific distance in *Archispirostreptus*, *Doratogonus* and *Spirostreptus* species was 14.87 % (Fig. 5). The genera *Bicoxidens*, *Archispirostreptus*, *Doratogonus*, *Orthoporoides*, *Plagiotaphrus*, *Cacuminostreptus* and *Spirostreptus* had a mean inter-generic distance of 21.26 % and the mean inter-order genetic distance was 28.51 % (Fig. 5). There was a large degree of overlap between the categories of genetic distances (Fig. 5). As expected, genetic distance increased with taxonomic distance, with the exception of the intra-specific and inter-specific comparisons. The mean intra-specific genetic distance for *Bicoxidens* species was higher than the mean inter-specific genetic distance in the *Archispirostreptus*, *Doratogonus* and *Spirostreptus* group. Both CO1 and 16S genetic distances for *B. flavicollis* A and C, and *B. flavicollis* D and C, respectively, were higher than expected (Table 1 & 2; Figs 1, 2 & 5).

There was high bootstrap support for all the major clades and there was some degree of congruence between the trees (Figs 3 & 4). Both the CO1 and 16S sequence datasets showed that the orders are distinct taxa (Figs 3 & 4). Bayesian, maximum parsimony and neighbour-joining analyses based on 520 nucleotides of the mitochondrial CO1 gene provided support for the monophyly of the Spirostreptida (Bayesian posterior probability 1.00, maximum parsimony bootstrap 87 % and neighbour-joining bootstrap 92 %). The monophyly of the Spirostreptida was even more strongly supported (Bayesian posterior probability 1.00, maximum parsimony bootstrap 100 % and neighbour-joining bootstrap 100 %) by the 16S rRNA dataset. Within the Spirostreptida clade, support for the *Doratogonus* subclade was good (Bayesian posterior probability 0.95 and neighbour-joining bootstrap 92 %), unlike for the unsupported and unresolved sister subclade which contained the Spirostreptidae species *B. aridis, B. flavicollis, O.*

pyrhocephalus, P. sulcifer, C. mazowensis, S. sebae, S. kruegeri, A. tumuliporus and *A. gigas*, and a harpagophorid genus *Thyropygus*. Based on the CO1 tree (Fig. 3) the genus *Bicoxidens* appears paraphyletic, *Bicoxidens flavicollis* occured in both clades, contrary to the results based on the 16S rRNA gene. *Plagiotaphrus sulcifer* and *A. tumuliporus* were distinct and well-supported lineages (Bayesian posterior probability 1.00, maximum parsimony bootstrap 100 %, neighbour-joining bootstrap 100 %).

Bayesian, maximum parsimony and neighbour-joining analyses based on 684 nucleotides of the mitochondrial 16S rRNA gene also provided strong support for the monophyly of the millipede orders Spirostreptida and Spirobolida: (Bayesian posterior probability 1.00, maximum parsimony bootstrap 100 % and neighbour-joining bootstrap 100 %). The strongly-supported Spirostreptida clade further formed strongly supported sister subclades. One of these contains *C. mazowensis* and a strongly-supported sister-group comprising *A. tumuliporus* and the harpagophorid *Thyropygus* sp.; the other clade contained the widely-distributed and colour-polymorphic *B. flavicollis*, which was further subdivided into two strongly-supported *B. flavicollis* sister clades separated by a mean 16S genetic distance of 6.6% (Table 2). The *Cacuminostreptus-Archispirostreptus-Thyropygus* subclade (Bayesian posterior probability 1.00, maximum parsimony bootstrap 100 % and neighbour-joining bootstrap 100 %) was consistent with the relationships observed in the CO1 tree. A 16S genetic distance of 21 % (Table 2) provides support for the genetic distinctiveness of *Cacuminostreptus* and *Archispirostreptus*.

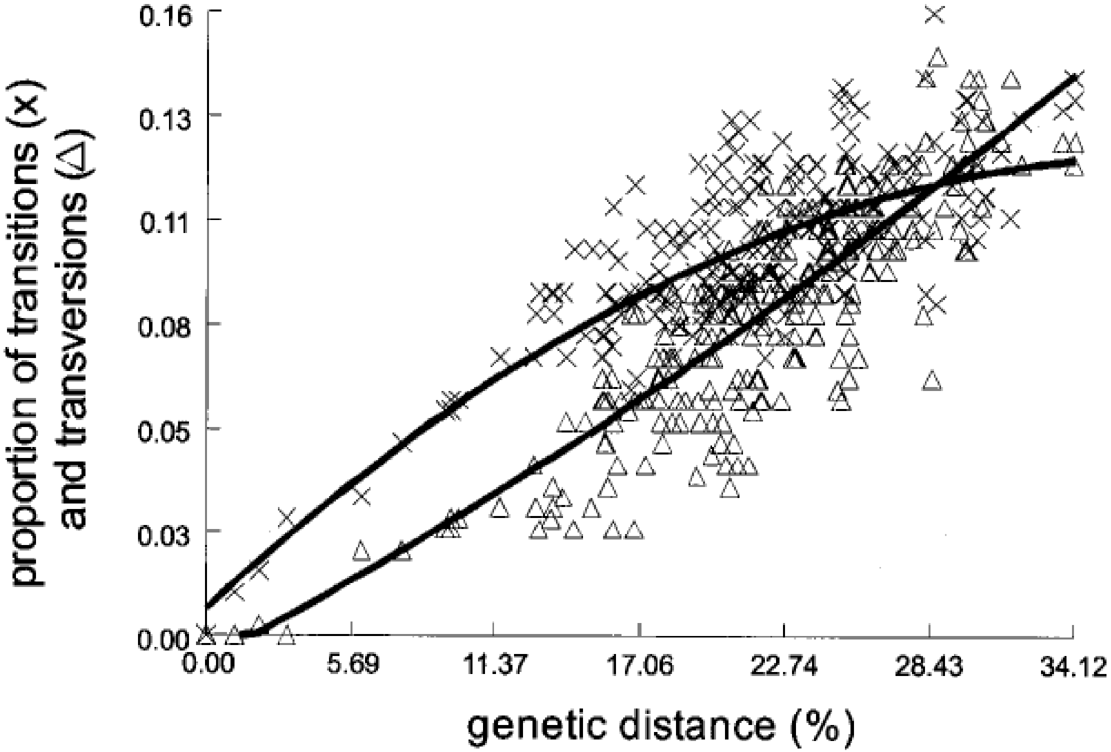

Figure 1: Saturation plot of a dataset comprising 520 nucleotides of the mitochondrial *cytochrome oxidase* 1 gene created in DAMBE (Xia & Xie, 2001).

