

**THE EVOLUTIONARY HISTORY AND TAXONOMY
OF THE *KOBUS LECHE* SPECIES COMPLEX
OF SOUTH-CENTRAL AFRICA
IN THE CONTEXT OF
PALAEO-DRAINAGE DYNAMICS**



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Declaration

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature

Date

Dedicated to my parents

Doreen Nesta Cotterill and the late Peter Cotterill

ABSTRACT

This multi-disciplinary study compiled taxonomic and biogeographical data to elucidate the extant diversity of lechwe antelopes (*Kobus leche* complex), and reconstruct their evolutionary history. Their diversification has been confined to wetlands across the south-central Africa plateaux. Lechwes are specialist grazers in water meadow floodplains; these stenotopic habitat requirements are invoked to explain why their evolution is atypical of terrestrial large mammals. Combined analyses of morphological (171 adult males), genetic (208 genotyped individuals) and palaeo-environmental datasets, revealed a recent (Middle Pleistocene) pulse of speciation in the *K. leche* complex. Multivariate morphometric analyses revealed the presence of five distinct groups that could be tied to the geography of the region. Furthermore, the genetic analyses supported the existence of at least four of these lineages, which show significant population separation at the level of the mtDNA control region. Most of the differences among populations were confined to frequency differences among populations and Bayesian analyses strongly suggest that the pattern obtained is the result of the retention of ancestral haplotypes with limited female gene flow among the extant populations. Evolution of the five lineages identified by the morphological and population genetic analyses were further investigated by making use of additional genetic data (mtDNA cyt b, SPTNB, SRY, Protamine 1, and b-Fibrinogen) and a subset of the samples. Topologies were largely unresolved due to the recent common ancestry of the lineages. Following the Evolutionary Species Concept, which was motivated by a philosophical review, five allopatric species could be recognized (*anselli*, *kafuensis*, *leche*, *robertsi* and *smithemani*). A model of drainage evolution compiled disparate facets of biological and geological evidence to detail interlinked histories of wetlands and their biota across the south-central Africa plateaux. This wetland archipelago is recognized as a distinct biogeographical unit in its own right - the Katanga-Chambeshi region. Evolutionary diversification of lechwes represents a dominant biogeographical signal reflecting how the aquatic biota have evolved in tandem with palaeo-drainage dynamics across this evolutionary theatre. Delimitation of key events in lechwe and drainage evolution was refined by archaeological dating of the Victoria Falls Formation, to decipher when the Zambezi river eroded the Batoka gorge. Demographic expansion in *K. leche s.s* (early Middle Pleistocene) corresponds to dessication of Palaeo-Lake Makakgadikgadi while more recent phylogeographic signals correspond to the tenure of Palaeo-Lake Buluzi. These speciation events in the Middle Pleistocene preceded peripatric speciation of *K. kafuensis* that accompanied the morphosis of the Kafue Flats (from palaeo-lake to floodplain), when the Kafue River attained its modern topology. The present study highlights that Lechwes represent a biota of evolutionary vibrant clades, rich in endemic species. As ecologically-dominant species in wetlands, lechwes deserve

priority conservation attention, which is challenged to perpetuate evolutionary and ecological processes across an archipelago straddling five countries.

Opsomming

Die multidisiplinêre studie bring saam taksonomiese en biogeografiese data om die evolusionêre geskiedenis en huidige diversiteit van basterwaterbokke (*Kobus leche* kompleks) te verklaar. Hulle diversifikasie is beperk tot vleilande regoor die suid-sentraal Afrika plato.

Basterwaterbokke is gespesialiseerde grasvreters in grasvloedvlaktes; hierdie stenotipiese habitatsvereiste word voorgedhou om te verduidelik hoekom die evolusie van hierdie diere a-tipies is vir terrestriële groot soogdiere. Gekombineerde analise van morfologie (171 volwasse manlike diere), geneties (208 genotipes) en plaee-omgewings datstelle toon aan dat daar 'n onlangse (middel Pleistoseen) pols van spesiasie plaasgevind het in die *K. lechwe* kompleks. Multivariate morfometriese analyses het aangetoon dat vyf verskillende groepe diere bestaan wat ook sin maak het op grond van geografiese ligging. Verdermeer, die genetiese analise het die bestaan van ten minste vier van hierdie lyne geondersteun wat betekenisvolle bevolkings isolasie vertoon het op die vlak van die mtDNA kontrole gebied. Meeste van die verskille tussen bevolkings was beperk tot frekwensieverkille tussen die bevolkings en Bayesian analise het sterk aanduidings getoon dat die patroon wat gekry is die gevolg was van die behoud van voorvaderlike haplotipes met beperkte vroulike geenvloei tussen die huidige bevolkings. Evolusie van die vyf lyne wat deur die morfologie en bevolkingsgenetika studies geidentifiseer is was verder ondersoek deur gebruik te maak van addisionele genetiese data (mtDNA cytb, SPTBN, SRY, Protamien 1, en b-Fibrinogeen) en 'n subset van die monsters. Topologieë was hoofsaaklik onopgelos as gevolg van die kort tyd tot die onlangse gemeenskaplike voorouer van lyne. Deur die Evolusionêre Spesies Konsep aan te hang, wat gemotiveer is deur 'n filosofiese oorsig, is vyf allopatriese spesies herken (*anselli*, *kafuensis*, *leche*, *robertsi* and *smithemani*). 'n Model wat dreinerings evolusie voorstel het verskeie fasette van biologiese en geologiese bewyse saamvat om die verbindingsgeskiedenis van vleilande en hulle biota oor die suid-sentraal Afrika plato te beskryf. Die vleiland argipelago word herken as 'n onafhanklike biogeografiese eenheid in sy eie reg – die Katanga-Chambeshi streek. Evolusionêre diversifikasie van basterwaterbokke verteenwoordig 'n dominante biogeografiese sein wat voortsel hoe die akwatiese biota ontwikkel het in tandem met die palaeo-dreinerings dinamika in hierdie evolusionêre konsert. Die afbakening van sleutelgebeure in basterwaterbok en dreinerigsevolusie is beter toegelig deur argeologiese datering wat gebaseer was op die vorming van die Victoria Valle om te bepaal wanneer die Zambezi rivier die Batoka skeurgroef

gevorm het. Demografiese uitbreiding binne *K. leche s.s* (gedurende die vroë Middel Pleistoseen) stem ooreen met die uitdroging van Palaeo-Meer Makakgadikgadi terwyl meer onlangse filogeografiese syne ooreenstem met die ontstaan van Palaeo-Meer Bulozi. Hierdie spesiasie gebeur in die Middel Pleistoseen het die peripatriese spesiasie van *K. kafuensis* voorafgegaan wat die morfose van die Kafue Vlakte vergesel het (van palaeo-meer na vloedvlakte), toe die Kafue Rivier sy huidige vorm aangeneem het. Die huidige studie het uitgelig dat basterwaterbokke verteenwoordig 'n biota van evolusionêre energieke eenhede, ryk aan endemiese spesies. As 'n ekologiese dominante spesie in vleilande, moet basterwaterbokke as 'n prioriteit gesien word in bewaring, waar dit dan die geleentheid sal hê om voort te bou op die evolusionêre en ekologiese prosesse van die archipelago wat oor vyf lande strek.

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Absorbed in studying the ecology, taxonomy and biogeography of Afrotropical Chiroptera, and challenged by nuances of cryptic speciation, my direct research (but certainly not interests) had circumvented Africa's antelopes. This was until 1994 when the most fortunate opportunity to participate in regional biodiversity studies across the Zambezi basin piqued my interest in lechwes and much else besides. Here, I thank all colleagues and collaborators in this rich experience, especially Jonathan Timberlake, Alan Sparrow, Moira FitzPatrick, Don Broadley, Vincent Katanekwa, Tony Morris-Davies, Isaac Mapaure, Brian Marshall, Dick Pitman, Sally Wynn, and Peter Mundy and many others who participated in these projects under the auspices of the Biodiversity Foundation for Africa (BFA), The Zambezi Society, and Canadian International Development Agency (CIDA), Harare.

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CONVENTIONS

Taxonomic authorities for names of taxa follow cited revisions, unless otherwise given for taxa that have recently been reclassified. The following conventions, defined below, are applied throughout this thesis.

Cyt b denotes the genetic sequence of the mtDNA protein-coding Cytochrome b gene.

DEM is the acronym for Digital Elevation Model, and in this study refers to the high resolution raster topographic database compiled as the SRTM-3 (Ustun *et al.* 2006). These geospatial data were analysed using propriety computer software in a GIS (Geographical Information System).

ESC is the acronym for Evolutionary Species Concept of Simpson (1951, 1961) explicated by Mayden (2002)

HVCR1 means Hyper-Variable Control Region I: the non-coding genetic sequence comprising the 5' portion of the Control Region (or D-Loop) of the mitochondrial DNA genome.

Kya means one thousand years ago B.P. (i.e. 1 000 yr Before Present)

Kyr denotes one thousand years

mtDNA refers to sequences of DNA that form part of the mitochondrial DNA genome.

nDNA refers to sequences of DNA comprising the nuclear DNA genome.

s.l. means *sensu lato*

SPTBN-1 refers to the non-coding sequence of Intron 1 in the B-spectrin nonerythrocytic gene, following Matthee *et al.* (2001)

SRY refers to the entire protein-coding sequence of the sex-determining region gene, the haplotypic Y chromosome marker that only occurs in male mammals.

s.s. means *sensu stricto*.

VFF is the acronym for the Victoria Falls Formation preserved along the Upper Zambezi River between eastern Namibia, southwest Zambia and northeast Zimbabwe. These late Neogene and Quaternary sediments were created along the Upper Zambezi in association with its erosion of the Batoka gorge.

Terminology and list of African landforms and regions, whose existence is discussed and/or proposed in this study. Names for landforms proposed in this study, but previously not mentioned in the literature, are appended by an asterisk. A brief explanation of the context of the principal landforms discussed in this study is listed below, with respect to their respective geographical location and their topological context with respect to modern drainage systems.

East African Rift System (EARS): The extensive geological system that extends from northeast Africa and Arabia south across East Africa to Mozambique. The South West Extension of the EARS extending across Zambia and Katanga (DRC) to Angola and Mozambique is a central feature to understanding the evolutionary history of lechwes and south-central African wetlands.

Eastern End Tertiary Drainage System (EETBD): Bell-Cross (1982) hypothesized that the middle and lower Zambezi formed a discrete drainage system - the EETBD. Its major tributaries included the Luangwa, Sanyati and Shire rivers.

High Africa: With respect to the bimodal topography of African analysed by Doucouré & de Wit (2003), High Africa refers here to the elevated hinterland of south-central Africa that forms the study area of this thesis. Its extent broadly corresponds to the Zambezian phytochorion of White (1983) which incorporates in turn the Katanga-Chambeshi region.

Katanga-Chambeshi region: Defined by (Cotterill 2004, 2005) as a biogeographical region in south-central Africa. This evolutionary theatre comprises an archipelago of inland basins and interconnecting rivers whose landforms and biota share an intricate history of evolution. The Palaeo-Chambeshi archipelago is represented today by the wetlands of Angola, Katanga, northeast and central Zambia, and northeast Botswana.

Lake Patrick: The palaeo-lake that covered 17 000 km² of the Kafue Flats in central Zambia. Its existence was postulated by Simms (2000).

Okavango-Kafue graben: The shallow rift valley that occupies much of northern Botswana, and extends northeast across the Machili Flats to the Kafue Flats in southern Zambia.

Palaeo-Chambeshi River: The large southwesterly flowing tributary that maintained PLM and may also have been an exoreic tributary of the Zambezi (Cotterill 2004). The configuration of the Palaeo-Chambeshi anteceded the Palaeo-Kafue and Upper Kafue and Upper Chambeshi systems of the Zambian Upper Congo system and central Zambia, respectively.

Palaeo-Kafila River*: The principal river postulated to have formed the Trans-Katanga drainage system. It ultimately became the northwesterly flowing headwater of the Lufira drainage system in Katanga, DRC. It anteceded the Kafila and Wiswila tributaries of the Lufira and Lower Luapula systems, respectively (Cotterill 2004).

Palaeo-Kafue River: The Upper Kafue after loss of its Upper Chambeshi headwaters, postulated to have existed when still connected to the Upper Zambezi. Its link with the latter was then broken, and the Palaeo-Kafue thereafter maintained Lake Patrick that inundated the Kafue Flats. The Palaeo-Kafue ultimately became the Upper Kafue late in the Pleistocene as a major north bank tributary of the Middle Zambezi.

Palaeo-Kunene River: The Upper Kunene River when it constituted an endoreic tributary of the Pliocene Palaeo-Lake Kunene in the Owambo basin (Hipondoka 2005).

Palaeo-Lake Bulozhi*: formed in western Zambia in the Upper Zambezi valley of Barotseland in the Middle Pleistocene, following on impoundment of the Upper Zambezi River at N'gonye (Sioma) Falls.

Palaeo-Lake Lufira*: Large, shallow lake that covered much of the Lufira depression in southeast Katanga. Intermittently part of the Trans-Katanga drainage system through the Pleistocene (Broadley & Cotterill 2004; Cotterill 2004).

Palaeo-Lake Makgadikgadi (PLM): Largest, persistent lake known to have occupied the Okavango graben in northeast Botswana and represented by massive fossil shorelines and off-shore sandbars, the Gidikwe and Mababe ridges (Grove 1969; Thomas & Shaw 1991). Evidence compiled in this study restricts the tenure of PLM within the late Pliocene to Early Pleistocene. PLM was probably maintained by an extensive endoreic drainage that included the Upper Zambezi and Palaeo-Chambeshi rivers.

Palaeo-Lake Thamalakhane (PLT): Large internal lake responsible for fossil shorelines at 936m and 920m altitudes in northeast Botswana (Shaw 1988; Thomas & Shaw 1991). PLT was likely maintained by Upper Zambezi system (and also possibly the Cuando and Cubango systems) during the Middle Pleistocene (Chapters 5).

Proto-Kafue River*: That portion of the Palaeo-Chambeshi system that then became the principal rivers of the Upper Kafue system. It included the Lufupa River.

Proto-Luongo River*: Today represented as the Upper Luongo River that formerly flowed south into the Palaeo-Chambeshi system. Today the Upper Luongo forms the swampy headwaters of a major east

bank tributary of the Lower Luapula River (Zambian Congo System). It was linked during at least part of its tenure with the north flowing Kalungwishi River across the Pambashye Swamps.

Trans-Katanga Drainage System*: Drainage system centred on Palaeo-Kafila and included Palaeo-Lake Lufira during part of the Pleistocene. Postulated to have linked Kamalondo and Lufira basins to the Palaeo-Chambeshi River.

Victoria Falls Formation (VFF): geological formation centred around Victoria Falls (Mosi wa Tunya) whose sediments reflect the flow regime of the Upper Zambezi in its incision of the Batoka gorge.

Nomenclature follows Clark (1950) and Dixey (1950). Its oldest sediments (**Older Gravels - OG I and OG II**) are of late Pliocene to Early Pleistocene age. They are superseded by two discrete deposits of aeolian **Kalahari Sands (KS I, and KS II)** during arid palaeo-climates, and the **Younger Gravels (YG I)** graded since late in the Middle Pleistocene.

Western End Tertiary Basin of Internal Drainage (WETBID): Bell-Cross (1982) hypothesized the endoreic rivers of the south-central African plateau formed a single system - the WETBID - during the Plio-Pleistocene. This included the Upper Cuanza, Upper Kunene, Upper Zambezi, Okavango, Upper Kafue and Chambeshi systems.

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The following raw data and articles (Adobe PDF files) are archived on the enclosed Compact Disc (inside of Back Cover):

1. Electronic Appendices G1-G5. Raw Sequence Data
2. Broadley, D. G. & F. P. D. Cotterill (2004) The reptiles of southeast Katanga, an overlooked 'hot spot'. *Afr. J. Herp.* 53: 35-61.
3. Cotterill, F. P. D. (2004) Drainage evolution in south-central Africa and vicariant speciation in Swamp-dwelling weaver birds and Swamp flycatchers. *The Honeyguide* 25(1): 7-25.
4. Cotterill, F. P. D. (2005) The Upemba lechwe *Kobus anselli*: an antelope new to science emphasizes the conservation importance of Katanga, Democratic Republic of Congo. *J. Zool., Lond.* 265: 113-132.
5. Cotterill, F. P. D. (2006). Taxonomic status and conservation importance of the avifauna of Katanga (southeast Congo basin) and its environs. *Ostrich* 77: 1-21.
6. Cotterill, F. P. D., A. E. Moore & G. Hughes. *unpublished ms.* Cichlid fishes evolved in a wetland archipelago. Submitted to *Nature* as a 'Brief Communications Arising' as criticism of Joyce *et al.* (2005) but rejected.