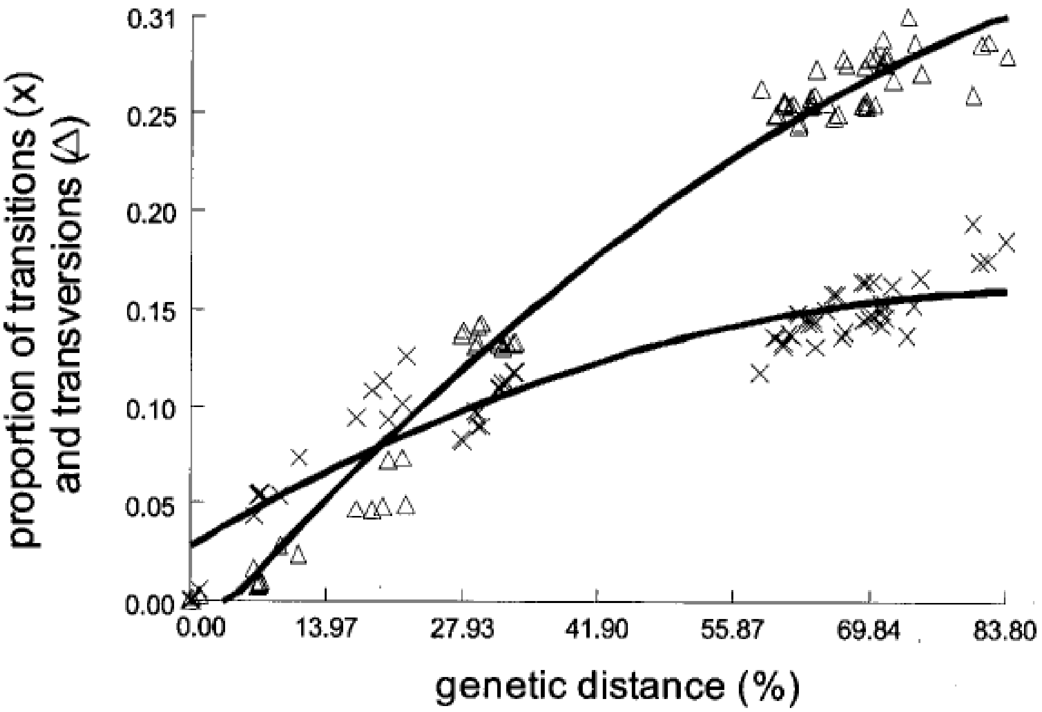

Figure 2: Saturation plot of a dataset comprising 684 nucleotides of the mitochondrial 16S rRNA gene created in DAMBE (Xia & Xie, 2001).

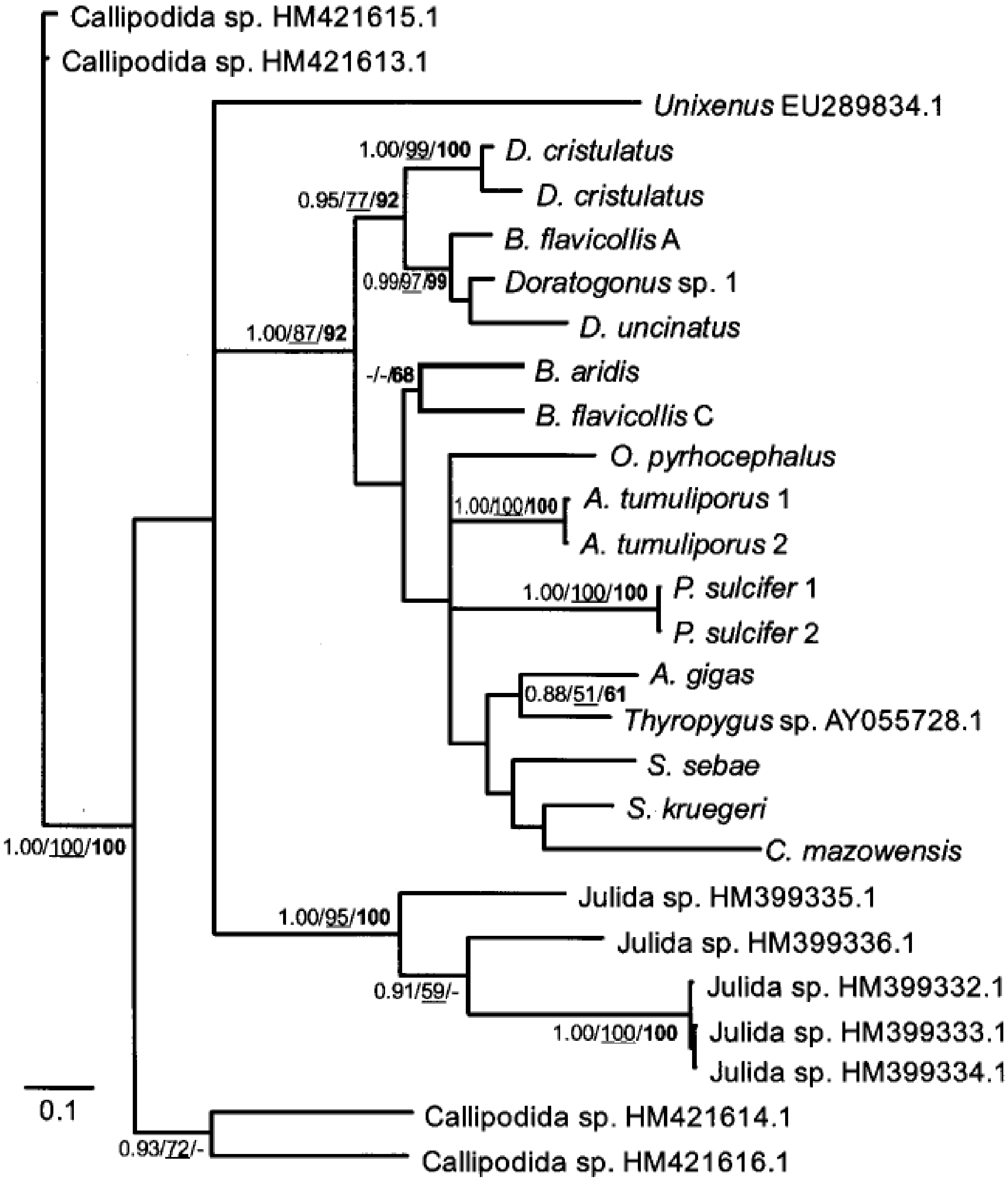

Figure 3: Bayesian Inference tree based on analysis of 520 nucleotides of the mitochondrial *cytochrome oxidase* 1 gene showing relationships between Spirostreptida species and outgroups Julida, Callipodida and Polyxenida (*Unixenus*) species. Numbers next to each outgroup are GenBank Accession numbers. This tree was congruent in structure with maximum parsimony

and neighbour-joining analyses of the same dataset. Nodal support values are indicated as (posterior probability, maximum parsimony bootstrap, **neighbour-joining bootstrap**). The scale bar (0.1) indicates the number of substitutions per site.