CHAPTER 1



The seasonally dry floodplain of the Bangweulu Flats during the end of the hot, dry season. October 1999.
Photograph: F. Cotterill

Group of female Red lechwe, *Kobus leche*, Busanga Plain, central Zambia
Photograph: F. Cotterill



CHAPTER 1. INTRODUCTION

"In the hundred or more years since Darwin's revolution began it has extended far beyond natural history, touching nearly every division of science and art. But the muse of history says here that when the future looks back through the lens of narrative, not only on Darwin's age, but also our own, it will see that the revolution of 1859 did not come to a close with us at the end of the Twentieth Century. It was not until the close of the Twentieth Century that the inertia of pre-evolutionary thought - of state questions and group-thinking - was at last overcome by the force of history - of change questions and tree-thinking - and Clio came down from the rafters of our museums, shook off the dust, and took her rightful place in the director's chair. A happy outcome of this, they will say, was the resurrection of the old term natural history: when the Darwinian revolution came to a close at the end of the Twentieth century, natural history became a discipline once again" R. J. O'Hara (1988: 153)

1.0 PROJECT OUTLINE

This study explores the evolution of a group of antelopes through the African Plio-Pleistocene. It focuses on how a species complex, *Kobus leche s. l.*, has evolved in relation to the geological history of their wetland habitats. Specialization of these bovids to their peri-aquatic habitats makes for interesting patterns of evolution interwoven with geological processes. I seek to understand the evolutionary history of these large mammals, by intensive study of their populations distributed across the elevated plateaux of south-central Africa. Resolving the taxonomy of these antelopes is integral to improving this knowledge, in tandem with a detailed study of their phylogeography. So, this study brings together biogeography and taxonomy to elucidate the real diversity of these organisms, and equally reconstruct their evolutionary history with respect to the landscapes where they have evolved. The primary data compiled into this thesis have been obtained from assessment and morphological studies of 343 natural science specimens preserved in the world's natural history museums. 171 were measured for morphometric analyses. Of these specimens, 89 are quintessential sources of the DNA sequenced in an integrated phylogeographic study. And molecular characters were also sequenced in selected specimens for a taxonomic revision. A combined dataset of morphological and molecular characters further revised the taxonomy of these antelopes. These combined datasets are complemented by a review of palaeo-drainage dynamics (hereafter the Geomorphic Dataset). The latter is interrelated with a review of published distributional data of selected indicator species, mainly fishes (hereafter the Biogeographic Dataset). Synthesis of the biogeographical and geomorphological history provides essential contributions to reconstruct the evolution of the *Kobus leche* complex, where interesting signals revealed in the phylogeographic study interrelate with patterns in the biogeographic dataset, and those exhibited in palaeo-drainage dynamics.

With respect to the scope and aims of the previous paragraph, the concept of a wetland archipelago is the valuable heuristic tool framing the entire study of landforms and biota (Cotterill 2004, 2006). The biogeographical context and rationale for delimiting this wetland archipelago are described in detail (Chapter 2), which focuses the operations of Chapters 4 and 5. These assemble a narrative of landscape evolution that brings together geological and geomorphological data, revealing how drainage across south-central Africa has evolved.

A narrative of landscape evolution details the evolutionary dynamics of this wetland archipelago through the late Cenozoic. Its lakes and rivers mantle the elevated plateau of "High Africa", whose anomalous topography is geological ancient (see Doucouré & de Wit 2003; McCarthy & Rubidge 2005, and the origins of High Africa receive due attention in Chapter 4.) Again, the resolution of this narrative benefits greatly from clarifications revealed in the biogeographical dataset. Thus, this study of lechwe antelopes has garnered historical information from disparate sources, which entailed forays from phylogeography, systematics and mammalogy into other subdisciplines. It necessitated devoting quite some detail to geology and geomorphology, and equally to archaeology and palaeoanthropology. More broadly, palaeoclimatology, hydrology, geomorphology, and geology have been brought to bear to answer key questions in a biogeographical study, which seeks to explicate the evolution of these large mammals with respect to their extant diversity. The nature of this cross-disciplinary study is explained and defended further below, with attention to key epistemological aspects and benefits.

1.1 KEY QUESTIONS AND OBJECTIVES

The encompassing aim of this study is to elucidate the species diversity of lechwe antelopes in south-central Africa; and reconstruct the recent evolutionary history of these mammals - focusing on their biogeography and phylogeography through the Plio-Pleistocene. This broad objective frames the following key questions:

1. How has vicariance of wetland habitats influenced the evolution of lechwes across south-central Africa? For example, did timings of evolutionary events in lechwe correspond to geological evidence of changes in wetland habitats? How do distributions of extant lechwes relate to the vicariant history of landscape change - notably rearrangements of drainage systems across south-central Africa?
2. What are the products of the vicariant evolution of lechwe antelopes? Can specimens of currently unclear taxonomic affinities be identified using molecular and morphological

techniques? These historical specimens vouch for outlying populations in eastern Angola, north Zambia, southern Congo Basin and Chisenga Island, Lake Mweru.

3. How can patterns and processes revealed in the evolutionary history of the *K. leche* complex, and their habitats, inform conservation plans and actions?

1.2 THE AFRICAN BOVIDAE AND LECHWE ANTELOPES

Before expanding on the above topics any further, it is pertinent to outline salient aspects of the natural history of the lechwe antelopes comprising the *Kobus leche* species complex. The extant representatives of African antelopes total at least 80 species that exploit forest, savanna and desert habitats. Only three species complexes are specialized to exploit aquatic habitats in Africa. One, a tragelaphid, the sitatunga, *Tragelaphus spekei* is truly swamp dwelling. The other two are the Nile lechwe, *Kobus megaceros* and the *K. leche* complex of the tribe Reduncini. Along with waterbuck, reedbuck, puku, and kob, lechwe comprise the bovid tribe Reduncini. Of all these reduncine antelopes, lechwes represent the most extreme adaptations to an aquatic life (Spinage 1986). Besides *K. megaceros*, endemic to a part of the Upper Nile drainage system, all other populations are included in the *K. leche* complex endemic to the Zambezi region of south-central Africa, where its five described taxa exhibit fragmented distributions. Each is restricted within a particular drainage system in south-central Africa, with their overall distribution confined within the Zambezi region. Historically, high densities of lechwe were restricted to floodplains across Angola, northeast Botswana, parts of Katanga, Democratic Republic of Congo (DRC) and Zambia. Interesting adaptations of these reduncine antelopes facilitate a semi-aquatic lifestyle. As obligate floodplain grazers, dependent on water meadow grasslands, their life histories are closely adapted to the ecological dynamics of perennial wetlands (Vesey-Fitzgerald, 1965; Cotterill 2000, 2005; Chapter 2).

1.3 THE CONSERVATION RELEVANCE OF THIS STUDY

The vast wetlands exploited by these lechwe not only constitute significant landforms, but are especially interesting products of Africa's ancient geomorphological history (Goudie 2005; Stankewicz & De Wit 2006). Equally, the integrity of the ecology and hydrology of these landscapes bears directly on the current well being of socio-economies and their future development. Many invaluable ecological goods and services accrue from wetlands, not least fish, hydroelectric power and tourism. For local and regional socio-economies, potable water is obviously of fundamental social, economic and strategic importance (Asselmann & Crutzen 1989). Patterns of its availability from the drainage catchments of south-central Africa underpin critical issues of geopolitical security across the

subcontinent. Forecasts predict escalating demands, and thus social and political tensions through the 21st century, as water scarcities become more acute (De Wit & Stankeiwicz 2006). Ecological evidence summarized in Chapter 2 reveals that lechwe antelopes hold pivotal roles in the ecological dynamics of wetlands, and especially those pertaining to important ecological goods and services.

All lechwe have suffered radical reductions in numbers and range since the end of the 19th century. Hughes (1933) emphasized how lechwes and pukus constituted a “thin red line” in great danger of extermination under burgeoning hunting pressure; and indeed, these antelopes had declined radically by the mid 20th century (Mitchell & Uys, 1961; Vesey-Fitzgerald, 1961). Lechwe populations have largely disappeared from western Zambia, Lukanga Swamps, and Angola. The range and numbers of Kafue lechwes have dwindled since the 1950s (Fig. 2.1). The isolated population on the Cuanza river (northern Luando Reserve), first reported by Crawford-Cabral (1967) barely survives. Adverse human impact on Katanga’s populations became catastrophic in the 1980s, when the population of Upemba lechwes was reduced greatly by poachers. So, in the absence of current knowledge of their status, these lechwe were mapped accordingly by East (1999) “as present but numbers unknown”. The Luapula population, south of Lake Mweru, appears to be extinct; whilst it appears Upemba lechwes barely survive in greatly reduced numbers (M. Hasson, *pers. comm*, August 2003).

The combined signals from indicator data (high endemism and species richness), together with aspects of geomorphological evolution, synthesized in this study reinforce recent reappraisals (Brooks *et al.* 2001; Linder 2001) that Katanga is a biodiversity hotspot in the larger Katanga-Chambeshi region (Fig. 2.1). The conservation values of Katanga have long been underappreciated (Broadley & Cotterill, 2004; Cotterill, 2004, 2005, 2006). It is very difficult to ignore imperative demands for knowledge to support conservation priorities and decisions. The picture emerging is that evolutionary dynamics through the Plio-Pleistocene have been of great significance in structuring the biodiversity of south-central Africa’s wetlands. The evolution of lechwe in the context of geobiotic patterns and processes extends novel historical insights to structure conservation planning, such that:

“Perpetuating species without ecosystems makes as much sense as preserving ecosystems without species. Perhaps the solution to this dispute includes the recognition that conservation is not about protecting objects, it is about protecting a process: life. Conservation is based on a mandate to maintain the threads of life as they arrive from the past, abide in the present, and depart for the future. Under the temporal perspective outlined above, the disciplines of systematics, ecology, and evolution each contribute uniquely and irreplaceably to conservation.” B. W. Bowen (1999: S9).

1.4 LECHWE DIVERSIFICATION AND WETLAND EVOLUTION: THE BIOGEOGRAPHICAL FRAMEWORK OF THIS STUDY

The unifying objective of this study is to elucidate the evolutionary history of lechwe antelopes with respect to dynamics of the wetland habitats in which they have evolved. As this study of lechwe antelopes accumulated new data, it became clear that an understanding of habitat evolution was quintessential to explain historical anomalies in lechwe evolution and biogeography. Relevant information unearthed in the geological literature demanded major investments into its revision and synthesis. In its own right, this process has revealed hitherto unrecognized events in Plio-Pleistocene geomorphology. These are all of direct relevance to lechwe evolution, and much else besides. In fact, beyond, and consequent to this thesis, this synthesis is developing into a major project (if not projects) to elucidate geological and geomorphological details centred around palaeo-drainage dynamics across south-central Africa. Constraints on resources has confined attention to more manageable aspects of this geological history - guided by the overarching objective of constructing a narrative of salient aspects of landscape evolution, sufficient to understand lechwe evolution.

One might argue that it would be satisfactory for such a study of lechwe antelopes to gather together a novel biological dataset, and then attempt to explicate its patterns (anomalous and other) using published reviews of African geomorphology. This strategy failed, because state of the art reviews of drainage evolution (namely Moore & Larkin 2001; Goudie 2005) - unquestionably of sound scientific merit - do not delimit ages of Plio-Pleistocene landforms in sufficiently fine detail to explicate critical events in lechwe diversification. With respect to the demands for such austere fine-scale resolution, known ages of the few studied landforms are vague at best.

It appears that the adage of panbiogeography that treats life as the fourth dimensional layer aptly applies to how lechwe antelopes have evolved in tandem with palaeo-drainage dynamics. These geobiotic dynamics appear to reflect correlated responses to common causes. The term 'geobiotic' is applied cautiously to describe these shared patterns - the close congruence exhibited in how aquatic biota have evolved in tandem with dynamics of palaeo-drainage. Geobiotic is admittedly a loaded, "catch-all" concept, yet this term figures prominently, if not structures, panbiogeography (e.g. Craw *et al* 1999; Heads 2004). This linking of abiotic and biotic dynamics assumes that patterns exhibited in known organisms are surrogate indicators of how an entire biota has evolved in tandem with their shared habitat. This ideal breaks down, as examples in this study reveal, so one has to be careful using this vague term, despite its heuristic pertinence!

This research revealed extinct landforms, whose existence was previously unrecognized. The emerging picture of Neogene and Quaternary palaeo-drainage dynamics exhibits fascinating intricacies across High Africa. The waxing and waning of palaeo-lakes and reshaping of river topologies reveals a history that appears even more elaborate than initially revealed in pioneering studies. This is especially true of Botswana, Katanga and Zambia. It can be seen, again and again, how changes of older landforms manifested in a plethora of nascent geobiotic patterns. So the importance of erosion surfaces receives deserving attention in how they control hydrological processes across wetlands. Quite literally, recurrences of tectonism underlie the deep history of uplift and rifting of Africa, which has controlled landscape evolution profoundly; such that very few of the continent's landforms have escaped its influences. These effects are apparent throughout south-central Africa, even though tectonism has tended to manifest as subtle effects.

An important aim in this study is to delimit tenures of palaeo-lakes, and the key events when drainage topologies changed. For our understanding of palaeo-environments (where these key events occurred) has an overwhelming bearing on the accuracy and precision with which such events in biotic evolution can be refined. The overall quality of such evidence needs to extend beyond criteria of its completeness, judged by how well patterns of events are detailed. For a critical criterion is how tightly it places spatial and temporal limits around key events. Together, all these factors influence the accuracy and precision of the historical narrative.

This criterion underlies a critical issue, which has structured this biologically focussed study. It pertains to serious discrepancies evident in certain geomorphological explanations. One might well skirt such controversies, but this would have severely hamstrung - if not mislead - this study in most serious respects. The crux of this dilemma arises from serious challenges of dating Quaternary sediments precisely. It especially applies to landforms older than the Late Pleistocene that cannot be dated with radiocarbon methods. This is one major reason why my scrutiny of geomorphological literature sought out alternative, more credible, evidence. It expanded to link aspects of the archaeological and palaeo-anthropological record to the Biogeographic and Geomorphic datasets. Invaluable revelations, and tighter temporal resolution accrued from this synthesis. A pertinent example underlines the importance and benefits of this strategy. One might follow Joyce *et al* (2005) and cite the geomorphological literature uncritically; where the postulated Palaeo-Lake Makgadikgadi (PLM) is interpreted to be a Holocene wetland, which inundated ~120 000km² of northeast Botswana. More reliable evidence reveals that these geochemical dates, purported to delimit a recent tenure of PLM, have serious

weaknesses. Most critically, a wealth of overlooked archaeological evidence reveals that PLM more likely ceased to exist much earlier in the Pleistocene (Chapters 4 & 5). A sobering lesson in this case is that one's critical reading of the earth science literature has to extend to judicious syntheses of valid evidence, if we are to elucidate credible biogeographical scenarios.

The time frame in this study extends from the late Neogene to late Quaternary, with key influences rooted in far deeper geological history. So, how far back in geological time is it reasonable to try and reconstruct the ultimate causes of lechwe evolution? (Here, it is obviously important to acknowledge that identification of dominant causes among several agencies that caused a phenomena - causal efficacy (Northcott 2006) - can be challenging in the extreme.) Obviously, how completely one pieces together historical evidence governs the antiquity of time frames that can be invoked as mechanisms of ultimate causation. This deeper boundary is difficult to delimit, but hinges on the presence, or rather absence, of key evidence. The most proximate, and thus recent, controls on lechwe biogeography are predominantly anthropogenic, and began to impact on populations in the late 1800s. The strongest controls invoked to explain evolution of lechwes centre on palaeo-drainage dynamics through the Quaternary. These dynamics of palaeo-drainage systems reflect in turn on the repeated uplift of Africa, whereby tectonism has controlled drainage profoundly. Moreover, this uplift had ancient antecedents initiated before Gondwana times. These geological determinants have directly controlled the origins and properties of wetlands through effects ranging from dramatic diastrophism through to subtle warping across Africa's hinterland. So it is important to acknowledge that the greater part of the landscapes across this vast plateau existed for crores (tens of millions) of years prior to the Quaternary. Thus, panoptic treatment of all available evidence, in search for ultimate causes, should logically extend back to origins of ancient geological formations. Allied with the older mobile belts, these ancient cratons have controlled the evolution of landscapes and biodiversity ever since their consolidation, ~1.8 billions years ago. Remarkable legacies of this history continue to frame biotic evolution through the Quaternary. For example, Squire et al. (2006) narrate key events on Gondwana (late Precambrian and early Phanerozoic) that conferred profound legacies on Earth thereafter. Since their initial emplacement, many of these landforms have changed in only subtle respects. Thus, the ancient legacy of these geological controls has overwhelming consequences for extant landforms and biodiversity across High Africa. Dominant determinants of properties of extant landscapes relate directly to events and environmental conditions existing during Mesozoic times on Gondwanaland.

1.5 THE MULTI-DISCIPLINARY RICHNESS OF BIOGEOGRAPHY

"These is probably no other field of biological enquiry that is as bewildering as biogeography. Evidence there is, in abundance, but it consists of patterns; from essentially worldwide, to taxa found in only one locality; from wholly contiguous, to taxa found today in several continents separated by hundreds or thousands of miles of open ocean. The biogeography of islands adds another layer of complexity, in the need to make sense of their varying patterns of diversity and of the ways in which their biota has been affected by the area or location of the island." (C. B. Cox 1998: 813)

Evolutionary biologists are repeatedly challenged to decipher particular patterns of biotic evolution in the context of the physical environment. So our studies of such biota comprising particular populations of organisms (or more correctly their ancestral lineages) have to equally scrutinize the landscapes in which biodiversity has persisted successfully through geological scales of space and time. This is business as usual in the majority of biogeographical studies; where it is very difficult, if not counter productive, to restrict one's explanations solely to biological patterns, and especially just to one's study taxa (lechwe antelopes in this respect). The multidisciplinary scope of biogeography holds whether one studies origins of early Life in the Archaean Eon, or the evolutionary dynamics of taxa that speciated through the Quaternary (Cox 1998). The knowledge assembled in such biogeographical enquiries is structured into explanatory narratives of evolutionary history. These invoke suites of mechanistic processes to explain extant patterns quantified in terms of the molecular, morphological, behavioural and ecological traits of the organisms. These narratives compile evidence from separate fields of scientific enquiry to explicate origins of such patterns. It is quite routine for a biogeographer to synthesize relevant evidence from many different studies to explain particular biotic patterns. This may bring together data from geochemistry, palaeontology, molecular genetics, animal behaviour, ecology (population, community and landscape), geomorphology, phylogeography, structural geology and systematics. Furthermore, it is difficult for any biogeographical study of deeper earth history to ignore how biotic evolution has been controlled by plate tectonics, which invariably dominate explicative narratives of biogeographical history. Each of these aspects of scientific knowledge contribute key facets to such syntheses to explain interlinked histories of biodiversity and landscapes. As argued below, biogeography clearly is a palaeontological science, as defined by Whewell (1837, 1847), and exemplified by geology (Cleland 2001; Didick & Orion 2003); and indeed Whewell (1847) considered geology the most representative palaeontological science in its searches into Deep Time, to explicate origins of modern entities in terms of chain of causes.

"Yet nothing in the realms of physics and chemistry is equivalent to the evolutionary causations that are controlled by genetic programs of all organisms. Simply to ignore a major determinant of all biological processes is both bad science and bad philosophy." E. Mayr (1996: 104)

1.6 HISTORY AND AETIOLOGY

"[A]Etiology is so fundamental to scientific classification that it is hard to exaggerate its importance. Its neglect has had so many disastrous consequences in the past that the point will be repeated time and again in the present work" M. T. Ghiselin (1997: 74)

More fundamentally, with respect to epistemology, this study is challenged by critical issues in aetiology, in its search to identify causal mechanisms that produced historical phenomena. These challenges centre on how well one can answer the question - What has really caused lechwe evolution? As pointed out decades back by Mayr (1962) and Simpson (1963a,b), extant properties of historically derived complexes reflect both proximate and ultimate agencies. The overall theatre of space and time within which phenomena have influenced another's state places outer boundaries around a study, or science (pertinently biogeography) that seeks to tease out patterns of causation into their respective historical roles. For example, in key respects (as detailed in Chapter 4), all Africa's landforms owe their existence to tectonics, and indeed to very ancient events of crustal faulting and warping. And as argued by Cracraft (1992), tectonics presents as an ultimate causative mechanism in many respects, especially when considered against more proximate controls on biotic evolution such as ecological determinants.

Epidemiology provides a well studied discipline with respect to how its practitioners decipher causal pathways responsible for diseases. In fact, appreciation of key philosophical tenets of aetiology are integral to successful epidemiology. Its searches for causes and origins of a disease address the broadest possible canvas of possible mechanisms. (Undoubtedly, life-and-death issues at stake motivate such exhaustive studies of diseases!) Surprisingly, it appears that biogeography and phylogeography have much to learn from epidemiology, when it comes to teasing out historical causes of observed patterns and processes. This means that this study of selected taxa of African large mammals stands to benefit immensely from disciplines, and corpuses of knowledge, that might seem remotely connected, if relevant at all, to the traditional terrain of mammalogy. An epidemiological example helps explain the scope and complexity of these issues.

As is well documented in *K. kafuensis* (Zeiger *et al.* 1998; Kock *et al.* 2002; Siamudaala *et al.* 2005), lechwe antelopes are susceptible to infection by bovine tuberculosis, *Mycoplasmadivium bovis*. Kafue lechwe constitute just one node in the epidemiology of this disease, nested within a complex web of interactions. This is primarily because the bacterium infects many hosts; and its transmission and virulence is complicated by non-linear responses to stochastic ecological factors. Virulence, manifestation, and thus transmission, of TB varies greatly between these vertebrate hosts, and equally in how individual organisms react (in time and space) to infection by their species' parasites. A spectrum of ecological determinants controls where and how virulently *M. bovis* infects particular hosts in the landscape. Clearly, aetiological understanding of any zoonosis is centred on what medical and veterinary research reveals of the microbe and its hosts. Thorough understanding of its virulence and transmission follows on studies that quantify how larger scale processes influence where and when the disease vector occurs in space and time, and susceptibilities of individuals and populations to infection. (With respect to humans, socio-economic factors exert critical controls on the epidemiology of TB in humans, especially where HIV infections are prevalent.) Equally, archaeology can reveal deep, historical dimensions to understand zoonoses such as tuberculosis. Evidence permitting, resolution can extend as far back in time as ancient DNA can be extracted from cadavers, and even deeper into geological strata, where tubercular lesions are preserved on fossilized bones.

This example highlights two key issues. One is the challenges we face to distinguish causes from effects. In this respect, macroecology continues to persist in scrutiny of neontological patterns, at the expense of deeper Earth history. Its ignorance of the interpretive strengths of the palaeobiological sciences is a myopic strategy if we are serious about understanding origins of ecological assemblages (Brooks & McClelland 1999, 2002). Indeed, disregard in ecology for the scientific relevance of evolutionary history reaches an absurd extreme in Peters (1991) *A Critique for Ecology*, which among several controversial conclusions, stated that "...some of the longest standing and most contentious issues in ecology evaporate when cause, mechanism and explanation are ignored." (Peters 1991: 146).

In its objectives to reconstruct evolutionary history, the science of phylogeography sits firmly within the mandate of biogeography. Here, phylogeography provides a set of powerful methodologies to unravel the finer tendrils of biogeographical patterns, and especially to decipher nuances of speciation events (Crisci *et al.* 2003). The ability to link phylogeographic patterns to palaeo-environmental conditions is a crux of the discipline (Hewitt 2004): for example relating patterns of genetic variation of plants to records of fossil pollen (Cruzan & Templeton 2000). Nevertheless, connections between gene

trees and population processes are complex; and disparate palaeo-environmental causes can result in gene trees of very similar structure (Nielsen 2006). I see this problem as an interesting example of pseudo-congruence; where corresponding patterns might invoke common causation.

As critically with respect to their explanatory scope, statistical analyses of phylogeographic patterns can only go so far. Ultimately, the viability of interpretations invoked to explain genetic patterns hinge on how reliably we understand palaeo-environments that caused the phylogeographic patterns we seek to understand. The precedent to interlink interrelated historical phenomena into a robust narrative, of evolutionary explication, places the phylogeographer in a challenging situation. One is tasked to reconstruct the best possible model of the palaeo-environment(s) where these organisms evolved. Only rarely does such a model already exist. For example, the glaciation history of the Quaternary Palaearctic exemplifies a robustly understood example of such an evolutionary theatre (Hewitt 2000, 2001, 2004). Nevertheless, one still has to relate the natural history of each species to these palaeo-environmental scenarios.

This aspect of phylogeographic interpretation needs to pay special attention to how these organisms exploit key resources in the landscape, and what determinants (e.g. physiological, behavioural, reproductive and interspecific interactions) influenced distributions of source and sink populations across a patchy landscape. (These demands present a rich field to develop and interrelate phylogeography with computer modelling of palaeo-environments with respect to interfacing the life history, behavioural ecology and ecophysiology of studied organisms with the palaeoecology and geology of landscapes.) In this respect, the quality of phylogeographic interpretations hinges on how reliably we understand life histories of the populations or species, we have sequenced. Most fortunately, three of the five principal taxa of the *K. leche* complex have been intensively studied with respect to their behaviour and ecology. Not least, relevant controls on their population dynamics are relatively well understood (Chapter 2). This knowledge has been brought to bear in this study to quantify demographic variables (pertinently generation time), and invoke criteria governing habitat selection by lechwes in palaeo-environments.

Phylogeography also faces the same challenges that hamstring biogeographical interpretations. How can current geobiotic patterns be confidently explained with respect to causes of their origins? Here again, we see how biogeography and phylogeography cannot ignore fundamental matters of aetiology; given the challenges to explicate origins of complex historical entities, which could have resulted from

any number of proximate and ultimate causes. As with phylogenetic trees elucidated by systematists, the AMOVAs, mismatch distributions and estimates of population history, we calculate using coalescent-based methods, can only be confidently related to real world history, if we have an equally robust understanding of the palaeo-environments where these genetic patterns evolved. An additional complication deserves greater recognition, especially as it is too rarely acknowledged in biogeography, and especially affects phylogeography. We are challenged by a scale-dependent problem, where the dynamic patterns (that we seek to interrelate) exhibit marked spectral differences - especially where demographic processes contrast against geological dynamics.

These dichotomies possibly create inductive lags in causative effects. This is illustrated by how dynamics of demographic processes, pertinently gene flow, outpace the slower palaeo-dynamics of evolving geomorphological systems. This contrast in spectra of these dynamics is exemplified where, for example, piracy of one river course by another may have taken many thousands of years to forge two separate drainage systems. Such a time lapse would provide ample time for persistent exchanges between fish faunas, and other aquatic organisms, over the period the two rivers individuate. A parallel situation likely applies to how vast floodplains expanded, concomitantly, as palaeo-lakes dwindled toward the end of their tenures. These geomorphological events provided broad windows of opportunity for aquatic biodiversity to respond. Thus, populations of organisms directly influenced by such protracted events might clock up many thousands of generations through these geological events. So it follows that phylogeographic patterns, pertinently gene trees, and profiles of accumulated mutations, may exhibit blurred spectra when compared against singular geological events. Nonetheless, there is a tendency to under represent this dichotomy between such interrelated biotic and abiotic patterns in our historical chronicles of biogeographical dynamics (Chapters 4-8).

The predilection of lechwe antelopes for aquatic landscapes created interesting challenges, and opportunities, in this study, with respect to how it has focussed searches for relevant knowledge in the earth sciences. Because key events in lechwe evolution span the Quaternary, it turned out that the archaeological record could contribute critical historical insights into the nature of landscape evolution over this recent period of earth history. In part, the huge research effort directed at reconstructing Quaternary palaeo-environments has been driven by our species' intense preoccupation to understand our origins, and latterly by burgeoning concerns to relate impacts of anthropogenic environmental changes to those preserved in the fossil record. Thus, inputs from archaeology and palaeoanthropology

can provide especially critical data, even though the ensemble makes for an unorthodox inter-disciplinary mix in pursuit of understanding how and where lechwe antelopes evolved.

The nature of evidence required to understand these patterns and processes exemplifies how biogeography, perhaps beyond any other science, is challenged to assimilate evidence from as many sources wheresoever it exists (Cox 1998). In this study, such syntheses of disparately-derived data have provided the only means to delimit critical events and unravel patterns of historical causation. Yet, rival methodologies in biogeography prescribe against syntheses, which seek to harness a spectrum of analytical methods toward understanding a plethora of disparate data. These divisions across science act to discourage a unified approach to problem solving. The research called for to understand intricate evolutionary patterns (of lechwe antelopes in this case), presents a pertinent example of how studies of historical phenomena need to transcend the orthodox boundaries traditionally delimiting scientific disciplines. Above all else, exhaustive explorations of historical entities not only decree that data and ideas flow freely, but that we contrast and complement different methods to understand evolutionary complexity.

"The kind of historical knowledge that scientists need can only be provided through the active participation of scientists themselves in the study of their own subject. History is too important to be left to the historians." M. T. Ghiselin (1997: 297)

1.8 NATURAL HISTORY AND PALAETIOLOGICAL KNOWLEDGE

It is critical to explicate how historical methodologies shared among the palaetiological sciences can chronicle intricacies of evolutionary history - in this case how the evolution and diversity of lechwe antelopes interrelates Plio-Pleistocene palaeo-drainage. Natural history encompasses those palaetiological sciences that seek to understand the evolutionary complexities of the natural world. In this respect, Gould (2002) has emphasized the epistemic powers of the methodologies that enable scientific enquiries to discern intricacies of earth history, whether abiotic or biotic. These methodologies furnishes natural history with its epistemological tools, which can reveal the origins and associations among entities that owe their existence to historical causes. In complementary or combined roles, they enable palaetiological studies to elucidate contexts, relationships and thus origins of evolutionary complexes. Gould (2002) has detailed how Charles Darwin employed them all in his eclectic, revolutionary research, and they structure and consolidate the scientific strengths of his seminal works (reviewed by Ghiselin 1984). Toward explication of the world's evolutionary

complexities, it is reasonable to conclude that natural history unites key palaeontological sciences; which seek to decipher evolutionary history. Yet, it might seem unfashionable in contemporary science (at least judged from orthodox positions) to construct synthetic arguments from disparate sources. As argued by Ghiselin (1971, 1986) different vocabularies, and even different grammars hinder cross-disciplinary pollinations, let alone syntheses. Nevertheless, such exercises can confer rich rewards.

To reiterate, *contra* Peters 1991, natural history encompasses those palaeontological sciences which employ the epistemic methodologies described by Gould (2002). Here, consilience confers especially powerful insights into historical complexities. A consilience of the inductions strengthens the Darwinian method in natural history, which draws on multiple lines of evidence to arrive at conclusions that explain quantified patterns (Magnus 2000; Gould 2002, 2003), such as all five theories elucidated in the *Origin of Species* (Darwin 1859, Ghiselin 1984; Mayr 1991). Such studies of historical associations characterize the nature and scope of geology, appropriately classified as an exemplar palaeontological science (O'Hara 1997; Dodick & Orion 2003). Where studies of what today appear as independent entities reveal unsuspected historical links, then our knowledge of their natural history gains considerable explanatory resolution. Thus, consilient explications follow on discovering that patterns elucidated amongst one set of entities (e.g. geological formations) serendipitously interrelate - in previously unsuspected ways - with seemingly disparately derived entities, such as biogeographical patterns.

In an epistemic context, consilience elucidates previously undetected links among historical patterns through independent discovery operations. Pertinent examples are where consilience reveals how speciation patterns interrelate with the individuation of geological formations caused by plate tectonics; thus discordance and congruence in the phylogeographic patterns of compared species can reveal influences of common causes. Elucidation of such historically structured knowledge involves an epistemology foreign to schools of inquiry that adhere to a strict dictum of Popperian falsification (see also Cohen 1994 and Cleland 2003). Moreover, any such exercise in falsification must obviously first obtain the patterns to construct a testable hypothesis, if indeed such singular historical discoveries are amenable to testing (Gould 2002, 2003).