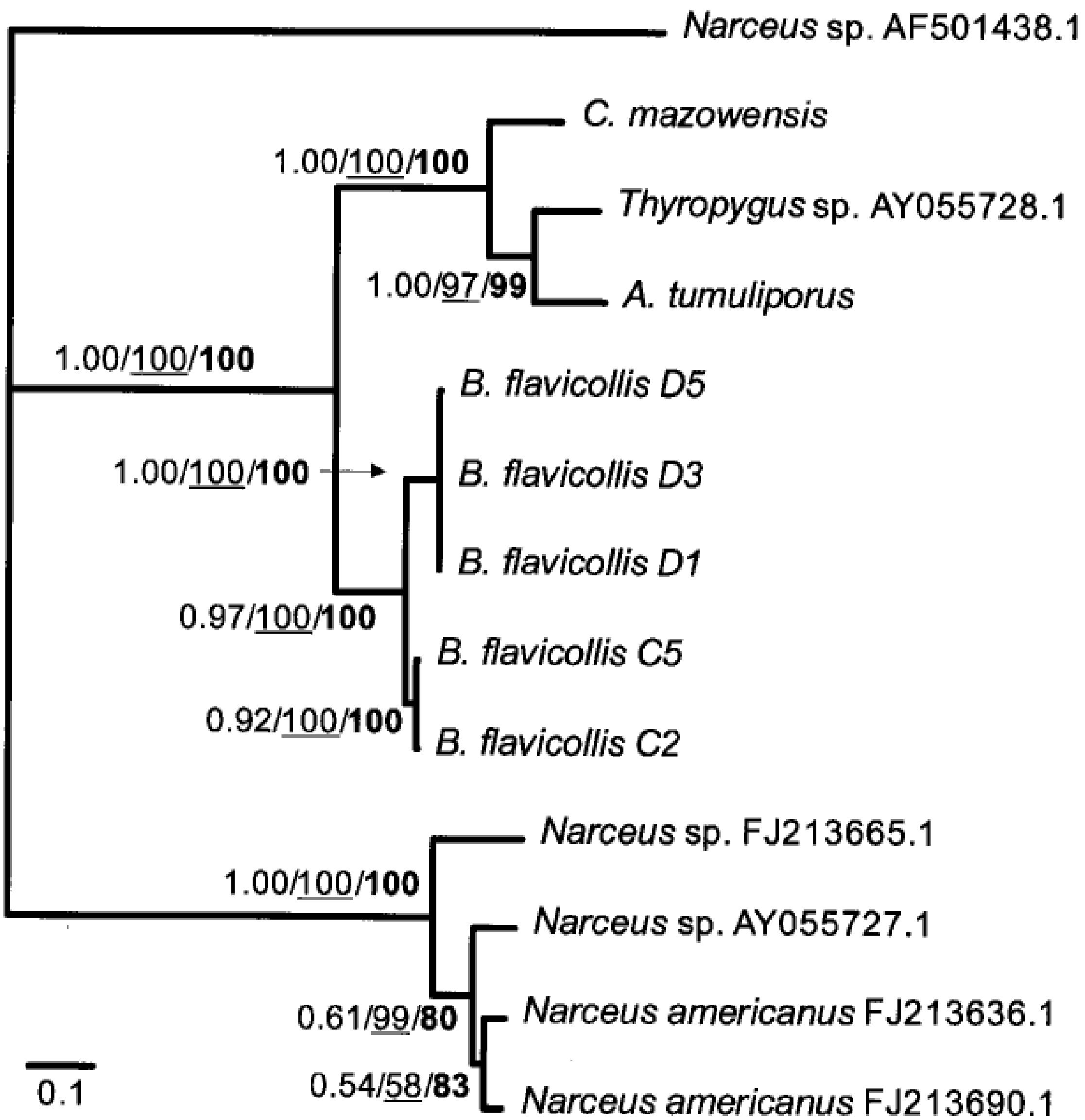

Figure 4: Bayesian Inference tree based on analysis of 684 nucleotides of the mitochondrial 16S rRNA gene showing relationships between Spirostreptida species and outgroups Spirobolida (*Anadenobolus* and *Narceus*) species. Numbers next to each outgroup are GenBank Accession numbers. This tree was congruent in structure with maximum parsimony and neighbour-joining analyses of the same dataset. Nodal support values are indicated as (posterior probability, maximum parsimony bootstrap, **neighbour-joining bootstrap**). The scale bar (0.1) indicates the number of substitutions per site.

Table 1: Pairwise comparisons of genetic divergence between spirostreptid species and the outgroups indicated by general time-reversible genetic distances (%) based on analysis of 520 nucleotides of the mitochondrial *cytochrome oxidase* 1 gene.

	Ag	At	Ba	BfA	BfC	Dc	D1	Du	Op	Ps	Sk	Ss	Cm	Th	Un	Ju
Ag																
At	19.47															
Ba	22.70	18.12														
BfA	20.90	20.20	17.76													
BfC	19.26	18.56	16.08	19.09												
Dc	24.34	21.97	16.64	13.95	20.69											
D1	23.06	21.43	19.19	7.48	20.57	11.58										
Du	28.79	24.77	24.10	13.20	27.59	16.79	10.10									
Op	23.19	18.64	18.94	22.28	21.72	16.32	20.33	25.00								
Ps	22.56	20.72	20.11	27.09	24.56	22.42	25.91	29.66	21.26							
Sk	16.75	17.99	19.85	16.81	19.28	17.78	17.20	21.31	16.27	23.12						
Ss	23.80	18.70	21.67	20.19	22.93	22.30	20.20	26.11	21.26	24.10	16.42					
Cm	28.29	22.49	25.84	25.77	25.23	23.07	21.16	21.49	19.99	23.33	19.10	18.48				
Th	16.86	18.55	18.91	19.79	22.41	20.37	20.39	25.10	19.26	21.94	17.34	20.10	22.10			
Un	33.39	30.17	29.44	30.07	32.91	28.98	29.99	36.14	31.13	31.60	29.87	32.49	29.88	31.69		
Ju	30.58	28.15	30.60	30.92	30.73	29.78	31.87	36.40	30.63	34.19	29.42	32.15	29.28	32.38	35.88	
Ca	28.42	31.06	33.34	28.23	29.36	30.05	28.83	32.92	30.29	33.62	28.77	33.58	30.02	26.64	30.85	29.37

Abbreviations: Ag, *A. gigas*; At, *A. tumuliporus*; Ba, *B. aridis*; BfA, *B. flavicollis* A; BfC, *B. flavicollis* C; Dc, *D. cristulatus*; D, *Doratogonus* sp. 1; Du, *D. uncinatus*; Op, *O. pyrhocephalus*; Ps, *P. sulcifer*; Sk, *S. kruegeri*; Ss, *S. sebae*; Cm, *C. mazowensis*; Th, *Thyropygus* sp.; Un, *Unixenus* sp.; Ju, Julida; Ca, Callipodida

Table 2: Pairwise comparisons of genetic divergence between *B. flavicollis*, *C. mazowensis*, *A. tumuliporus* and the outgroups indicated by general time-reversible genetic distances (%) based on 684 nucleotides of the mitochondrial 16S rRNA gene.

	Th	Cm	BfD5	BfD3	BfD1	BfC5	BfC2	At	Nam	Ng	Nan
Th											
Cm	19.66										
BfD5	31.91	29.43									
BfD3	31.69	29.21	0.15								
BfD1	31.69	29.21	0.15	0.00							
BfC5	29.00	27.21	6.66	6.50	6.50						
BfC2	28.85	27.03	6.48	6.30	6.32	1.54					
At	16.83	21.00	32.99	33.21	33.21	31.83	31.33				
Nam	72.43	60.89	67.26	66.88	66.88	63.40	63.46	65.23			
Ng	76.86	65.75	70.29	69.93	69.93	71.62	70.78	73.14	18.77		
Nan	72.34	60.78	64.18	63.81	63.81	61.62	61.64	67.73	11.24	22.23	
Ae	74.65	73.00	71.34	71.74	71.74	69.19	69.19	70.89	81.92	80.89	82.35

Abbreviations: Th, *Thyropygus* sp.; Cm, *C. mazowensis*; BfD5, *B. flavicollis* D5; BfD3, *B. flavicollis* D3; BfD1, *B. flavicollis* D1; BfC5, *B. flavicollis* C5; BfC2, *B. flavicollis* C2; At, *A. tumuliporus*; Nam, *N. americanus*; Ng, *N. gordanus*; Nan, *N. annularis*; Ae, *A. excisus*