With respect to its structure and cross-disciplinary interpretation of independent datasets (molecular, morphological, biogeographical and geomorphology), this study falls squarely under the auspices of

natural history (*sensu* O'Hara 1988). Its enquiries have progressively drawn independent datasets into a synthesis of accumulating evidence: with published data combined with new evidence. Then when considered together, several independently derived sets of facts reveal a great deal about how lechwes have evolved across a wetland archipelago. This synthesis has interlinked previously unrelated patterns of facts into an explanatory network, which extends to discern previously unsuspected aspects of knowledge. Each of these patterns exemplify a colligation of facts, precursory ingredients for our palaeontological epistemology to structure into consilient explications. This methodology of Whewellian consilience is employed progressively. I dissect out individual patterns in historical complexes, and then apply emergent findings from revealed colligations to explicate facets of evolutionary history. As importantly, discordant signals have revealed links among entities that existed in Quaternary palaeo-environments. This discovery process is aptly demonstrated in the synthesis of what otherwise appear as isolated events in the biotic and geomorphological history of south-central Africa, which turn out to yield invaluable consilient insights (Chapters 4 & 5). Structured by a taxonomic revision (Chapter 7), details of the evolutionary history of lechwe antelopes - especially phylogeographic patterns (Chapter 6) are interpreted through the same palaeontological strategy.

Thus, complementary palaeontological investigations into the relatively recent history of a wetland archipelago has combined many parcels of scattered evidence. A synthesis of interlinked biotic and geological patterns is framed within a metaphysics of historically derived entities, which are treated as individuals (following Ghiselin 1997, 2005a,b). Moreover, this ontology is critical to we treat the species category, and actual species (pertinently lechwes) where it prescribes how such species can be characterized (Chapter 3). The category of the species is quintessential if this study is to classify and discuss ideas, data and findings. Tensions over different concepts of the species category continues to fan a contentious debate in contemporary biology and the philosophy of science. Several conflicting concepts of species are in widespread use, even though they classify biodiversity in incompatible ways. These errors in taxonomies tend to ramify widely, and manifest in inaccurate and imprecise decisions. The sources of dissension in this debate sit firmly in the domain of metaphysics; where they turn out to fall, with surprising neatness, into the domains of ontology and epistemology. I devote quite some space to articulate a solution to this problem. This necessitates recourse to fundamental matters of metaphysics, with attention to complementary subjects arising in ontology and epistemology. Eminently, these disciplines interface - intricately linked - to structure the foundations of what Ghiselin (2002a) has aptly termed the "new evolutionary ontology".

1.9 CONCLUSIONS

Where ever historical processes have determined the patterns whose origins we seek to elucidate, then the disciplinary scope of a study has to be broadened in order to seek out these hidden connections and cryptic pathways of causation (Richards 1992). Analogously to Mayr (1961), many of us may be happy to classify such patterns along a simple, dichotomous aetiological schema dividing proximate from ultimate. Even though geological phenomena are usually classified as ultimate controls on living entities by biologists, divvying up these abiotic and biotic patterns is not always straightforward. This especially applies to this study, which seeks to decipher the history of recently speciated biota, inextricably linked with complex palaeo-environmental dynamics.

Last, but by no means least, criteria of scholarship have important bearings on how one studies historical phenomena. This is not the place to review citation patterns. Nonetheless, much of the current literature, in certain academic disciplines, exhibits the unfortunate tendency to ignore important evidence because it was published decades back, perhaps because it is judged obsolescent, if not obsolete. Fortunately, thorough citation remains the quintessential practice if taxonomy is to meet its fundamental scientific objectives. Sparse citation can perhaps be excused where contributions embroider prevailing theory, or alternatively challenge the orthodoxy with genuine, new ideas. This study highlights, repeatedly, how primary discoveries published decades back can continue to provide critical platforms on which to frame modern knowledge. Exemplary platforms for this study include Clark (1950) for archaeology; Du Toit (1933) and Dixey (1944, 1955a,b) for geomorphology; while key metaphysical foundations articulated by Simpson (1940, 1951) continue to structure evolutionary biology and systematics. This situation reminds one of Lawton's (1994a) argument that there is little new under the sun with respect to established research terrain, unless where one ventures across utterly unexplored frontiers of scientific exploration!

1.10 THE SCOPE AND STRUCTURE OF THIS THESIS

Adequate attention to these interrelated questions has necessitated research into the variation of three character sets. One represents the morphological differences within and among principal populations of the *K. leche* complex. The second and third databases comprise molecular genetic sequence data to describe and resolve lechwe phylogeography and taxonomy, respectively. Where necessary, morphological and genetic data on related reduncine species are also included: namely the Nile lechwe, *K. megaceros*, Waterbucks of the *K. defassa* and *K. ellipsiprymnus* species complexes, and Puku, *K. vardoni*. As explained above, attention to interrelated historical phenomena lengthened this thesis. I summarize below the overall structure of this thesis with respect to the stated objectives. A resume of the scope, aims and salient aspects of each chapter are presented in the respective paragraphs below:

Chapter One, the present introduction establishes the scope and background to the project, and presents the interrelated objectives of this study (above). The multidisciplinary scope of the thesis is emphasized, given the aims of understanding the historically derived properties of lechwe antelopes in the context of present and antecedent environments. These disciplines primarily involve zoology and mammalogy, systematics, phylogeography, geology, geomorphology and molecular genetics. Because archaeological data can help constrain the dates and tenures of landforms, this study has also drawn together pertinent evidence from the archaeological record, given the focus on Quaternary history (over the past 1.6 million years). The underlying philosophical tenets of this investigation are discussed. I briefly explain how the research focus on historical entities (evolution of lechwes and their habitats) establishes the aetiological scope of the thesis, especially the geological context of explications for evolutionary origins.

Chapter Two has two interrelated aims. One is to summarize knowledge about the evolution of the Reduncini, and review the behaviour, ecology and natural history of the *K. leche* complex. This review focuses on the natural history of lechwe antelopes in the context of their floodplain habitats, to cover a major portion of south-central Africa. My second, allied, aim is to identify the natural region that frames the overall study, and here the knowledge, already synthesized, provides essential background to delimit this study area. Synthesis of traditionally disparate subjects in Chapter 2 highlights important aspects of the ecology of lechwes, and the tight dependency of lechwes on floodplains. It is clear that these antelopes are important interactors in the overall ecology of drainage systems. Lechwes influence vegetation structure of floodplains, and thus important aspects of the spatial and temporal patterns of primary production. Intimate associations between lechwes and

floodplains has manifested in many mutualistic associations between lechwes and other aquatic organisms, as evident in the foraging behaviour of waterbirds. Understanding where lechwes occur, and have evolved, sets the scene to identify the natural region that can frame the geographical scope of this study. The final section of Chapter two seeks to marry traditionally disparate classifications of aquatic versus terrestrial landscapes. It turns out that the Zambezi grasslands, dominating the Zambezi phytoregion (White 1983), are of key relevance to understanding, and studying, lechwe antelopes, especially with respect to landscape evolution. Vegetation maps accurately reveal a patchy distribution of islands of grasslands and floodplains. They constitute a proxy indicator of where populations of lechwes can disperse and persist in the landscape. These islands are maintained by seasonal flooding of large rivers, and together form an archipelago of wetlands. This wetland archipelago has framed evolutionary dynamics of a diverse biota since at least the Neogene; and its spatial domain conveniently frames the scope and studies of this thesis. Its overall extent is defined as the Katanga-Chambeshi region.

Chapter Three presents a detailed argument to define the taxonomic treatment applied to the *K. lechwe* complex, and in fact all biodiversity. Here the nature of the species category is critical, with respect to how the evolutionary entities that comprise biodiversity are defined, characterized, and studied. The microtaxonomic focus of this study accents the question of “What is a species?”. Different definitions of the species category, and how they are applied, can lead to disparate classifications of biodiversity, which differ in recognized taxa and their topology. Scientific consequences of taxonomic errors tend to be serious. Two examples are how evolutionary history is interpreted and conservation priorities are decided. Both are central concerns in this study, which seeks to explain the evolutionary history of large mammals with respect to geological events. A vast, contentious and complex literature is relevant to these questions. They are of a fundamentally philosophical nature, and it turns out that their solution lies firmly within the territory of metaphysics. A pertinent aspect of this controversy pertains to trinomial taxonomy - especially relevant to classify complexes of closely related vertebrates such as lechwes. Are there coherent philosophical reasons that justify use of the category of the subspecies, or one (among several of the defined) Evolutionary Significant Units (ESUs)? Many possible ways exist to defend one’s taxonomic treatment. Invariably, this entails arguing in favour of one species concept against many competitors. In addressing these underlying issues, the first section of Chapter 3 begins with an examination of the philosophical tenets that frame the species debate. This begins by reviewing the ontology of biodiversity that evolutionary biologists are challenged to study and characterize. I consider how living entities are most objectively conceptualized and studied, with central attention to

evolutionary patterns and processes. I focus on how unique lineages manifest as historical products of evolutionary processes. This ontological stage frames consideration of species and speciation. I then discuss how to objectively evaluate evidence for speciation events, and characterize species. The chapter concludes with a summary of this philosophical argument, which is structured by the Individuality Thesis of Ghiselin (1997).

Chapter Four reviews the evolutionary history of the study region described in Chapter 2, and its findings are refined further in Chapters 5. The aim of Chapter 4 is to present a synopsis of the evolutionary history of the Katanga-Chambeshi region. I focus on modern and antecedent drainage systems. This review is framed by Africa's geological history, which structures much new geomorphological data synthesized with biogeographical patterns. Its reconstruction pertains primarily to late Cenozoic history: late Neogene and Quaternary (~4 million years to Present), and I focus on landforms relevant to the evolutionary dynamics of lechwe antelopes. Very ancient aspects of Africa's geological history frame this review in important ways, and the continent's unusual topography receives due attention. The extreme elevation of Africa's hinterland reflects its persistent uplift over hundreds of millions of years. This has profoundly controlled the nature of drainage within and off Africa. Dynamics associated with the East African Rift System have been as critical in forming and modifying landforms throughout the Katanga-Chambeshi region. Vicissitudes of past climates are also important, especially with respect to wetlands, so its understanding stands to benefit from consideration of extant landforms. Published data were unfortunately found to be very incomplete, and also outdated. Where available, geomorphological reconstructions of several important drainage systems are now over fifty years old. Whilst the evolution of the Zambezi river is comparatively well understood, the timings of many geomorphological events are not tightly constrained. This review also reveals that geochemical dates of Quaternary landforms are unreliable, which constitutes a critical weakness. So I extended this literature review in Chapter 4 to refine key geomorphological events in finer detail. This employed and synthesized two datasets. One comprises remotely-sensed geospatial data, analysed in a GIS context. This rendered fine-grained representations of topographic structure, which greatly facilitates deciphering and interpreting aspects of drainage evolution directly relevant to understanding lechwe evolution. The second dataset - the Biogeographic dataset brought together distributional data for certain groups of aquatic organisms, especially fishes. Patterns in fishes' distributions reveal key aspects of drainage evolution. These collective insights are summarized at the end of Chapter 5 in a model that reconstructs drainage history.

Chapter Five refines the findings of Chapter 4 into a more precise context. Its encompassing aim is to refine the tenures of formations and tenures of wetlands in the Katanga-Chambeshi region. Thus, insights into the evolution of landforms, revealed in Chapter 4, are now integrated with chronological data to reconstruct the evolution of the Katanga-Chambeshi region. It turns out that facets of the archaeological record hold centre stage in this endeavour. Where evidence permits, the resulting narrative describes principal changes in palaeo-drainage since Miocene times, and emphasizes key events invoked to explain how drainage topologies changed over the past five million years.

Attainment of the first aim entails a focused study of the erosion history of the Batoka gorge: created by the Zambezi river through the westward retreat of the Victoria Falls (Mosi-wa-Tunya). It pays special attention to the stratigraphy of the Victoria Falls Formation (VFF). The general lack of geochemical dates, and unreliability of nearly all those published for lacustrine and alluvial sediments in the region dictated a recourse to a chronological record of Quaternary history, represented in tenures of Africa's Stone Age cultures. Fortuitously, the VFF is rich in stone age artefacts, previously studied in detail by Clark (1950). The history of erosion of the Batoka basalts by the Zambezi exhibits distinct controls by a combination of tectonics and Pleistocene palaeo-climates. These events interacted intimately with tenures of palaeo-lakes in the region. Key sediments testifying to these events can be reliably dated by the stone age artefacts they preserve. Chapter 5 first describes the representative details in these archaeological, climatic, and geomorphological datasets. Their synthesis is structured by refined chronologies delimiting tenures of stone age cultures over the past decade. The chronology of sedimentary events revealed in the revised stratigraphy presents pertinent findings relating to tenures of palaeo-lakes in northeast Botswana and Zambia. They also provide hitherto unavailable constraints on timings of river capture events, perceived critical to the vicariant evolution of lechwe antelopes. The final section of Chapter 5 presents a revised model of drainage evolution for the Katanga-Chambeshi region. Where possible it places principal findings of Chapters 4 into the temporal framework of Chapter 5. This narrative can now be related to aspects of the evolutionary histories whereby lechwe antelopes populated changing landscapes.

Chapter Six describes, analyses and applies findings represented in the dataset comprising 208 mtDNA sequences of the control region marker for the entire *K. leche* complex. Nearly half this total sample (89) was obtained from museum specimens. It provides otherwise unattainable insights into important populations (including extirpated populations). Subject to limits of sample sizes and resolution of sequenced markers, phylogeographic analyses reveal salient aspects of the evolutionary histories of each lineage. The overall phylogeographic structure exhibited in these populations is

explained in the context of the wetland archipelago in which these antelopes have evolved. Comparisons of the four principal populations analysed in this phylogeographic study reveal important differences between populations. Emphasis is placed on estimates of lineage divergences, and aspects of demographic histories of lechwes. These findings are discussed in the context of the geological history of the Katanga-Chambeshi region presented in Chapters 4 and 5.

Chapter Seven describes and interprets two datasets. One describes the variation in the morphology of the *K. leche* complex, as represented by cranial and pelage characters of 171 specimens. These analyses of morphological characters are followed by the analysis and discussion of variation obtained in the second, genetic dataset, of molecular markers sequenced in this study, which complement the phylogeographic study of Chapter 6. These are the mtDNA marker Cytochrome b gene region; intron 1 of the nuclear gene B-spectrin nonerythrocytic 1 (SPTBN-1), and a haplotypic Y chromosome marker. The latter comprised the complete sequence of the sex-determining region (SRY) and adjacent non-coding sequence. Intron-7 of β -Fibrinogen and the entire sequence of Protamine 1 were also sequenced. The combined evidence revealed in these morphological and molecular datasets is compared and discussed - in order to reappraise the diversity of the *K. leche* complex. Here I revise and discuss the taxonomy of these large mammals, with recourse to the philosophical argument presented in Chapter 3. These findings and discussion are also structured by the narrative of evolution of the Katanga-Chambeshi region (Chapters 4 and 5).

Chapter Eight synthesizes the findings of the entire study. I present a synopsis of the evolutionary history of the *Kobus leche* complex, as revealed by phylogeographic and taxonomic studies. It centres on how phylogeographic and taxonomic patterns causally relate with the palaeo-environmental narrative. The broader relevance of new insights obtained into Quaternary landscape evolution are discussed with respect to biogeographical and evolutionary insights. The multiple lines of evidence, brought together in this thesis, reveal hitherto unknown aspects of the evolutionary history of an archipelago of wetlands. Where possible, the aetiological aspects of these findings are emphasized, with respect to elucidation of interacting controls over lechwe evolution, and the spatial and temporal context of evolutionary events. The significance of changes in biota and landforms (notably their shared links), are helpfully understood within the framework of an interrelated biogeographical unit, the Katanga-Chambeshi region. These phenomena deserve due attention in the study and management of wetlands and their biodiversity.