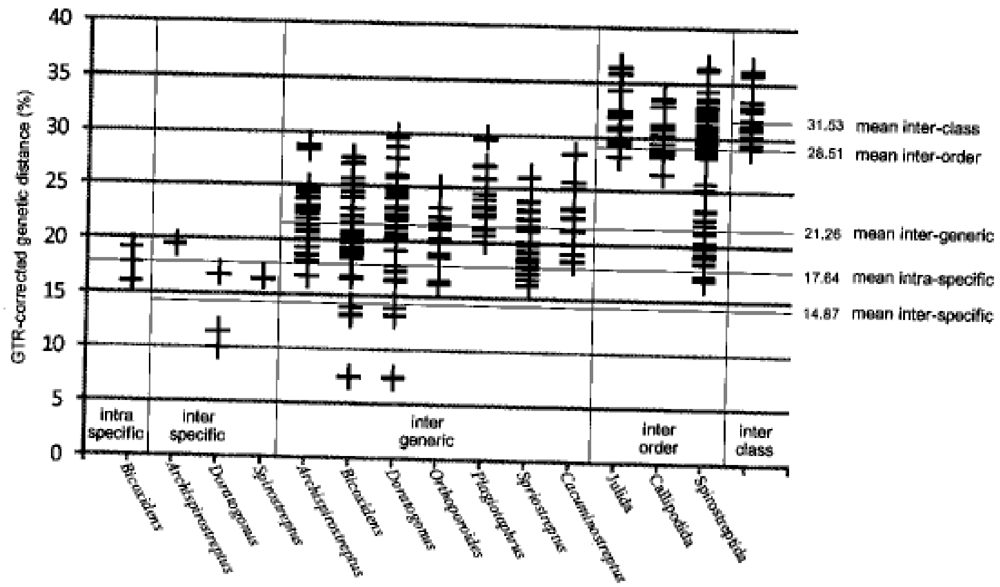

Figure 5: Comparisons of genetic distances separating millipede taxa at inter-specific, inter-generic, inter-order and intra-class level based on analysis of 520 nucleotides of the mitochondrial *cytochrome oxidase* 1 gene. This figure is based on an analysis of the distances in Table 1.

7.5 Discussion

Despite recent advances in molecular techniques, the need for fresh material for good quality DNA extraction and sequencing (Carvalho & Vieira, 2000) may be necessary because preserved specimens are unsuitable for sequencing (Meier, 2008). In this study, DNA of good quality could only be extracted from fresh specimens or millipedes which had been preserved in ethanol for less than five years. This implies that taxa of uncertain taxonomic status and other preserved specimens, including those which have been collected once only, can not be studied using molecular tools, thus hinder phylogenetic studies of the taxa. In addition to this, many museum specimens could not be used in DNA extraction because they were considered valuable (Meier, 2008), further reducing the size of the sample available for molecular work. Furthermore, DNA extracted from most specimens did not amplify despite repeated attempts using different primer sets, different temperature profiles and several DNA concentrations. This was probably a result of the poor quality of extracted DNA, or inhibition of PCR. Meier (2008) reported that ethyl acetate which is used to kill insects and formaldehyde which is used as a preservative degrade DNA, and result in low amplification of DNA. Although these chemicals were not used in this study, several other chemicals and conditions could have affected the quality of extracted DNA. The defensive secretions that are produced by millipedes (Hopkin & Read, 1992; Huth, 2000; Arab *et al.*, 2003), the length of time that specimens had been preserved and the method of preservation are factors that could have reduced the quality of DNA, and could explain the lack of gene amplification and sequencing in most specimens. Unfortunately, these variables could not be controlled in this study because preserved specimens were borrowed from museums where they were kept under different conditions.

Most millipedes produce defensive secretions; the Spirostreptida produce mainly benzoquinones (Hopkin & Read, 1992; Huth, 2000; Arab *et al.*, 2003), whilst the Polydesmida produce hydrogen cyanide (Arab *et al.*, 2003). The chemistry of the secretions differs among taxa (Hopkin & Read, 1992) and between sexes (Huth, 2000). Huth (2000) reported that males tended to have higher proportions of certain quinones than females. This could be a critical factor considering that only males were used in this study, because species identification requires using male genitalia (Hamer, 1999). These chemicals could have affected the quality of DNA, or inhibited amplification of DNA. Therefore, the quality of DNA and success of PCR could depend on the taxa, the sex, duration of preservation and the method of preservation (see Carvalho & Vieira, 2000). In addition, the temperature at which preserved specimens were kept could have affected the quality of DNA (see Carvalho & Vieira, 2000). As such, more work on preservation methods, optimizing PCR and the possible influence of chemical secretions on PCR, is required before DNA methods can be fully exploited for millipede taxonomy.

The saturation analyses plots showed that both CO1 and 16S rRNA genes are useful genetic markers in spirostreptid taxonomy and provide useful phylogenetic signals. Whether these genetic markers are the most phylogenetically informative in millipedes require investigation. The view that CO1 sequences allow discrimination of fauna, and that the CO1 gene can be a universal marker (Hebert *et al.*, 2003; Lefébure *et al.*, 2006), is widely disputed because morphologically distinct species could have similar CO1 sequences (Wiemers & Fiedler, 2007; Meier *et al.*, 2006). In addition, Vences *et al.* (2005) demonstrated that 16S rRNA was a better marker than CO1 in amphibians, and proposed its use in vertebrates. In some taxa, DNA sequences are not sufficiently divergent, or may be too divergent to differentiate species (Meier *et al.*, 2006). Besides these opposing views, other debates are on the suitability of maternally inherited mitochondrial genes when nuclear sequences could be used (Meier, 2008), the fact that 16S is easier to amplify and that CO1 evolves faster than 16S (Lefébure *et al.*, 2006).

Although the datasets were of different sizes, taxa belonging to the same Order clustered together, as expected, in both the CO1 and 16S DNA phylogenetic trees. In general, clustering of the genera in the trees are consistent with classifications based on genital morphology. Both the CO1 and 16S DNA sequences illustrated that the Spirostreptida is monophyletic, and that the genera (in this study) are genetically distinct. However, whether morphologic and genetic divergences are coupled is unclear. The high CO1 and 16S sequence divergences (> 20 %) between the genera also supported the erection of the new genus *Cacuminostreptus* (see Mwabvu *et al.*, 2010). Concordance between morphological and sequence data demonstrates that gonopod morphology is a reliable index of taxon validity in spirostreptids. Because proposed names of taxa are hypotheses, they are considered reliable when different types of data are congruent (Padial & De la Riva, 2010). Concordance between the different types of characters makes taxonomic data widely accepted and reliable, which benefits biodiversity conservation planning, especially in millipedes, with many species local or site endemics (Hamer & Slotow 2002), making them IUCN threatened (Hamer, 2009) and prioritizing them for conservation.

It is interesting that *Thyropygus* sp. and *Archispirostreptus* have a sister group relationship in both trees, although genital morphology-based taxonomy places the two genera in different families, Harpagophoridae and Spirostreptidae, respectively. However, at this stage it is premature to question the relationship based on genital morphology because of inadequate sequence comparisons among the taxa. More importantly, *A. gigas* and *A. tumuliporus* do not form a subclade within the Spirostreptida clade although based on gonopod morphology they are congeneric; this was unexpected. Although inter-specific (but intra-generic) genetic divergence of 22.60 % is high, it is difficult to explain their separation because all the species in the genus were not studied, and intra-specific variations were not determined. However, given lower intra-generic sequence divergence (< 10 %) in the Lepidoptera *Cymothoe* (Van Velzen *et al.*, 2007), the two species may possibly belong in different genera. Furthermore, the large degree of overlap in different categories of CO1 genetic distances indicates that genetic and morphological variations are not correlated, and that some taxonomic assignments could be incorrect. Therefore, there is need to increase taxon sampling in order to assess intra-generic and intra-specific divergence in the group.

The occurrence of a strongly-supported clade in the CO1 phylogeny containing *Bicoxidens flavicollis* A, *Doratogonus uncinatus* and *Doratogonus* sp. 1 was unexpected because the two genera have distinct gonopods. In the phylogeny, *Bicoxidens* is not monophyletic, with *B. flavicollis* C and *B. aridis* occurring in a distinct, although very poorly-supported clade. *B. flavicollis* is a colour-polymorphic and widely-distributed species (Mwabvu *et al.*, 2007). The CO1 genetic distance separating *B. flavicollis* forms A and C (19.09%) is larger than the mean inter-specific distance (14.87%); in the 16S dataset, *B. flavicollis* C and D form a well-supported clade. Thus the notion that *B. flavicollis* A, D and C are distinct species warrants further investigation. Comparable data from the 16S rRNA region is unfortunately not available, as this region did not sequence successfully for *B. flavicollis* A. The high CO1 genetic distances among *Bicoxidens* species (*B. aridis*, *B. flavicollis* A and *B. flavicollis* C) and high 16S genetic distances between *B. flavicollis* C and D samples (6.66 %) suggest the existence of more than one species or genera. The presence of cryptic species in *Bicoxidens* would be supported by Lefébure *et al.* (2006), who proposed designation of species in Crustacea using CO1 divergence threshold of below 16 %. In addition, compared to intra-specific divergence values of below 2 % from several phylogeographic studies (see Bond, 2004), genetic variability among specimens of *B. flavicollis* was high. Therefore, if 2 % divergence is used as a threshold value for species designation genetic distance of 6 % further supports the presence of a cryptic species which could not be identified using genitalic morphology. The high genetic variability in *Bicoxidens* is not surprising because the species are small-bodied, with poor dispersal ability (Mwabvu *et al.*, 2007), and as they tend to have very narrow distributions, there is presumably restricted gene flow.

As previously mentioned, the 16S tree separates *Bicoxidens* into a clade, however, there is no congruency with the CO1 tree which places specimens of *B. flavicollis* (from different localities and with indistinguishable gonopods) in separate clades. Incongruency between the trees could be explained, in part, by the differences in the rates of evolution of the genes (Lefébure *et al.*, 2006) and the different sizes of the datasets. Therefore, taxon sampling should increase and further investigations into the suitability of the genes that are used currently are required because some genetic markers may be suitable for specific taxa (see Vences *et al.*, 2005)

Although DNA samples proved difficult to amplify or clone and sequence, even after repeated attempts, which resulted in fewer taxa being studied, sequence data are useful in spirostreptid taxonomy. Sequences demonstrated a general increase in divergence with increasing taxonomic level as indicated by the mean inter-specific, inter-generic and inter-order genetic distances. Greater genetic distinctiveness among taxa than expected emphasises the need to review taxonomies based on gonopod morphology. Because gonopod morphological change may not be correlated with genetic change (Adams *et al.*, 2009) morphological species might be hiding considerable levels of cryptic variation.

Besides increasing taxon sampling, more work on genetic marker selection, DNA amplification and sequencing more taxa is required before sequences can be fully utilised in spirostreptid taxonomy. Adding sequences of more taxa to datasets could resolve phylogenies and provide a clearer picture of the phylogenetic relationships in the Spirostreptida. Although the use of sequences contributes to improved taxonomies, Rubinoff *et al.* (2006) argue that DNA sequences can not be used alone because they rely on morphological and ecological data to identify specimens, and because no single threshold genetic distance can be assigned to designate species in different groups. Their view further reinforces the importance of integrative taxonomy (see Padial & De la Riva, 2010). In spirostreptid millipedes, clear inter-generic and intra-generic phylogenetic relationships can only be established once more sequences become available.

Future research could include a phylogeographic study of the Spirostreptida and investigate levels of genetic variation in the genera, that is, after taxonomic revisions of the genera. Molecular research could reveal greater cryptic diversity and high levels of intra-specific genetic variation in these genera after complete taxon sampling and sequencing. It is critical that reliable and corroborated systematic data are available for use in biodiversity assessment and conservation planning before species become extinct. Therefore, extensive sampling throughout the distribution range of the taxa has to be conducted. Until more samples are studied using different types of data, species delimitation, biogeographical trends and threats to millipedes will be difficult to determine. Furthermore, research should clarify the possible influence of preservation methods and millipede defensive secretions on DNA quality and amplification. This is critical because many taxa may be extinct or have been collected once, thus leaving museum specimens as the only source of material for genetic studies. In addition, the potential of defensive secretions in chemo-taxonomy could also be investigated to establish whether they are sufficiently distinct to differentiate taxa.

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Appendix 1: List of taxa from which DNA was extracted, DNA concentrations, year of collection and preservation method. Appendix 2 gives details of where the specimens are housed.

Taxon	**Year**	**Preservation**	**DNA concentration (ng/ul)**
A. tumuliporus	2007	70 % ethanol	26.88
A. divergens	1977	70 % ethanol	16.53
A. gigas	2000	Ethanol	16.59
B. aridis	1997	70 % ethanol	25.60
B. nigerrimus	1994	Ethanol	13.50
B. brincki	1994	70 % ethanol	11.63
B. nyathi	1994	70 % ethanol	4.66
B. matopoensis	1985	70 % ethanol	11.55
B. flavicollis	1991	Ethanol	7.54
B. flavicollis	2008	100 % ethanol	13.00
B. flavicollis	2009	100 % ethanol	79.30
C vumbaensis	2008	100 % ethanol	19.43
C. triangulatus	1989	70 % ethanol	13.68
C. mazowensis	2007	100 % ethanol	18.36
C. conatus	1996	70 % ethanol	27.00
Calostreptus	2008	100 % ethanol	9.00
Doratogonus sp.1	2008	100 % ethanol	41.80
D. uncinatus	2008	100 % ethanol	75.35

D. cristulatus	2008	100 % ethanol	6.59
O. pyrhocephalus	2008	100 % ethanol	3.36
N. kymatorhabdus	1978	Unknown	5.59
P. sulcifer	1997	70 % ethanol	21.52
S. unciger	1961	Unknown	2.81
S. tripartitus	1975	Unknown	------
S. batokensis	1995	70 % ethanol	23.62
S. heros	2005	70 % ethanol	64.34
S. kruegeri	2009	100 % ethanol	83.06
S. sebae	2008	100 % ethanol	82.17
Z. munda	2008	100 % ethanol	21.47

Appendix 2: List of specimens from which DNA was extracted, museum housing the specimens and accession numbers (or museum housing the specimens if the specimens are uncatalogued), geographical coordinates and localities.

Taxon	**Accession #**	**Coordinates**	**Locality, Country**
A. tumuliporus	NMSA21941	18^{0}57'S, 32^{0}27'E	Marange, Zimbabwe
A. divergens	ZMUC	0^{0}59'N, 36^{0}03'E	Lake Baringo Lodge, Kenya
A. gigas	MRAC20254	03° 25' S, 38° 46'E	Tsavo, Kenya
B. aridis	NMZ/D819	1630B1	Mushumbi Pools, Zimbabwe
B. nigerrimus	NMZ/D753	2030A4	Taru Dam, Zimbabwe
B. brincki	NMZ/D756	2230A4	Pande Mine, Zimbabwe
B. nyathi	NMZ/D747	2030B4	Mudzwiru River, Zimbabwe
B. matopoensis	NMZ/D356	2129A4	Doddieburn, Zimbabwe
B. flavicollis	NMZ/D648	2032D1	Maguge, Mozambique
B. flavicollis	NMZ	18^0 40'S, 31^{0}30'E	Chihota, Zimbabwe
B. flavicollis	NMZ	18°30'S, 32°30'E	Muterere, Mutasa, Zimbabwe
C vumbaensis	NMSA21937	18^0 12'S, 32^0 43'E	Zindi, Zimbabwe
C. triangulatus	NMZ/D568	1631A3	Mavuradona, Zimbabwe
C. mazowensis	NMSA21944	17^0 49'S, 31^0 02'E	Highlands, Zimbabwe
C. conatus	NMZ/D844	2231A2	Beitbridge, Zimbabwe
Calostreptus	NMZ	17^0 30'S, 30^0 58'E	Mazowe Dam, Zimbabwe
Doratogonus sp.1	NMZ	18^0 40'S, 31^{0}30'E	Chihota, Zimbabwe
D. uncinatus	NMZ	17^0 30'S, 30^0 58'E	Mazowe Dam, Zimbabwe