CHAPTER 2



▲
A breeding herd of Red Lechwe, *Kobus leche*, on a water meadow in a narrow channel of the Lufupa River at the end of the hot, dry season. Busanga Swamps, Kafue National Park. October 2002.
Photograph: F. Cotterill

A female Red lechwe, *Kobus leche* with her young lamb effect swift passage across a floodplain.
Photograph: Mitsuaki Iwago



CHAPTER 2 THE NATURAL HISTORY OF LECHWE ANTELOPES IN A WETLAND ARCHIPELAGO

“It can be shown that the lechwe is the dominant herbivore on the range it utilises, and that it is not possible to maintain herds of domestic stock wholly on their range. Therefore it is postulated that the lechwe herds constitute a resource of national importance, and that this can be profitably developed by conservation of this species of antelope. It also follows that without lechwe these specialised pastures would be a wasted asset.” L. D. E. F. Vesey-Fitzgerald (1963:143)

2.1 INTRODUCTION

This chapter has two objectives. One is to review published knowledge of the natural history of lechwe, *K. leche*, antelopes. The second is to define and describe the geographical area under study. The ecology and behaviour of lechwes, in the context of their unique specializations to floodplain habitats in south-central Africa will be described. In addition the wetland habitats inhabited by lechwe will be described with attention to their ecological importance and geomorphological significance. Synthesis of scattered evidence reveals that lechwes are unique among large African mammals in their dependency on floodplain grasslands and they play an important role in the ecological dynamics of these productive landscapes. It has been hypothesized that several wetland plants have evolved adaptive responses in their growth patterns in response to sustained disturbances from lechwes. Since the salient attributes of lechwe pastures are relatively well understood, it is feasible to map these islands of habitats across south-central Africa.

In an attempt to reconstruct historical ranges before human depredations reduced lechwe populations, specific attention is paid to the historical status of lechwe populations confined to principal wetlands. The modern distribution patterns largely reflect the fragmented artefacts of much larger populations. They clearly represent only the survivors of severe extirpations that have impacted on these antelopes since the mid-1800s. From an evolutionary perspective these human-induced changes in lechwe distributions deserve detailed attention, because a review of the evolutionary history of the *K. leche* complex would yield most misleading results if based solely on extant populations.

It is reasonable to expect an evolutionary study to approximate the spatial domain where the study organisms have evolved. In this case of lechwe antelopes, identification of the central African wetland regions turns out to be a revealing exercise. Aspects of the natural history of lechwes reveals salient attributes of their habitat requirements and constraints prescribing where populations can and cannot persist. This might suggest that such an overall study area, defined by these key properties would make for

a large region; so one could logically review whether well known natural regions (especially biomes and ecoregions) set such a convenient framework. Unfortunately, classifications of aquatic and terrestrial landscapes have developed along very different traditions. Moreover, any attempt to define a study area, framing a study of lechwe evolution, is challenged to integrate wetlands (and also interlinking drainage systems) with respect to terrestrial habitats. Historical evidence is critical; and here the geology and geomorphology of these landscapes provides both important evidence and essential context. Equally, dynamics of past climates cannot be ignored. It turns out that this study of lechwe evolution is served best by recognizing that the region's wetlands comprise an archipelago. The outer limits to this natural region correspond to the spatial domain within which aquatic biota and landforms share a common heritage of evolutionary interactions. This evolutionary theatre, an archipelago of inland basins and interconnecting rivers is termed the Katanga-Chambeshi region (Cotterill 2004, 2005); and its total extent is similar in important respects to that of the Zambezian phytochorion defined by White (1983, 1993).

2.2 NATURAL HISTORY AND ECOLOGY

2.2.1 Evolution

Lechwe antelope belong to the Reduncini whose origin dates back 10-12 Mya (Vrba 1985). Approximately 6.5 million years ago, as represented by fossils in East Africa, reduncines were well represented among the grazing bovids that had come to dominate grazing assemblages (Turner & Antón 2004). Diagnostic characters of reduncine antelopes include transverse ridges on the horns (typically present only in males); a large maxillary tuberosity; and no less than three diagnostic dental characters (Gentry 1990). The phylogenetic relationships of Grey rhebok, *Pelea capreolus*, presented persistent problems to bovid classification, but recent morphological and molecular evidence reveals it is a primitive taxon within the Reduncini (Bronner *et al.* 2003). The group formerly also occurred in Asia (as of 5 million years ago), although published records need to be treated with caution, as most fossil evidence for this claim has not withstood scrutiny (Vrba 1995a). Kingdon (1982) suggested that ancestral reduncines dispersed out of Africa along the Nile valley to Asia. Nevertheless, the identity of the closest extant relatives of the Reduncini proved challenging to discern, an uncertainty revealed in contrasting classifications of the Bovidae. Vrba (1979) concluded that the Reduncini diverged from a clade which ultimately formed the Neotragini (steenbok, suni, royal antelope, and grysbok). This treatment was followed by Meester *et al.* (1986) and Skinner and Smithers (1990). Based on morphology, neotragines are considered to be primitive antelopes, as exemplified by *Raphicerus sharpei*, Sharpe's grysbok. This suggestion was based principally on puku, *Kobus vardoni*, which

possess a vestigial preorbital gland common to all neotragines. Additional evidence is represented in the ontogeny of horn growth in waterbucks, lechwes and reedbucks. Primitive swept back horns (a shared neotragine trait) in juveniles develop into the longer, lyrate horns of adult reduncines (Vrba *et al.* 1994). Indeed, reduncine evolution exhibits a trend leading to elaboration of horns and scent glands (Kingdon 1982).

In a different taxonomic treatment, Gentry (1990) treated Reduncini as sister to the Hippotragini (oryx, sable, roan and allies), but acknowledged the understanding of bovid relationships (above the genus level) to be poor. A derived character shared among these antelopes is the enlarged basioccipital bone at the rear of the skull, which anchors insertion of the enlarged longus capitis muscle. This adaptation permits powerful and rapid downward head movements in alcelaphines, hippotragines and reduncines (Gentry 1990). Nevertheless, as Kingdon (1982) argued, its possession might not necessarily reflect common ancestry. Separate fossils from Langebaanweg, South Africa and Pinjor, Siwaliks (Pakistan) suggest the Reduncini to be paraphyletic. In this respect, Gentry (1990) noted that certain characters in *Ourebia* (traditionally treated as a neotragine) are more reminiscent of reduncines than neotragines. For example, the subauricular glands of oribi, *Ourebia ourebi*, are very similar to mountain reedbuck, *Redunca fulvorufula* (Kingdon 1982; Vrba *et al.*, 1994). Dependence of oribi on mesic habitats, with surface water, and their loud whistling call (reminiscent of reedbucks) further supports inclusion of *Ourebia* in the Reduncini. Most neotragines occur in dry forest, savanna and desert. Given its resemblance to neotragines, with reduncine affinities, *Ourebia ourebi* could be a primitive reduncine. The phylogeny of the Bovidae still await detailed study to resolve higher level relationships (Hernández Fernández & Vrba 2005). More recently, molecular characters rejected many of the morphological similarities based on convergence, but confirmed the Reduncini to be monophyletic, with *Pelea capreolus* a primitive member of this group (Gatesy *et al.* 1997; Matthee & Robinson 1999a; Hassanin and Douzery 1999). Higher level investigations into the family Bovidae strongly suggest a sister taxon relationship between the Hippotragini and Alcelaphini (Gatesy *et al.* 1997; Matthee & Robinson 1999a; Hassanin and Douzery 1999; Matthee & Davis 2001; Matthee *et al.* 2001), but the exact position of the Reduncini remained uncertain (also see Hernández Fernández & Vrba 2005). At the lower taxonomic level (among species) the evolutionary associations among species seems more clear. A mtDNA cytochrome b phylogeny reveal the waterbucks of the *K. defassa* and *K. ellipsiprymnus* complexes to be the closest living relatives of the extant *K. megaceros* and *K. leche* complex (Birungi & Arctander 2001; Chapter 7).

Fossils very similar to extant *K. leche* were recovered from Twin Rivers, used by Middle Stone Age *Homo* (Lupemban culture). Twin Rivers borders the Kafue Flats in central Zambia. These lechwes were part of a large mammal assemblage also including taxa similar to today, with the notable presence of Square-lipped rhinoceros, *Ceratotherium simum* (Clark & Brown 2001; Chapter 5). Lechwe fossils can be invoked to indicate distinctly pluvial palaeo-environments, assuming these antelopes depended on sufficiently large perennial wetlands. It is thus interesting that lechwe antelopes occurred at Florisbad on the South African plateau (28° 46' S, 26° 04' E) during the Middle Pleistocene (Brink 1987, 1988). Broom (1913) described these fossil lechwe as the extinct *K. venterae*, which Klein (1984) lumped into *K. leche*. Nevertheless, Brink (1987) emphasized that the cranial morphology of these Florisbad fossils is distinctly different from extant lechwes. Early Pleistocene fossils of lechwe in the Cornelia sediments, east of Florisbad, were also assigned to *K. leche*, although their similarity to *K. venterae* was noted (Butzer *et al.* 1974). With reference to Lake Ngami, the historical southern limit in the overall range known for these antelopes (Fig. 2.1), these fossils extend the former range of the *K. leche* complex over 950 km south (Brink 1987).

2.2.2 Historical Attention, Previous Studies and Conservation Concerns

The spectacular diversity of African vertebrates has attracted societal and scientific interest for centuries since their first scientific descriptions. This is especially true of the large mammals. The halcyon era for scientific discoveries of large mammals extended from the late 1700s into the early 1900s; when the Red lechwe, *K. leche* and Black lechwe *K. smithemani* were formerly described in 1850 and 1899 respectively (Spinage 1995; Grubb 1993, 2005, Chapter 7). At the close of the 19th century, knowledge of the Bovidae had accumulated sufficient to fill four volumes of an inaugural synthesis - *Book of Antelopes* (Sclater & Thomas 1894-1900). It was followed by the five volume *Catalogue of Ungulate Mammals in the British Museum (Natural History)*. The treatment of the Reduncini in its Volume II by Lydekker and Blaine (1914) summarized what little was then known about the taxonomy and distribution of the *K. leche* complex. Thereafter, the natural history of lechwes was mentioned in several publications (e.g. Lyell 1913); and two partial reviews of lechwe taxonomy were also published (Derscheid 1926; Barclay 1933).

Attention to lechwes burgeoned through the 1950s, especially in Zambia, particularly with conservation concern mounting over declining populations on the Kafue Flats and Bangweulu Swamps (Ansell 1955; Grimwood *et al.* 1958; Allen 1963; Mitchell & Uys 1963). These led to summaries of natural history of the principal populations (Ansell 1964, 1968; Smithers 1971), and aspects of reproduction (Robinette & Child

1964). Accounts of the status of surveyed populations have appeared regularly since the 1960s in Zambia (Hanks 1969; Grimsdell & Bell 1972, 1973; Kamweneshe 2000). The ecology and conservation status of Red lechwe in northeast Botswana was also reported on (Lent 1969; Child 1975; Robbel & Child 1975). The prescient insights of Vesey-Fitzgerald (1963, 1965) stand out today, in his emphasis that lechwes are uniquely adapted to exploit water meadows in floodplains. This succinct emphasis on the significance of “lechwe pastures” predated thorough studies in the 1970s (Rees 1978a-d) on the ecology of *K. kafuensis*, and by Ellenbroek (1987) of the plant ecology of the Kafue floodplain. By comparison, detailed information about the biology of the equatorial endemic, the Nile lechwe, *K. megaceros*, is sparse. Virtually all that is known about this threatened wetland specialist was published by Falchetti *et al.* (1993). The total population was estimated at approximately 30 000 - 40 000 animals in 1983, confined, more or less entirely, in the Sudd region of southern Sudan. The population in southeast Ethiopia is nearly extinct (Falchetti 1998; East 1999).

These studies of Kafue lechwe were paralleled by detailed studies of Black lechwe (Grimsdell & Bell 1975) and Red lechwe in Botswana (Williamson 1979, 1981). The extension to 1985 of the latter study in Linyanti culminated in five papers (Williamson 1990, 1991, 1992, 1993, 1994). This population of *K. leche* is one of the three taxa whose behavioural ecology has been studied in detail. The demonstration that Kafue lechwe are also lek breeders (Schuster 1976) followed on the first description of a lek breeding system in a mammal. This was described in another closely related reduncine antelope, *Kobus kob*, in Uganda by Buechner (1961). It was followed by a detailed study of the breeding biology of *K. kafuensis* (Nefdt 1995, 1996), which was later compared with *K. smithemani* (Thirgood *et al.* 1992; Nefdt & Thirgood 1997) and also *K. kob* (Deustch & Nefdt 1992).

Attention to the conservation of lechwes in Botswana and Zambia persisted (e.g. Schuster 1980; Howard *et al.* 1984; Thirgood *et al.* 1994), and has continued (e.g. Ross *et al.* 1998; Kamweneshe 2000; Kamweneshe *et al.* 2002). These testify to dwindling populations, emphasizing alarms sounded well before the 1950s (Hughes 1933; Brelsford 1944). All populations of the *K. leche* complex have suffered severe reductions in range and numbers under burgeoning human impacts. When considered on a palaeoecological time scale, humans very recently became a dominant agent of disturbance in lechwe habitats. This is either through direct depredation, habitat modification (especially through fires and hydrological developments) or competition from domestic herbivores. Batwa swamp dwellers in the Bangweulu Swamps depended on Black lechwe as a source of protein second only to fish (Von Rosen 1916; Crabtree 1917; Hughes 1933).

Dried fish and lechwe meat were traded for subsistence goods with tribes around the Bangweulu basin. Brelsford (1946) identified an increased decline of Black lechwes during the 1930s and 1940s. This followed the growth of commercial hunting after the First World War, where after lechwe meat began to be exported from Bangweulu to feed mineworkers on the Zambian CopperBelt (Grimsdell & Bell 1975).

Since their discovery by westerners in the 19th century, lechwe antelopes have been coveted as hunting trophies. The importance of lechwes as trophies was emphasized in many natural history writings, including Selous (1881, 1908), Letcher (1910, 1912) and Lyell (1913). Hughes (1933) emphasized that hunting expeditions to the Bangweulu Swamps primarily targeted Black lechwe as trophies. Lechwe continue to feature prominently in safari areas of Botswana and Zambia; where they are premium hunting trophies as part and parcel of lucrative safari and tourism industries (East 1999). This is exemplified for *K. kafuensis*, where annual income from national and trophy hunting generated a minimum of US\$47 459 and US\$60 315, respectively, between 1995 and 1999 (Siamudaala *et al.* 2005)

2.2.3 Behavioural and Ecological Adaptations

Lechwes are uniquely adapted to exploit the rich pastures of floodplains and swampy wetlands, and have evolved interesting specializations to this environment. While sitatunga, *Tragelaphus spekei*, are highly specialized to life in dense, permanent swamps that extend over deep water, lechwes exploit the shallower margins of wetlands (Spinage 1986; Cotterill 2000). Adaptation to perennially swampy habitats has entailed the evolution of interesting specializations to exploit the rich grazing available in the unpredictable environment of floodplains, where disturbances are frequent. These latter principally entail floods, cursorial predators, and seasonal fires. Parasite loads also appear to be important in the ecology of lechwes (Kingdon 1982; Stafford 1991; Kock *et al.* 2002).

The evolution of leks in lechwe and other ungulates is characterized by clustered territories defended by a minority of dominant males, while females form large unstable groups (Clutton-Brock *et al.* 1997). The different mating systems of lechwes reflect adaptations to local conditions of resource availability. Male Red lechwe in Linyanti defended discrete patches of habitat exploited by oestrus females. Black lechwe on the Bangweulu Flats also demonstrated a form of resource-defense polygyny, which is interpreted as a behavioural response to grazing resources distributed across a more homogenous grazing environment compared to Kafue lechwe. Compared to Black lechwes, female Kafue lechwes forage more erratically; so it

appears that encounters rates with males are relatively lower. It has been inferred the lek mating system of *K. kafiensis* has evolved as an adaptive response to patterns of habitat selection by females and larger female herds (Nefdt & Thirgood 1997).

The evolution of lechwe life histories is interpreted as an adaptation to high levels of predation, and the regime of stochastic disturbances that characterizes their physical environment. Dependency on floodplains expose lechwe antelopes to frequent disturbances: including diseases, parasites, fluctuating water levels associated with climatic extremes (floods through droughts), fires and predation. To optimize reproductive success, females time the most energetically costly investments of reproductive efforts to coincide with periods when floodwaters recede. Their high reproductive output is a function of rapid growth to maturity, with a relatively young age at first reproduction in females. Reproductive outputs are high compared to antelopes of similar body size. For example, Red and Black lechwes reach adult size at 2.5 years and 1.5 years, respectively; and female Black lechwe in good condition can bear young at just one year old. Lechwe lambs are comparatively precocial, once they have survived the critical lying-out period (Robinette & Child 1964; Grimsdell & Bell 1975; Williamson 1991, 1992). Comparisons of studied species have revealed that density dependent effects regulate population growth. Condition of female Red lechwe in the Linyanti was poorer compared to females of Black lechwe in Bangweulu; and the latter grow faster and reach sexual maturity at a younger age. Nearly 100% of these adult females were fecund compared to only 83% of Red lechwes in Linyanti (Williamson 1991). The higher reproductive output in *K. smithemani* manifests in a population increase of 25% per annum that followed from a drop in heavy predation pressure. It appeared that this population was then far below carrying capacity, and yearling females were breeding (Grimsdell & Bell 1975). Lechwe also exhibit interesting plasticity in life history traits. Nefdt (1996) revealed the calving peak has shifted by five months in *K. kafiensis*, since impoundment of the Kafue river in the 1970s. The majority of females now exhibit a peak in lambing to optimize parturition with the artificial flooding regime of the Kafue Flats.