D. cristulatus	NMSA	29^{0} 51'S, 30^{0} 58'E	PigeonValley, Dbn,
O. pyrhocephalus	NMSA	29^{0} 51'S, 30^{0} 58'E	Pigeon Valley, Dbn, SA
N. kymatorhabdus	ZMUC	22^{0}32'S, 17^{0}41'E	Daan Viljoen Game Park, Nm
P. sulcifer	NMZ/D830	16^{0}S, 30^{0}E	Mushumbi Pools, Zimbabwe
S. unciger	NMSA8896	25^{0}44'S, 28^{0}11'E	Pretoria, South Africa
S. tripartitus	ZMUC	12^{0}33'S, 13^{0}24'E	Egito, Angola
S. batokensis	NMZ/D835	1726C3	Batoka Gorge, Zimbabwe
S. heros	NMZ/D835	22^{0}02'S, 30^{0} 00'E	Beitbridge, Zimbabwe
S. kruegeri	NMZ	20^{0}56'S, 29^{0}00'E	Gwanda, Zimbabwe
S. sebae	NMSA21967	19^{0}00'S, 32^{0}40'E	Marange, Zimbabwe
Zinophora munda	NMZ	17^{0} 30'S, 30^{0} 58'E	Mazowe Dam, Zimbabwe

Abbreviations:

MRAC - Royal Museum of Central Africa, Tervuren, Belgium

NMSA - Natal Museum, Pietermaritzburg, South Africa

NMZ - Natural History Museum, Bulawayo, Zimbabwe

ZMUC - Natural History Museum (Zoological Museum), University of Copenhagen, Copenhagen, Denmark

Dbn - Durban

Nm - Namibia

SA - South Africa

N - *Namibostreptus*

CHAPTER 8

GENERAL DISCUSSION & CONCLUSION

8.1 Introduction

Taxonomic revisions of the spirostreptid genera *Bicoxidens, Plagiotaphrus, Spirostreptus* and *Archispirostreptus* stabilised their taxonomy, and corroborated Hamer's (2000) observations that the Spirostreptidae contains poorly defined and heterogeneous genera, with many endemic and undescribed species. In addition, the geographical distributions of the genera are poorly known and the levels of endemism have not been determined. The results also demonstrated that genitalic morphology discriminated genera. Furthermore, DNA gene sequence divergences illustrated expected increase with taxonomic level and generic divergences were concordant with classifications based on genitalic morphology. The results of the molecular study, which was the first on Southern African spirostreptid genera, support increased future use of DNA sequences to identify cryptic species and determine phylogenetic relationships among taxa.

8.2 Taxonomic changes in the genera

Taxonomic revisions often result in taxonomic inflation, that is, an increase in the number of recognized taxa after splitting inclusive groups (Isaac *et al.*, 2004; Garnett & Christidis, 2007; Morrison III *et al.*, 2009). The results of this study illustrated that, in millipedes, the number of known species increased mostly due to new discoveries in previously unsurveyed biomes, rather than due to taxonomic inflation (see Mwabvu *et al.*, 2007; 2009a; 2009b; Mwabvu *et al.*, 2010). Padial and Dela Riva (2006) also reported that increases in the number of amphibian species were mainly a result of new discoveries rather than taxonomic inflation. This further supports the view that most of the earth's biological diversity has not been discovered (see Gaston & Spicer, 1998) and puts into context the estimate of 12 % millipede species having been described (Sierwald & Bond, 2007). Increases in the number of species due to new discoveries are expected in poorly known groups, such as millipedes, whereas taxonomic inflation is common in taxa that are well known (Padial & De la Riva, 2006).

Two new genera (*Namibostreptus* and *Cacuminostreptus*) and eleven new species were described in this study. These descriptions support my hypotheses that generic boundaries were too inclusive and that many millipede species are undescribed. Similar observations were reported by Hamer (2000), Hamer and Slotow (2009) and Hamer (2009). More new species of spirostreptids continue to be discovered, particularly from previously unsurveyed localities in Southern Africa (see Hamer, 2009; Mwabvu *et al.*, 2010) and Eastern Africa (Van den Spiegel, 2001; Van den Spiegel, 2004; Mwabvu & Van den Spiegel, 2009). It is likely that more species await discovery because other Southern African biomes, such as grassland, have not been well surveyed for millipedes (Hamer & Slotow, 2009), and some museum collections have not been processed (Sierwald & Bond, 2007). Furthermore, because millipedes are a poorly known group in which trinominal nomenclature (naming of subspecies) is uncommon (Enghoff *pers. comm.*), there are few subspecies that could potentially be elevated to species rank after taxonomic revisions. Although morphological characters will remain important in taxonomy (Padial & De la Riva, 2010) using sequence data to delineate species will result in more species being recognized, as such, Sierwald and Bond (2007) estimated that millipede genitalic and other morphological characters could underestimate the number of species by a factor of three.

In this study, taxonomic uncertainties in the Spirostreptidae were highlighted by the splitting of two genera, the three species which were re-assigned to other genera, four new synonymies that were established, and the two names treated as *nomina dubia* and two as *incertae sedis*. In most of the problematic cases, species descriptions had been based on non-genitalic characters which vary intraspecifically and were taxonomically redundant. This demonstrated that some taxa had been incorrectly identified and that morphology-based classifications need to be re-assessed using other characters, such as gene sequences, in order to produce taxonomies that have been corroborated independently, and are likely to be stable and reliable hypotheses (Padial & De la Riva, 2010). Therefore, revisions of the four genera using genitalic characters erected monophyletic taxa with clearly defined synapomorphies by correcting generic and species boundaries. Besides stabilising the taxonomy of these genera, keys to species identification, which are important tools in future research and biodiversity assessment, were produced.

8.3 Morphology in millipede taxonomy

Non-genitalic morphological characters in the Spirostreptidae are homoplastic. For example, *Archispirostreptus*, *Plagiotaphrus*, *Namibostreptus*, *Cacuminostreptus* and *Spirostreptus* have the same body colour and overlapping body size ranges, thus body colour and size are taxonomically uninformative. Considering the similar preferences for sheltered and moist habitats (Hamer, 2000; Hamer & Slotow, 2000; Hamer & Slotow, 2009) morphological convergences in millipedes are not surprising. Body size also varies intra-specifically. This is consistent with Enghoff (1992) and Bond and Sierwald (2002) who reported that body size in conspecifics is influenced by habitat type. The shape of the collum was the only non-genitalic character which showed differences between genera. This suggests that some characters are more informative in some groups than others (Krabbe, 1979), thus variation in morphological characters requires further investigation for use in taxonomy of millipedes.

Given that other external body features are influenced by habitat conditions (Krabbe, 1979), male gonopod morphological characteristics proved to be reliable indices of taxonomic validity, and did not show major qualitative intra-specific variation. Bond and Sierwald (2002) reported similar observations in a spirobolid millipede *Anadenobolus excises* Karsch. The low intra-specific variation in genitalia, which has been observed in other arthropods, is probably a result of sexual selection pressure to be compatible with conspecific females (Huber *et al.*, 2005). Thus speciation was assumed to be correlated with changes in gonopod morphology (Huber *et al.*, 2005). According to Hamer (2000) the gonopod telopodite provides taxonomically useful characters for species delimitation in a spirostreptid millipede *Doratogonus*. However, in *Archispirostreptus, Plagiotaphrus, Bicoxidens* and *Spirostreptus* the gonopod coxites distinguish species whilst the telopodite differentiates the genera.