Episodes of unprecedented flooding (e.g of the Bangweulu basin in 1937, Grimsdell & Bell 1975) can cause unprecedented mortality, notably through drowning (especially of juveniles). The relative scarcity of forage during floods manifests in lower fecundity and higher mortality; even though lechwe can graze in water meadows flooded to over a metre, rapidly cropping growing swathes of aquatic plants (Williamson 1991, 1992). Several studies suggest that parasites and diseases are important in the population ecology of Kafue

lechwe, which host a diversity of microbial pathogens and parasites (Stafford 1991; Kock *et al.* 2002). It appears that *K. kafiensis* possesses relatively high resistance to disease as these antelopes harbour bovine tuberculosis, *Mycobacterium bovis*, which manifests virulently in other bovid species, including waterbucks, hippotragines and alcelaphines (Zieger *et al.* 1998; Kock *et al.* 2002; Siamudaala *et al.* 2005). Lechwe also host several external parasites, of which larvae of warble flies (Diptera: Oestridae) appear to be most prevalent. They infected up to 95% of young lechwes sampled (Howard 1975, 1980; Stafford 1991).

2.3 ECOLOGY OF AFRICAN WETLANDS

2.3.1 Overview

African floodplains are highly productive landscapes, where turnovers of herbaceous plants are high. This is a function of the seasonal flooding regime; and accumulation and retention of nutrients into aquatic plants, which exhibit many adaptations enabling rapid growth (Howard-Williams & Gaudet 1985). The ecology of floodplains is dominated by the seasonal hydrological regime of its catchment. The properties and dynamics of the principal rivers and lakes strongly regulate flooding of surrounding floodplains. Africa's wetlands are unique in the dominance of floating swamps, principally *Cyperus papyrus*, on deeper, permanent water bodies. Autotrophic production in these floating swamps is very high compared to rooted swamps. For example, papyrus production in the Upemba Swamps averages 48 - 148 t ha⁻¹ yr⁻¹. Remarkably, this productivity of papyrus occurs under a regime of low nutrient conditions, yet exceeds productivity of intensively farmed tropical seed crops, because nutrients and carbon trapped in large rhizomes of papyrus sustain rapid growth of young culms. Nevertheless, the biomass of large mammals supported in these floating swamps is far lower than that in terrestrial savannas on eutrophic soils, such as the Serengeti-Mara grasslands (Thompson *et al.* 1979; Howard-Williams & Gaudet 1985; Fritz & Duncan 1994). These mats of *Papyrus* and *Typha* can be colonized by other plants, including wetland adapted grasses (*Vossia* spp.), which may be marginally exploited by lechwe.

The floodplains and floating swamps are linked by trophic processes. Here, the euhydrophytic zone of floating aquatic plants in shallower water forms an important ecotone between deeper, open water, and the shallower water meadows (Thompson *et al.* 1979; Denny 1985). This ecotone between floating swamps and floodplains approximates the limits in water depth where lechwe forage (although they readily swim deep channels). Trophic dynamics between floating swamps and the surrounding floodplains have yet to be thoroughly quantified. Nevertheless, in addition to water flow, fluxes of nutrients, and energy across these

landscapes appears to be influenced strongly by vertebrates: notably fishes, hippopotamuses, and also lechwes, sitatunga, and waterbirds.

2.3.2 Ecology of Lechwes in Wetlands

Lechwe antelopes graze entirely on the comparatively high quality forage in wetlands. The bulk of their forage includes grass species restricted to water meadows and floodplains (Rees 1978a-d; Williamson 1979), which are high in crude protein, and palatable even when dry (Gaudet 1992). These landscapes are buffered against the marked seasonality that controls the phenology and productivity of grasslands in terrestrial savannas (Walker 1987). Ecologically dominant species in lechwe pastures include C3 metabolizers, assemblages which differ from those in tropical savannas dominated by C4 species (Ellenbroek 1987). Initial inundation of floodwater initiates decomposition releasing nutrients that foster population blooms, first in phytoplankton, and then zooplankton (Gaudet 1992). The late B. L. Mitchell first suggested a close relationship between lechwes, waterbirds, and fishes on the Kafue Flats, where manuring and substrate disturbance by feeding lechwes accentuate these blooms, mutually benefiting fishes and birds (Anonymous 1958: 235). Mitchell & Uys (1961) further emphasized the significance of an association of foraging birds (especially ducks and geese) with the huge herds of feeding Kafue lechwes. Censuses by Douthwaite (1977) of waterbirds revealed that 8 000 waterfowl/km of shoreline, on average, foraged amongst grazing Kafue lechwe herds. Conversely, an average of only 340 waterfowl/km were counted along an analogous stretch of floodplain, from which lechwes had been extirpated. Douthwaite (1977, 1978) suggested trampling of taller perennial grasses by lechwes enhances access by waterfowl to seeding annuals that flourish in these disturbed patches. Grazing pressure by lechwes was demonstrated to be extremely high, notably in patches of the *Vossia - Echinochloa* assemblages after floodwaters begin to recede. Primary productivity in these patches may exceed $40 \text{ t ha}^{-1} \text{ yr}^{-1}$ (Ellenbroek 1987). These flooded grasslands shelter fish fry and provide forage for larger herbivorous fishes, also benefiting from heavy manuring by the lechwe herds (Williams 1971). This is important in south-central African floodplains, whose soils are inherently low in nutrients being derived from ancient parent rocks (Grimsdell & Dell 1975). The evidence for mutualistic benefits are circumstantial, but certainly worthy of closer study and experimental testing.

2.3.3 Lechwe Diets: Feeding Behaviour, and Coevolution

Ecological associations between lechwes and floodplain vegetation are complex and intrinsically dynamic. The incomplete information available (Vesey Fitzgerald 1965; Grimsdell & Bell 1975; Ellenbroek 1987;

Williamson 1979, 1990) reveals distinct differences in the autecology of lechwes between different environments. The stochastic dynamics of lechwe pastures are exemplified by the Linyanti Swamps. On four occasions (July 1975, March, 1976, August 1976 and March 1977) a vertical increase of only 3-4 cm in floodwaters, measured at the Cuando river, flooded the entire floodplain of 1 200 km² (Williamson 1979). These higher water levels reduced the lechwes' access to quality forage, and their body condition indices declined, especially in yearling females (Williamson 1991, 1992). Similarly, vertical fluctuations around ~2 m of floodwaters across the Bangweulu depression fluctuates seasonally across a margin of 45 km. Large herds of Black lechwes migrate across this floodplain to exploit benefits of the seasonal flood (Grimsdell & Bell 1975).

Floodplains also exhibit distinct patterning in landscape structure, which reflect a subtle heterogeneity in topography. Ellenbroek's (1987) detailed studies of the Kafue Flats revealed that what appears to be a topographically uniform landscape is actually a dynamic mosaic of habitat patches, whose extent and longevity are determined by their subtle differences at the mesoscale (1 - 1000 m²). When the clay-rich vertisols on the Kafue Flats dry out, the surface warps and domes into ridges (20 - 60 cm in height) and small basins (2 - 7 m diameter). Their irregularities across the floodplain determines the patchiness of inundated water-meadows at the mesoscale (Ellenbroek 1987).

Overall, seasonal changes in hydrology govern the trophic regime, and dynamics within and across this mosaic. These larger scale determinants are complemented by mesoscale dynamics governed by these localized patterns in soil composition and topography, which act to attenuate, and also magnify, impacts of flooding across the floodplain. In consequence, primary productivity varies patchily in concert with the hydrological regime. Acting in concert, all these factors determine where, and for how long, herbivores exploit different patches. Intensities and durations of lechwe grazing behaviour varies across this mosaic. Habitat exploitation is very intense, but transient; as the animals concentrate their grazing along the shifting flood line; so grazing pressure forms a wave-like pattern across the landscape, as these lechwe herds track optimal patches of grazing habitats in tandem with hydrological dynamics. The overall result is that lechwe behaviour constitutes a dominant determinant on the composition and dynamics of the vegetated landscape.

The association of lechwes with floodplains appears to have been sufficiently ancient, because close associations have evolved between lechwes and other aquatic organisms. These associations also relate

closely with ecological dynamics governing the landscape; and point to coevolutionary dependencies, originally suggested by Vesey Fitzgerald (1963, 1965). Ellenbroek (1987) demonstrated that high densities of Kafue lechwe, through their grazing and trampling, exercised dominant control over spatial and temporal patterns of primary production of grasslands across the seasonally inundated Kafue Flats. The high rates of recruitment in these plants on the annually replenished eutrophic substrate were interpreted as an adaptation primarily to heavy grazing pressure. This trampling of the soil under high densities of lechwes may contribute to longer term changes in geochemical properties of the clay soils. Trampling is most intense as floodwaters recede. It breaks up the dense mats of grass on the drying floodplain. This disturbance facilitates seeding of *Echinochloa* grasses and their subsequent germination. Allocation of growth in some of these plants is asymmetric, such that most phytomass of the plant is confined under the water surface. Equally, growth tactics of different grass species suggest these plants have evolved growth tactics to optimize somatic investment so as to benefit not just from the predictable chronology of seasonal flooding, but further when periods of grazing pressure are minimized. Such a phenological adaptation manifests, for example, in the annual plant, *Vernonia glabra*. These plants mature quickly, and have seeded before lechwe have invaded the patches dominated by *V. glabra*. Other species of annual plants appear to survive the lechwe invasion by growing within the vegetation swathe (Ellenbroek 1987).

Other characteristics of plant assemblages, exemplified by the species composition in the *Nymphaeae caerulea* lagoon community, also cannot be attributed solely to dynamics of seasonal flooding. Certain plant species fare better under the regime of heavy disturbance of intense lechwe grazing. No less than four dominant grasses in these water meadows are C3 metabolizers. Here, underwater, these C3 plants avoid heavy grazing, but grow adequately in the lower light conditions. One such species is *Oryza longistaminata*, which even though sensitive to heavy grazing, enjoys a competitive advantage over faster growing C4 grasses. Its C3 metabolism allows it to sprout from geophytic rhizomes even though inundated; and it can grow efficiently at depths down to 2m underwater. The near monospecific composition of the *Paspalidium obtusifolium* water meadow is interpreted as a function of heavy grazing pressure by lechwe, when the C3 *P. obtusifolium* out competes the C4 photosynthesizers, *Vossia cuspidata* and *Echinochloa scabra*. Where grazing pressure is lighter, both C4 species dominate these patches changing the composition and structure of the vegetation considerably. *Leersia denudata* provides yet another example of this trade-off between lechwe herbivory, and the physical conditions favouring C3 versus C4 grasses. As a C4 metabolizer, *Panicum repens* requires relatively strong sunlight to photosynthesize efficiently; so when submerged alongside the C3 *L.*

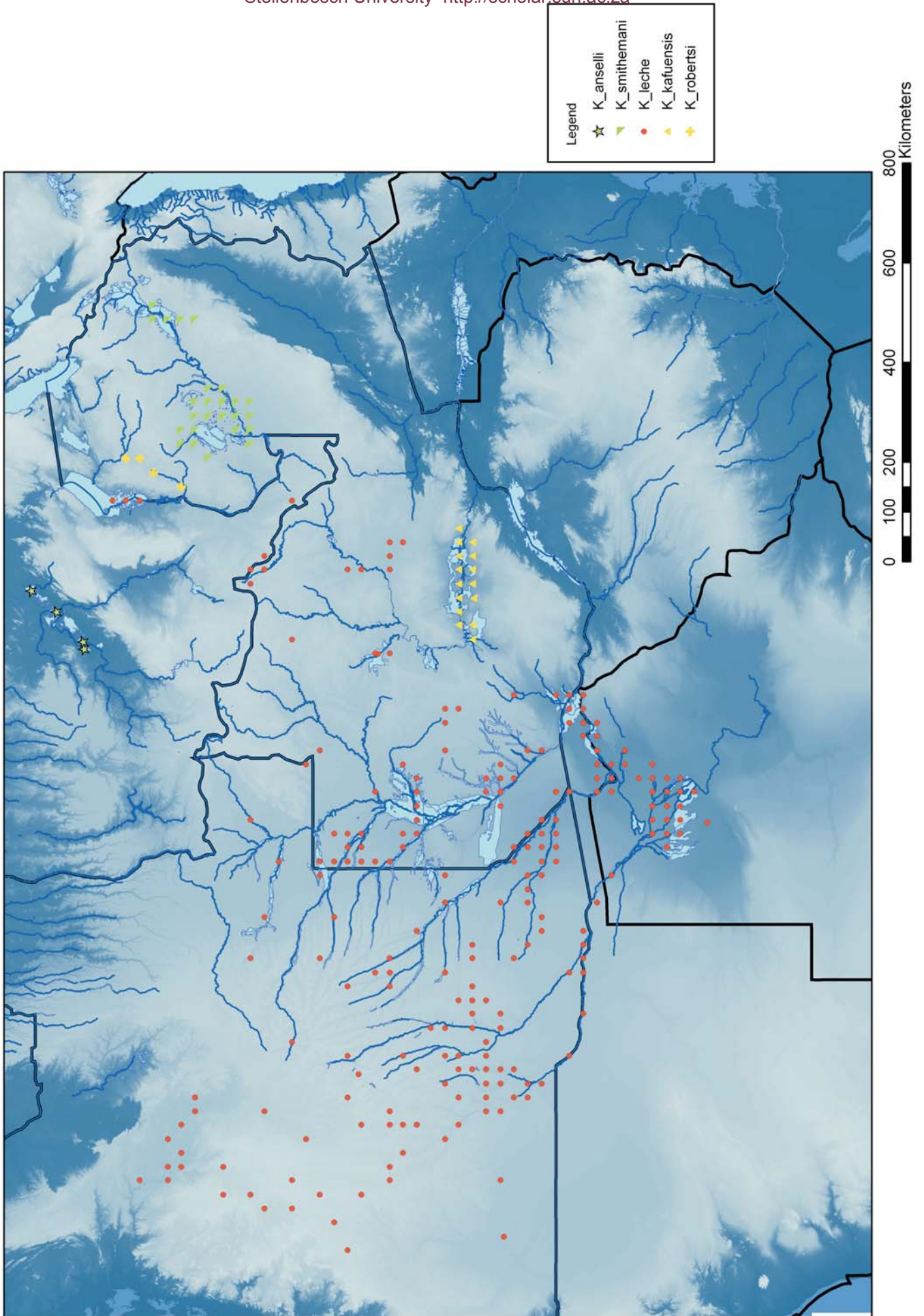
demudata, its growth is strongly inhibited. The combined evidence reveals that all these C3 grasses have evolved convergent solutions to reduce heavy grazing by growing underwater, where they also out compete more vigorous C4 species (Ellenbroek 1987).

The intricacies of these dynamics reveal the importance of lechwes not only in trophic pathways, but also as ecological engineers in floodplains. Furthermore, as revealed in studies of the Kafue Flats, ecological specializations of lechwe antelopes to exploit floodplain habitats points to positive feedback mechanisms operating across and within interactive webs (*sensu* Martinez 1995). I suggest that dynamics and structure of these floodplains can be revealingly conceptualized in terms of landscape ecology. The domain of interactions dominated by lechwes centre on habitat patches whose grain sizes approximate $\sim 1 \text{ m}^2$ and less; and these patches form a mosaic across entire floodplains. The ecological conditions vary among and within these patches, hosting different plant assemblages contingent on local edaphic conditions, and past and prevailing disturbance regimes. This landscape is dynamic, characterized by disturbances that modify its habitats across a spectrum of spatial and temporal scales.

It is also instructive to acknowledge how critical microbes are to energy conversion, not only as decomposers in the substrate, but equally in bovid alimentary tracts. Imai *et al.* (1992) documented a high diversity of Protozoa in the rumens of *K. kafuensis*, that included descriptions of four species new to science. The rumen flora of these Kafue lechwe was interpreted as representing an evolutionary conserved assemblage. Overall, the diversity of their rumen flora exceeds that of other grazing bovids (Imai *et al.* 1992).

Historical records provide further evidence that reveal how dependent lechwe are on floodplain habitats. Changes in the range of Red lechwe in northern Botswana since the mid 19th century exemplify the susceptibility of these antelopes to dynamics of wetlands. The explorer, David Livingstone, and his companions, first encountered *K. leche* near Lake Ngami in 1849 (Spinage 1995); where Andersson (1856) recorded lechwes in abundance around its Taoghe Delta. This was when the Ngami depression supported a

Figure 2.1 (Following Page). Distribution of lechwe antelopes of the *Kobus leche* complex, including Upemba lechwe, *K. anselli*; Kafue lechwe, *K. kafuensis*; Red lechwe, *K. leche s. s.*; Robert's lechwe, *K. robertsi* (historically extinct); and Black lechwe, *K. smithemani*. The localities are vouched for by museum specimens (Appendix 1), and also literature records: Crawford-Cabral (1967), Crawford-Cabral & Verissimo (2005), Schouteden (1947), Ansell (1978), Griffin & Grobler (1991), and Smithers (1971).



perennial swamp. Today, the landscape supports open, semiarid grassland, and is rarely flooded, because flow through the Taoghe river dwindles upstream in the Okavango Delta. In 1970, the closest lechwe to Lake Ngami then occurred just north of Maun - over 60kms to the north (Smithers 1971; Fig. 2.1). This example illustrates how vagaries of habitat change can alter lechwe distributions rapidly. It further exemplifies how subtle changes in hydrological patterns control the ecology of lechwes.

2.4 THE PRINCIPAL WETLANDS OF SOUTH-CENTRAL AFRICA

In this section, I describe the salient features of the principal wetlands in south-central Africa populated by lechwe antelopes. I summarize published knowledge for those floodplains that support, or supported, populations. For convenience, salient attributes, including the overall extent of floodplain habitat are tabulated (Table 2.1). Each brief summary also reviews the lechwe population, with respect to its status and published studies. The ranges of Black, Robert's, Upemba and Kafue lechwe exhibit a tight fidelity to islands of wetland in their respective drainage systems. The exception, at least when considered historically, is the total range occupied by Red lechwes across Angola and western Zambia. Distributional data compiled by Crawford-Cabral & Verissimo (2005), and additional historical records, confirm that *K. leche* occurred widely through the gently-sloping valleys of the Cubango, Cuando and Upper Zambezi drainage systems, within suitable floodplain habitat. Overall, *K. leche* was patchily distributed across western Zambia, where Ansell (1978) documented their former occurrence throughout the extensive floodplains of the Upper Zambezi (Barotseland). This range appears to have been contiguous with populations occurring along drainage lines in eastern Angola. Their range extended along the Kasempa river, and apparently contiguously east to Upper Kafue tributaries: notably along larger, broad river valleys, especially the Nashinga, Lukanga and Busanga Swamps. These floodplains form localized lechwe habitat within the valleys of the Nashinga, Upper Kafue and Lufupa rivers, respectively (Fig. 2.1). The overall extent of these lechwe habitats across the archipelago is mapped in Fig. 2.2.

2.4.1 BOTSWANA

2.4.1.1 Linyanti-Chobe

Williamson (1979, 1981) estimated a total of 15 000 *K. leche* in the Linyanti, but this population has declined markedly over the past decade (Ross *et al.* 1998). Northcote (2005) described how poachers from the Caprivi Strip of Namibia, and unsustainable hunting quotas within Botswana decimated these herds of Red lechwe along the Linyanti and Chobe rivers through the 1990s.

2.4.1.2 Okavango

The biota, ecology and geomorphology of this region have been relatively well studied (McCarthy *et al.* 2000; Timberlake 2000a,b; Haddon & McCarthy 2005). East (1999) estimated that over 68 000 Red lechwe occurred in the Okavango Delta. This population is believed to be healthy especially in the Moremi Game Reserve; but concerns were expressed that these populations are declining under impacts of rural development and encroaching human settlements (Ross *et al.* 1998).

2.4.2 KATANGA, DEMOCRATIC REPUBLIC OF CONGO (DRC)

The Katanga region (formerly Shaba) occupies the southeast corner of the Democratic Republic of Congo (DRC, formerly Zaire). The geology of Katanga and neighbouring Zambia comprises Proterozoic formations influenced by a long and complex tectonic history (Porada & Berhorst, 2000). Geomorphology, vegetation, and boundaries of Katanga have been described in detail elsewhere (Alexandre & Alexandre-Pyre, 1987; Bailey, 1986; Banister, 1986; Broadley & Cotterill, 2004; Cotterill 2004, 2005, 2006). High heterogeneity of the landscape is invoked as the dominant control on the high species richness and endemism of Katanga's habitats. This varied relief across Katanga was enhanced by tectonic activity initiated in the Pliocene, and extended southwest from the EARS (Tanganyika) across Katanga and northeast Zambia (Mondegue *et al.*, 1989; Sebagenzi & Kaputo, 2002; Tack *et al.* 2003). Lying in a transition zone between moist forest and mesic miombo savanna, the floristic diversity of Katanga and adjacent northeast Zambia has been enriched by both Guineo-Congolian and Zambebian elements. This is exemplified by the high richness and endemism of savanna plants in the Miombo Ecoregion (Frost *et al.* 2002). Phytogeographically, Malaisse (1997) proposed that Katanga lies in the centre of a "Katanga-Bemba Region", as the northern subregion of the Zambebian Phytochorion (Fig. 2.2). Hitherto underappreciated, the biogeographical and conservation importance of the reptile and bird faunas of the region were described recently by Broadley & Cotterill (2004) and Cotterill (2004, 2006).

2.4.2.1 Lake Mweru and the Kashiobwe (Lower Luapula) Flats

Lake Mweru receives most of its inflow from northeast Zambia, notably from the Chambeshi-Bangweulu system through the Luapula river (Thieme *et al.* 2005). Lechwe were first reported on the Kashiobwe Flats by Sharpe (1893). The population appeared to number about 300 in 1954, and were considered extinct by May 1966 (Hanks 1969). These lechwe have hardly been studied. Only two museum specimens appear to exist, which are classified as *K. leche* (Ansell & Banfield 1979; Cotterill 2005; Fig. 2.1, Chapters 6 & 7).

Table 2.1. Areas of principal floodplains and shallow lakes within the Palaeo-Chambeshi archipelago. Predicted extents of floodplains also included for palaeo-wetlands*. As estimated below, the total area of extant wetlands (excluding Etosha Pan) comprises approximately 149 700 km². The overall fluctuations in annual inundation of each seasonal floodplain is summarized, where known. Where quantified, the percentage denotes the relative extent of seasonally flooded habitat potentially available to organisms, including lechwe antelopes, which are floodplain specialists. Sources of these data include: Bangweulu (Grimsdell & Bell 1975; Manning 1983), Linyanti (Williamson 1979). Statistics for all other wetlands from Gaudet (1992), Matondo & Mortensen (1998) and Sahin (2002). (* denotes extinct wetland, which existed during tenure of palaeo-drainage system.)

Wetland	Total Area (km²)	Area of Low Water (km²) (Percentage total area = seasonal floodplains)	Catchment (km²)
Owambo Depression* (includes Etosha Basin)	236 000	Unknown	106 500
Okavango Delta	19 000	12 880 (68%)	121 900 (Cuito contributes ~45% of total inflow)
Chobe Floodplain	200	Unknown	170 000
Linyanti Swamps	1 200	Unknown	150 000
Cuanza Floodplains	52 300	Unknown	Unknown
Lufira Flats*	22 400	Unknown	11 980 (modern Upper Lufira river only)
Upemba Swamps	11 800	4 760 (40.3%)	187 800 (includes Lufira river)
Barotse Floodplains	9 000	8 300 (92.2%)	274 920
Liuwa Plains	3 500	Unknown	Unknown
Bangweulu Swamps	11 700	4784 (41%)	190 000
Kalungwishi-Luongo	6 800	Unknown	26 696
Luapula (Kashiobwe) Flats	3 000	Unknown	71 372, below Bangweulu basin; 172 866 entire catchment
Kafue Flats	6 000	500 - 4650 (8 - 78%)	153 060
Lukanga Swamps	2 500	Unknown	77 800

2.4.2.2 Lufira Depression

This large wetland does not appear to ever have supported lechwe historically. Nevertheless, its importance as a dispersal route for these antelope (amongst other biota) during the Pleistocene has been invoked in biogeographical scenarios (Broadley & Cotterill 2004; Cotterill 2004, 2005).

2.4.2.3 Upemba Swamps

Sustained by the Upper Lualaba and Lufira rivers flowing across the Kamalondo graben, the Upemba Swamps form one of Africa's largest wetlands (Bailey, 1986, Figs 2.1 & 2.2). Upemba Swamps comprise a complex mosaic of lakes within extensive swamps of *Phragmites* and *Cyperus papyrus*, surrounded in turn by floodplains (De Witte 1966; Thompson *et al.* 1979; Malaisse 1997).

The existence of Upemba lechwe was materially documented by museum specimens collected in December 1924. The existence of this population was mentioned repeatedly (Schouteden 1947; Mitchell & Uys 1961; Ansell 1974, 1978; Verschuren 1975) and most recently by East (1999). Their taxonomic and biogeographical significance was long ignored and formally described only recently (Cotterill 2005). In all respects the biology and status of *Kobus anselli* is very poorly known. This antelope appears to be Critically Endangered (Cotterill 2005). It is interesting to note that the Kamalondo depression has supported relatively dense human settlements for millennia. Archaeological evidence reveals that large, permanent settlements have existed around, and within, the Upemba Swamps since at least 1400 yrs BP. For centuries, the Kamalondo depression supported the central settlements of the ancient Luba Empire. The evidence from excavated middens reveals that humans have exploited the Upemba Swamps for protein and other raw materials over the millennia (De Maret 2005). Nevertheless, these lechwe obviously persisted successfully in Upemba Swamps despite human hunting. This was until the estimated 20 000 animals (reported by Verschuren 1975) were decimated by commercial poaching during the 1980s (M. Hasson *in litt.*).

2.4.3 ZAMBIA NORTHEAST

2.4.3.1 Bangweulu Basin and Bwela Flats

The Bangweulu basin has formed by down-warping of an ancient craton. More recently, faulting has modified both the topography and drainage along its western margin (Chapter 4). Dixey (1955a,b) noted the geomorphology of the Bangweulu basin differs little from that in which Lake Victoria has formed in east Africa. This similarity likely reflects their juxta-positioning as highlands of comparable height between

active rift valleys. Cole (1986) described lake alluvium extending beyond the present margin of the floodplain, which would suggest the existence of a larger palaeo-lake earlier in the Quaternary.

The Bangweulu basin receives run off from 17 principal rivers, but only 10 % of this run off flows out of the southwest corner of the depression into the Upper Luapula river, the majority is lost to evaporation. Historical records over the past century reveal that the basin has gradually tilted to the north west, where run off pools locally - forming Lake Bangweulu. This trend has been associated with high floods that impacted negatively on human settlements and populations of large mammals, especially Black lechwe (Debenham 1952; Grimsdell & Bell 1975, 1976). Certain large mammals have been studied quite intensively, namely *Kobus smithemani* (Grimsdell & Bell 1975; Thirgood *et al.* 1992, 1994; Nefdt & Thirgood 1997; Kamweneshe 2000) and *Tragelaphus spekei* (Manning 1983). The other endemic antelope, the Bangweulu tsessebe *Damaliscus superstes*, awaits study of details of its status and ecology (Cotterill 2003a,b). Knowledge of all other biodiversity, even the fishes of Bangweulu is patchy at best (Jackson 1986, 2001), and herpetofaunal knowledge is even poorer (Broadley & Cotterill 2004). The flora has barely been studied (Timberlake *et al.* 2000).

The Black lechwe population of Bangweulu Swamps became firmly established as a flagship species for conservation concerns in the then Northern Rhodesia after the 2nd World War. Concern over a catastrophic decline in this endemic large mammal catalyzed activities of the Game Preservation Society of Northern Rhodesia (subsequently the Wildlife Society of Zambia). Its official journal was aptly named “Black Lechwe”. Concern culminated with a detailed long-term study (mid 1969 to December 1973) that culminated in a detailed report of the species’ ecology with a detailed management plan (Grimsdell & Bell 1975).

Figure 2.2. (Following Page) Overview of the principal wetlands and drainage systems within the Katanga-Chambeshi region. This map was generated from a Digital Elevation Model (DEM) and integrated with GIS datasets as described in Chapter 4. The extent of the Katanga-Chambeshi region is denoted by the continuous red line, and falls within the Zambezian phytochorion of White (1983) - not shown. Major rivers are labeled in italicized text. The fine dotted line depicts the Southern Equatorial Divide: the extant watershed between the Congo and Zambezi drainage systems. Principal wetlands and rift valleys (including lechwe habitats) are labeled: Ba = Bangweulu Basin; Br = Barotseland Floodplain; Bu = Busanga Swamps; Ca = Cameia depression; Et = Etosha Basin; Ka = Kafue Flats; Ku = Kunene Floodplain; Lf = Lufira Depression; Lo = Luando Floodplain; Lp = Luapula Flats; Lu = Lukanga Swamps; Lw = Liuwa Plains; Ly = Linyanti and Chobe Floodplains; Ma = Magkadikgadi Pans; Mu = Lake Mweru; Mw = Mweru-Wantipa Depression; Ng = Lake Ngami; Ok = Okavango Delta; Pb = Pambashye Swamps (Luongo-Kalungwishi rivers); Ru = Rukwa graben; Ta = Lake Tanganyika; and Up = Upemba Swamps (in the Kamalondo Depression).

Around 1900, the Black Lechwe population was estimated at over 200 000, perhaps 350 000 individuals (Hughes 1933). This estimate set the upper limit to subsequent demographic models (Grimsdell & Bell 1975). There was a gradual decline through 1900 - 1936 under intense hunting pressure; this culminated in a drastic reduction in numbers from ~150 000 to between 60 000 - 40 000 animals. Unusually high flooding was a major cause of this decline. Higher hunting pressure from 1945 - 1969 reduced the population to ~16 000, where it stabilized; and officially and enforced conservation underwrote a 25% population increase, with at least 25 000 animals present in October 1973. It had increased to ~30 000 in 1975 (Bell & Grimsdell 1973; Grimsdell & Bell 1975, 1976). Most censuses estimate the population as persisting at around 30 000 individuals (Kamweneshe 2000).

The isolated population of Black lechwes in the Chinsali district on the Bwela Flats, northeast of Bangweulu has received comparatively less attention. D. G. Lancaster, then Assistant Game Warden of the country stated that Black lechwe “...range as far east as the Nshinga Swamp in the Chinsali District, where a small herd is strictly preserved.” (Lancaster 1950: 39). Until 1939, herds numbering up to 1 000 could be seen on the Chinsali floodplains. By August 1960, this population had dwindled to between 50 - 100 animals (Mitchell & Uys 1961; Allen 1963). This population was, surprisingly, still extant in the mid 1970s (I. Manning *in litt.* November 2004), and was bolstered by a reintroduction in 1974 and 1975, with animals from the neighbourhood of Chikuni Island, Bangweulu (Ansell 1978).. Today, this populations appears to be extinct, and few scientific specimens exist (Appendix 1).

2.4.3.2 Mweru-Wantipa Depression

The shallow depression of the Mweru Wantipa depression lies between the Mweru and Tanganyika rift valleys. Vesey-Fitzgerald (1970) mapped extensive floodplain grasslands across this region. These landscapes supported large herds of lechwes, where Sharpe (1893) recorded large herds in 1892. All these lechwe have since vanished, unaccounted for in the subsequent settlement and development of the region (Ansell 1978). No voucher specimens of this population appear to exist in any of the world’s museums.

2.4.4 ZAMBIA CENTRAL - UPPER KAFUE DRAINAGE

2.4.4.1 Busanga Swamps and Luswishi River

Vesey-Fitzgerald (1970) mapped extensive valley grasslands along major reaches of the Upper Kafue river. These correspond to units mapped by White (1983). The hydrological regime across the Busanga floodplain is controlled by seasonal run off through the Lufupa river, augmented by the relatively high annual rainfall

contained in the remarkably flat terrain. The relationship between vegetation of the flat landscape of the Busanga depression, with respect to controls by flooding and edaphic factors, was described by Cole (1963). The Busanga Swamps are almost entirely included within the protected area complex of the Kafue National Park, and Kasonso-Busanga Game Management Area, but permanent human settlements are established in the latter (Leonard 2005).