Although genitalic morphology is widely used to distinguish species, there is evidence suggesting that it may not reflect species boundaries (Huber *et al.*, 2005; Dayrat, 2005). Thus there is a drive to investigate the validity of genitalic morphology-based classifications using molecular characters (Lee, 2004; Dayrat, 2005) because there appears to be no correlation between sequence divergence and reproduction isolation (Lee, 2004).

8.4 Gene sequences in taxonomy

Based on the results of this first study of genetic variation in the spirostreptid millipedes, the use of DNA sequences in millipede taxonomy has potential to compliment genitalic morphology, particularly in identifying cryptic taxa. Both the mitochondrial CO1 and 16S rRNA genes discriminated taxa, and provided useful phylogenetic signals in the spirostreptids. In addition, classifications based on genitalic morphology and genetic evidence were concordant. However, the high mean sequence divergence suggests slow morphological evolution relative to molecular evolution (Lee, 2004), thus gonopod morphology may have failed to identify cryptic species and thus underestimated species richness in the genera. This further supports the view that genetic variation and genital morphology are not necessarily correlated (Bond & Sierwald, 2002; Lee, 2004).Therefore, intra-specific genetic variation requires further investigation in order to identify any cryptic diversity. High intra-specific genetic distance in *B. flavicollis* compared to lower divergence values in other studies (Bond, 2004; Meier *et al.*, 2006; Lefébure *et al.*, 2006; Pfenninger *et al.*, 2006; van Velzen *et al.*, 2007) strongly suggest the presence of cryptic species. Unfortunately, because few invertebrates have been sequenced (Lefébure *et al.*, 2006), there are few comparable studies. In addition, it is not possible to compare the performances of the CO1 and 16S rRNA genes in this study in detail because different species were sequenced for the two genes. At present the GenBank sequence database for millipedes is very small, as a result, only male genitalic morphology-based keys are available for identifying millipedes. More sequencing of millipedes would provide important data to use in identification and phylogenetic analysis. Given that DNA barcoding and DNA taxonomy could speed up identification and delineation of species, sequencing of millipedes is critical because many species have not been described (Sierwald & Bond, 2007), and face extinction because of man's activities (Hamer & Slotow, 2009). Thus, inferring phylogenies using molecular data would facilitate selection of appropriate taxa and areas for conservation. Based on the levels of genetic divergence among taxa and their phylogenetic relationships, areas/taxa that have unique genotypes could be selected for conservation.

Although molecular data give faster and consistent identification (Dayrat, 2005), and reveal more cryptic species (Huber *et al.*, 2005), than morphological characters do, at this stage few spirostreptid millipedes have been sequenced, which makes it impractical to use the sequences in systematics. Furthermore, several aspects of DNA data need standardization and further investigation. For example, the notion that CO1 is a universal marker which is unique to species (Hebert *et al.*, 2003) is widely disputed because morphologically distinct species could have similar CO1 sequences (Wiemers & Fiedler, 2007). Thus it is incorrect to assume that the genes that are used in DNA taxonomy are correlated with reproductive isolation (Meier *et al.*, 2006). Different genetic markers may be suitable for specific taxa, for example Vences *et al.* (2005) found 16S rRNA to be a better marker than CO1 in amphibians. Most importantly, intra-specific and inter-specific divergence threshold values to designate taxa should not be arbitrary, particularly in cases where intra-specific and inter-specific divergences overlap (Meier *et al.*, 2006). Divergence threshold values should probably be specific to taxonomic groups because many published studies have shown wide variation between groups (Bond, 2004; Meier *et al.*, 2006; Lefébure *et al.*, 2006; Pfenninger *et al.*, 2006; van Velzen *et al.*, 2007). It is likely that more informative and reliable data could be obtained if multiple genetic markers are used in molecular studies. Until these questions are adequately addressed and taxon sampling increased, misidentification of taxa could become widespread, and defeat the purpose of using molecular data in taxonomy of millipedes.

8.5 Distribution of taxa

Many species were recorded for the first time in previously unsurveyed localities. New distribution records from Southern Africa (see Mwabvu, 2005; Mwabvu *et al.*, 2009a; 2009b; Mwabvu *et al.*, 2010) and from Eastern Africa (Van den Spiegel, 2001; Van den Spiegel, 2004; Mwabvu & Van den Spiegel, 2009) were reported. As more biomes, such as grassland, are surveyed for millipedes (Hamer & Slotow, 2009), as museum collections are processed (Sierwald & Bond, 2007) and taxonomic revisions of genera are undertaken, new distribution patterns of species will emerge.

Although the genera are widely distributed, many species have restricted distributions and are endemic in the savanna. However, the levels of endemism are lower in the South African savanna than in forests (Hamer *et al.*, 2006). Hamer and Slotow (2000) reported high endemism in *Doratogonus* which led them to conclude that one area cannot conserve many species because of high degrees of localised endemism in millipedes. Hamer and Slotow (2009) also reported high levels of endemism in the Drakensberg mountains in South Africa. *Bicoxidens*, *Plagiotaphrus*, *Cacuminostreptus* and *Spirostreptus* are endemic to Southern Africa, and most species are restricted to woodland in the wetter, eastern half of Southern Africa. The exceptions are the large-bodied species of *Spirostreptus* which occur in drier and sparsely vegetated savanna. This is not surprising because millipedes are vulnerable to desiccation due to their inability to close their spiracles completely (Hopkin & Read, 1992), and because they have limited dispersal ability (Hamer & Slotow, 2002). As such, most millipedes cannot cross barriers, such as arid areas, or survive under xeric conditions. Consequently, species occur where moisture and shelter are present (Hamer & Slotow, 2009). For example, small-bodied *Bicoxidens* species are restricted to relatively high rainfall areas and Miombo woodland, and display high levels of endemism (Mwabvu *et al.*, 2007). In this case, woody vegetation provides moist microhabitats and shelter, and protects small-bodied species that are more vulnerable to desiccation (Hamer & Slotow, 2000).

What was surprising was that the genus *Spirostreptus* is not as widespread as *Archispirostreptus* whose body size and mobility are comparable. *Spirostreptus* species dominate arid environments in Southern Africa (Mwabvu *et al.*, 2009b), thus suggesting a body size-desiccation resistance correlation (Enghoff, 1992). The genus spreads westwards into Botswana, Namibia and Angola, but not eastwards into the eastern highlands of Zimbabwe. This suggests that high altitude (and associated vegetation types and climatic conditions) is probably a challenging barrier to the spread of this genus. *Archispirostreptus* is widely distributed in Africa and the Arabian Peninsula (Mwabvu *et al.*, 2010). The distribution pattern of *Archispirostreptus* probably indicates the influence of past climate change. The genus probably had a continuous distribution before parts of Africa became drier, and forests contracted in the late Pliocene and early Pleistocene (Werger & Coetzee, 1978). Fragmentation of forests may have led to allopatric speciation after isolation of small populations (Hamer & Slotow, 2009). Isolated occurrence of small populations of *Archispirostreptus lugubris villiersi* in remnant refugia in North Africa corroborates this explanation (Schubart, 1951).

Restricted distribution of species and high levels of endemism occur in all the genera in this study. Many *Archispirostreptus* species with narrow distributions are known from single localities despite intensive sampling in the East African mountain system (Mwabvu & Van den Spiegel, 2009). This is consistent with reports that montane forests are centres of high species richness and high levels of endemism (see Myers, 1988; Hoffman, 1993; Hamer & Slotow, 2009). Similarly high levels of endemism in afromontane forests were also reported in earthworms (Horn *et al.*, 2007) and spiders (Foord *et al.*, 2008) in South Africa. With respect to millipedes, these patterns appear to be associated with high altitude and woodland or forests. Given that high altitude areas have heterogeneous habitats (Hoffman, 1993), the poor vagility of millipedes and their preference for specific habitats, small populations could become isolated, diverge and speciate (Hamer & Slotow, 2000), resulting in many species with narrow, non-overlapping distributions. Further evidence of the high levels of endemism in millipedes comes from recently collected and undescribed species from the eastern highlands of Zimbabwe (Mwabvu, *pers. obs.*).

Although localised endemism is high in millipede species, different genera were recorded in close proximity, in many cases metres away from each other. These observations indicate similar habitat preferences among different genera. As such, these patterns could have broader implications for conservation of millipedes and other non-volant soil invertebrates. Given that a single species within a genus contains the ancestral diversity inherent to that genus, where different genera occur in the same localities, the genetic diversity of all species belonging to those genera, could be conserved in a single locality thereby effectively conserving greater genetic diversity (see Rodrigues & Gaston, 2002). For that reason, areas of overlapping generic distributions could be identified and targeted for protection. The areas could include forest and woodland patches, where species could be facing extinction because of habitat loss (see Hamer & Slotow, 2009). Thus, it is critical to establish phylogenetic relationships among the taxa and the extent of genetic variation so that the data can be used in conservation (Posadas *et al.*, 2001; Rodrigues & Gaston, 2002).

Based on Hamer and Slotow's (2002) classification of endemism, most species in this study are site and local endemics. These patterns of distribution are probably linked to greater diversification in woodland and at high altitude (Hamer & Slotow, 2009) and the effect of past climate changes on forest size (Hamer *et al.* 2006). The high levels of endemism in these genera are consistent with observations for *Doratogonus* (Hamer, 2000; Hamer & Slotow, 2000) and highlight the challenges of trying to conserve localised endemic species (Hamer & Slotow, 2002).

Although the absence of species from surveyed areas suggests that they do not occur there, the absence could also be because the species are rare or occur in small, patchy areas which could have been missed in random or scattered sampling (Hamer & Slotow, 2009). With more localities being surveyed and additional material in museums being processed, new distribution records will be captured. However, several collecting gaps still exist in most parts of Eastern Africa, Central Africa, and the northern half of Africa. Therefore, the distribution patterns of genera remain incomplete and should be interpreted cautiously because they could be a collecting artifact.

8.6 Conclusion

Given that the use of different types of data in taxonomy presents reliable data for biogeographic and ecological studies, and for addressing conservation issues, morphological and sequence data should be integrated (see Padial & De la Riva, 2010). Because genitalic morphology may fail to detect cryptic species, genetic data could compliment or be used to re-assess morphology-based taxonomy, particularly in poorly known invertebrate groups. As such, because genetic data are largely concordant with morphologic evidence, the two types of data could be used in integrative taxonomy to produce more stable taxonomies. When reliable taxonomic data are available for use in monitoring programmes and conservation planning there is likely to be fewer cases of arbitrary decisions making.

The role of genetics and phylogenies in conservation is an important one. Phylogenies and genetic distances will show relationships between populations and facilitate identification of unique populations. Because unique genotypes may perform key roles in the ecosystem, they may have to be targeted for conservation. More critically, areas with recent radiations of taxa or showing fast diversification of taxa can be identified and targeted for protection. However, before DNA sequence data can be utilized fully in millipede taxonomy and phylogeography more taxa should be sequenced and genetic variation among taxa determined. Prior to this, DNA extraction techniques, amplification and sequencing protocols appropriate for millipedes need to be developed. Presently available protocols appeared inappropriate for successful amplification, cloning and sequencing of millipede DNA. However, many reasons, among them the presence of defensive chemicals and the effect of preservation, could have caused unsuccessful amplification of most samples.

Given that millipedes have high levels of endemism and that several biomes are under threat because of direct or indirect human activities (Hamer & Slotow, 2009), it may be impractical to survey all localities and designate large areas for protection. Thus, conserving habitats and endemics outside protected areas could be difficult because of increasing demand for resources and land. The solution could be educating rural communities on sustainable use of resources and providing communities with alternatives to what they see as available in nature and feel entitled to. Without the involvement of governments and full cooperation of communities, conservation of millipedes and other non-volant soil invertebrates is unlikely to succeed.

Given that it is not possible to identify all invertebrate species because of their enormous diversity, environmental monitoring may have to be based on a single indicator taxon which reflects the response of other taxa (Uys *et al.*, 2010). As the number of described species and data on distribution increase, millipedes could become important indicators in biodiversity monitoring and ecosystem management, and surrogate taxa for other poorly known soil invertebrates that also have restricted distribution (see Lovell *et al.*, 2007). Unfortunately, there may be incongruency between invertebrate groups (Lovell *et al.*, 2007) because different taxa respond differently to environmental changes (Uys *et al.*, 2010). This led Lovell *et al.* (2007) to propose using many taxa in conservation and environmental monitoring. Considering that many genera are poorly known, that few species are listed as endangered and the slow pace of taxonomic research, blanket protection of threatened or rare biomes could be a more effective approach to conservation at present. Additionally, sequencing described species and submitting the sequences to the GenBank database should be prioritized. When sequences become available for use with genitalic morphology in integrative taxonomy, stable and more reliable taxonomies are produced. Most importantly, accurate circumscriptions will have far reaching implications for biogeographic interpretations, phylogenetic conclusions and biodiversity conservation.

8.7 Recommended Future Research Directions

Given that millipedes are a poorly known group, with many undescribed taxa and unknown distributions (see Hamer, 1997; Hamer, 2000; Sierwald & Bond, 2007), additional taxonomic and biogeograhic data are required in order to improve the predictive value of the data and make them more useful for conservation planning. Although greater understanding of diversity and distribution patterns of genera was achieved in the study, several questions need to be addressed.

Future taxonomic research on millipedes should focus on:

1. Revising more genera, describing new taxa, comparing patterns of distribution among taxa, and sequencing all the described species of millipedes.
2. Increasing taxon sampling in order to examine intra-specific and inter-specific variation, levels of endemism and cryptic diversity using gene sequences.
3. Identifying suitable genetic markers for distinguishing taxa and estimating phylogenies. Because large genetic variation among taxa was observed in this study, more conserved genes such as 18S (Dowton & Austin, 1994) should be sequenced to determine their suitability as genetic markers in millipedes. Other genes that could be sequenced include 28S, *cytochrome b* and 12S. In addition, millipede sequences should be added to the existing GenBank database.
4. Developing appropriate PCR protocol for millipedes. Given that most DNA samples in this study did not amplify, the effects of defensive secretions and methods of preservation of millipedes on DNA quality and amplification have to be investigated.
5. Assessing the potential of integrative taxonomy and using multiple genetic markers to construct phylogenies.
6. Establishing the potential of chemo-taxonomy in species differentiation, given that all spirostreptids produce defensive secretions. Chemo-taxonomy could be developed if the chemistry and relative proportions of chemicals are unique to taxa.
7. Behavioral or breeding experiments to determine reproductive isolation, particularly in widely distributed or closely related taxa. Although they are time-consuming, these experiments could compliment taxonomic data.
8. Ecological questions relating to inter-taxonomic interactions, coexistence and activity patterns of species could also be investigated to determine their role in diversification.

8.8 References

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