The first report of the Red lechwe population confined to the Busanga floodplain, counted only 71 animals in October 1948 (Ansell 1955). They had increased to 463 by October 1960 (Mitchell & Uys 1961), and to 1163 by July 1971 (Grimsdell and Bell, 1972). A subsequent report estimated this population at 3400 individuals in 1985: from wet and dry season censuses (Howard and Chabwela 1987). They appeared locally numerous in October 2002 (F. P. D. Cotterill *pers. obs.*), but the precise current status of this population is not known (Leonard 2005). The statusposition of a small population of Red lechwes along the Luswishi river, south of Ndola, is also unclear; where Mitchell & Uys (1961) reported 150 animals. Very few scientific specimens are preserved of either population (Appendix 1).

2.4.4.2 Kafue Flats

This region has been intensively studied through the second half of the 20th century. Through the same period burgeoning human settlement has altered the landscape and its wildlife significantly. Impoundments of the Kafue river upstream at the Itzhi-Tezhi rapids, and downstream in the Kafue Gorge, have radically changed the natural hydrological regime (Ellenbroek 1987; Chabwela & Ellenbroek 1990; Kamweneshe *et al.* 2002). These studies preceded, accompanied, and have followed the construction of these hydroelectrical developments. Agricultural developments on the Kafue Flats have focused around Namwala (in the west) and Mazabuka (in the east). These have encroached on the seasonal floodplain since the 1940s alongside with human pressures. The latter has also increased overall with the growth of commercial and subsistence fisheries across the Kafue Flats.

All the above-mentioned factors have caused a massive decline in the numbers and range of the endemic Kafue lechwe, *K. kafuensis*. The first documented total for the entire population estimated 350 000 individuals (Pitman 1933). They had declined to an estimated total of 26 000 by 1955 (Ansell 1955). Mitchell & Uys (1961) summarized the history of the decline of Kafue lechwe from an estimate of 190 000 since 1934. Since then their range has imploded east from Kafue Bridge and west from Namwala to a localized population (Fig. 2.1). Major impacts through the 1950s included traditional hunts, termed the chila, by the Ila

people of the region. Through the 1980s and 1990s, poaching pressure on Kafue lechwes intensified with increased availability of modern firearms, and the burgeoning bushmeat market in Zambia. Nevertheless, numbers of *K. kafuensis* increased again from an estimated 47 000 to 65 000 in the mid 1990s (East 1999). This remaining population occupies a narrow portion of floodplain (only 15 and 35 km wide along the southern and northern margins, respectively) within the Blue Lagoon and Lochinvar National Parks. The total population was estimated at 42 000 individuals in 2002. The population is under serious threat, as its steady state through the 1990s reflects heavy poaching, despite sound recruitment, after a steady decline since the 1970s (Kamweneshe *et al.* 2002). Veterinary studies have revealed that *K. kafuensis* also appears to be at high risk from diseases and parasites (Stafford 1991; Zieger *et al.* 1998; Kock *et al.* 2002; Siamudaala *et al.* 2005).

2.4.4.3 Lukanga Swamps

The ecology and biodiversity of the Lukanga Swamps is poorly known, even less so than Bangweulu Swamps (Leonard 2005). The hydrological regime of the Lukanga swamps is quite different from the neighbouring Kafue Flats (Kamweneshe & Beilfuss 2002). Selous (1881) “found the Lechwee [sic] antelope in large herds” in the environs of the Lukanga Swamps in 1888. The precipitous decline of these herds passed undocumented, until approximately 800 were estimated to occur around the Kafue - Lukanga confluence (Hanks 1969). The most recent survey in 2002 reported these lechwe to be under heavy human pressure, with no legislated protection. Less than 100 Red lechwe appear to remain in the entire region (Kamweneshe & Beilfuss 2002).

2.4.5 ZAMBIA-UPPER ZAMBEZI DRAINAGE

2.4.5.1 Liuwa Plains

The Liuwa population has always been poorly known (Benson 1969). A recent aerial census over 10-12 December 2004 estimated 966 red lechwe (Viljoen 2005). In fact, human depredations on Red lechwe populations throughout Barotseland have been severe. Very few lechwe still occurred in the Kasempa district by 1960 (Mitchell & Uys 1961). The Liuwa population appears to be the only surviving remnant in all of western Zambia.

2.4.5.2 Simahala Flats, Mambova

Seasonal flooding along the Upper Zambezi river maintains this wetland across the upper end of the Okavango graben along the Namibian/Zambian border. Here the river meanders across this broad gentle-

sloping flood plain of the Okavango-Kafue graben, within the Linyanti and Chobe faults, demarcated by the Katimo Mulilo and Mambova rapids, respectively. Red lechwes occurred, reportedly in large herds, throughout the Zambezi floodplain, but only ~1 000 existed along the Simalaha Flats by 1960 (Ansell 1960; Mitchell & Uys 1961). Their current status is not known, but very few, if any, appeared to survive (East 1999).

2.4.6 ANGOLA AND NAMIBIA

Until Crawford-Cabral & Verissimo (2005) recently published detailed data, the status and wide distribution of lechwe antelopes across the Okavango and Upper Zambezi catchments was underappreciated (Fig. 2.1). This database documents what have become historical records, since nearly all lechwe populations (alongside all Angola's wildlife) were widely exterminated during the decades of civil war. What little can be gleaned from historical reports suggests that numbers of lechwe were characteristically high. In 1928, Reitz (1999: 438) encountered large numbers of lechwe on the Congo-Zambezi watershed, west of Luashi and Chilongo, in eastern Angola - a region today close to the Zambian border. Similarly, Stratham (1924) met large concentrations of lechwe in 1923 in a traverse from west to east across southern Angola. These were localized in the larger rivers. For example, "great herds of lechwe and roan antelopes" were recorded around the upper reaches of the Cubango river (Stratham 1924: 6).

This is the place to record the remarkable historical record represented by two specimens (MNKB 68375 and 68376 %) collected from Karibib Etosa Pan (*sic*), by von Birlow in February 1906. These comprise two skull preserved in the Von Humbolt Museum of Natural History, Berlin. This locality record escaped the attention of Shortridge (1934), and is not mentioned in any other literature reviewed in this study. The habitat does not appear suitable, and these specimens require careful consideration before their provenance can be accepted as genuine. They may instead have been collected further east in the Caprivi near the Cubango.

Crawford-Cabral & Verissimo (2005) mapped the occurrence of lechwe in the Cameia basin. This is a significant wetland, also very poorly known, through which the Upper Zambezi river circumscribes its course along the southeast edge of this depression (Figs 2.1 & 2.2). These lechwe all seem to be extinct; as they have also been extirpated across much of Angola. The most northwestern population on the Cuanza floodplains had been drastically reduced by 1992 (Crawford-Cabral & Verissimo 2005), but still survived in 2004 (J. Anderson & R. D. Estes *in litt.* November 2005).

2.4.6.1 Owambo Depression, Etosha Pan and Lake Kunene

A recent study by Hipondoka (2005) revealed new and important aspects of drainage evolution centred around Etosha Pan, Namibia within the much larger Owambo depression. The Pliocene Lake Kunene was followed by a Palaeo-Lake Etosha stage. This geomorphological evidence reveals that the Etosha basin supported an immense Pliocene lake, which persisted late into the Pleistocene. These palaeo-lakes present interesting implications for the biogeography of lechwe antelopes. Past links during the Quaternary between the western margin of the Magkadikgadi and Okavango depressions with the Etosha basin, along the Okavango - Omuthiya fossil drainage line, would have aided dispersals of aquatic organisms into the Kunene system (Chapter 4; Fig. 2.1).

This former link can be invoked to explain how a population of lechwes came to be isolated along the Upper Kunene valley. The evidence for their former occurrence at approximately 16° 45'S; 15° 22'E is based on herds of lechwes described by the Earl of Mayo in 1881. Skins of three animals were preserved and sent back to England (Earl of Mayo 1883), but do not appear to have been published on, let alone still exist. Based on Hipondoka's (2005) reconstructions of palaeo-climates and hydrographic history, there is an interesting possibility that the Etosha basin supported populations of lechwes under more mesic conditions during the Holocene (Chapter 4).

2.5 NATURAL REGIONS AND THE EVOLUTION OF LANDFORMS

2.5.1 Biomes versus Phytochoria

Africa has been divided up into natural regions according to many different biogeographical and ecological classifications. The different units reflect on the corresponding criteria employed. These criteria have included broad patterns evinced in the biota (especially plants), allied with physiographic indicators mapped for geology, soils, topography and climate. Vegetation structure is common to nearly all treatments that have classified Africa into natural regions; where the largest units form biomes, and trend to ecoregions and vegetated landscapes of smaller extent. Even though quite different criteria underlie these classifications, nearly all have described south-central Africa as dominated principally tree-dense savanna. This perspective has influenced faunal classifications. Klein (1984), for example, emphasized that the Zambebian mammal fauna is adapted to habitats of wooded grassland. Moreover, neontological studies of the region's savannas have emphasized the ecology of woodlands. These are dominated by the *Colophospermum mopane*, mopane, woodlands in low-altitude valleys while vast miombo woodlands cover large regions of plateau. Studies of herbaceous plants have focussed on their diversity and ecological dynamics, with respect to the

dominating canopy of larger trees (Cole 1982; Walker 1987; Frost 1996; Furley 2004). Statements along the lines that miombo constitute the greatest dry forests on earth (Adams & McShane 1992) are common.

Birds are purported to be the best known group of organisms, worldwide; and this belief has been applied to the African context (Bibby *et al* 1992; Brooks *et al.* 2001). Nevertheless, weaknesses in entrenched avian taxonomies obscure some biogeographical signals (Zink 2004). This especially applies to the Zambezi and Katanga-Chambeshi regions, when a taxonomy structured by the Biological Species Concept (BSC) is replaced by the Evolutionary Species Concept (ESC) (Cotterill 2006, unpublished data). Only a complete continental analysis of datasets (restructured by thorough taxonomic revision with the ESC) will reveal whether faunal classifications of Afrotropical birds are changed significantly. Nevertheless, pioneered by Moreau (1966), recent analyses of the traditional dataset (based on Hall & Moreau 1970, Snow 1978 and Crowe & Crowe 1982) consistently recovered a Zambezi avifauna, with a distinct hotspot of higher endemism and species richness in Katanga (De Klerk *et al.* 2002a,b, 2004; Fjelds  2003; Dillon and Fjelds  2005). It is important to note that numbers of avian endemics in this Katanga hotspot has been repeatedly under represented in these studies (Cotterill 2006).

Given these terrestrial biases and research paradigms, it is interesting to compare what criteria have been employed to classify Africa's aquatic landforms into natural regions. At the continental level, Roberts (1975) divided Africa into principal units based on the largest drainage basins. More local classifications have applied extant watersheds as boundaries to delimit aquatic regions into contiguous hydrological basins. This strategy was recently applied by Thieme *et al.* (2005) to classify Africa's wetlands into a mosaic of freshwater ecoregions. Unfortunately, these extant hydrographic units camouflage complex patterns of evolutionary history. This especially applies when we acknowledge the shared affinities of biota inherited from antecedent drainage systems. In south-central Africa, pioneering studies of fish biogeography by Bell-Cross (1968, 1972, 1982) and Jackson (1962, 1986) emphasized how evolutionary insights confer valuable resolution on our knowledge of aquatic assemblages, and the landscapes in which they have evolved. Skelton's (1994) biogeographical review reveals how a classification of wetlands biased toward extant ecological and geomorphological boundaries deprecates the importance of these evolutionary regions. For example, the Upper Kafue basin is indeed linked to the Middle Zambezi basin today. Yet, until late in the Quaternary it shared many millions of years of history linked with wetlands to its north and west, especially the Upper Zambezi and Okavango systems. If conservation of biodiversity is their central objective, management plans for wetlands cannot ignore the evolutionary history of extant wetlands.

Fishes have been the taxa of choice to delimit aquatic landforms into natural regions (Roberts 1975; Bell-Cross 1982; Skelton 1994). Unfortunately, knowledge of distributions of Afrotropical Amphibia fall short in completeness, when compared to what we know about Aves, Mammalia and especially angiosperms, with respect to how well taxa and habitats have been sampled. Nonetheless, the available data were sufficient for Poynton & Broadley (1991) to conclude that the Zambebian amphibian fauna is composite. Taxa that characterize the East African lowland and Afromontane faunas complement the Zambebian plateau component. Overall, incomplete knowledge of Afrotropical amphibians can be gauged by the occurrence of only five endemics recorded in the Kamalondo drainage system. This statistic appears anomalously low, when compared to the high endemism of vertebrates in the Kamalondo, especially fishes (Malaisse 1997; Section 4.11). Overall, taxonomic uncertainties hamstring biogeographical analyses of Afrotropical amphibians (Poynton & Broadley 1991; Channing 2002). This is most unfortunate, as their diversity and specialized habitat requirements offer great potential as a proxy to help reveal the evolutionary history of African wetlands.

Many terrestrial classifications have tended to place more emphasis on neontological patterns, at the expense of evolutionary history underlying affinities of landscapes. An important exception are the geographical patterns of floral endemism that underlie how phytochoria have been delimited across Africa (White 1965, 1971, 1976a, 1993), mapped in White's (1983) *Vegetation Map of Africa*. This is the most comprehensive, biotically-focussed classification available for the terrestrial landscapes of Africa. Pertinently to this study, the Zambebian phytochorion with no less than 8 500 species (54% endemic), covers much of south-central Africa. A more quantitative biogeographical revision identified broadly similar units. The largest Zambebian region recovered in this analysis was much larger than that originally mapped by White; nevertheless, the central Zambebian area recovered in Linder *et al.*'s (2004) analysis corresponds closely to the Katanga-Chambeshi region (Cotterill 2004, 2005, 2006) described in this study (Fig. 2.2).

Overall, it appears that phytochoria are a more biogeographically informative criterion to delimit continental land masses into the larger natural regions that reflect patterns of biodiversity evolution (Linder *et al.* 2004). White (1983, 1993) delimited natural units within his principal phytochoria principally on patterns represented in distributions of dominant plant species and contiguous landforms. Emphasis was placed on more local regions of endemism. These tend to be less well known and subject to taxonomic biases in the indicators employed. The extent of the Zambebian phytochorion (3.77 million km²) also corresponds closely to the Miombo Super-Ecoregion of the World Wide Fund for Nature, and the Miombo-Mopane Wilderness

Area recently delimited by Frost, *et al.* (2002). Delineation of the latter are both derived from White's original definition of the Zambezi phytogeography.

Apartly, White's (1983) mapping of vegetated landscapes within the Zambezi phytogeography corrects the vague, misleading generalization that south-central Africa is covered principally by tree savanna. Zambezi grasslands constitute the single largest unit mapped among all vegetation units in the Zambezi phytogeography. Furthermore, dambo grasslands cover a significant portion within the regions mapped as miombo woodlands (White 1983). This is because dambos dominate depressions within wooded interfluvies, and they anastomose along the majority of drainage lines across the high plateau (Von der Heyden 2004; Cotterill 2005; Chapter 4).

The floodplains supporting lechwe antelopes (Cotterill 2005) reveal how broad ecotones within wetlands constitute dynamic landforms representing both aquatic and terrestrial habitats. Wetlands are tightly coupled to ecological and biogeochemical processes that propagate from both their terrestrial and aquatic components. These landscapes are challenging to delimit and classify unequivocally (Forman 1995a,b). So, it is challenging to integrate regional classifications of Africa's aquatic biota and landforms with respect to the terrestrial entities. Unfortunately, disparate differences characterize the respective criteria applied to delimit, study and manage aquatic versus terrestrial regions. Considerable investments in studies of aquatic and terrestrial systems have developed independently; and this polarity in research focus has dominated significant arenas of biological research in Africa. Thus, advances in biogeographical studies, classifications of natural regions, and conservation planning still proceed separately for terrestrial and aquatic landscapes. A recent testimony to this dichotomy is represented in the isolated, yet considerable investments in studies of Afrotropical terrestrial and freshwater ecoregions by Burgess *et al.* (2004) and Thieme *et al.* (2005), respectively. Delimiting an encompassing natural region within which to frame this study of lechwe antelopes must reconcile biogeographical patterns revealed by these contrasting approaches to classifying terrestrial versus aquatic landscapes. It requires a bridging of two secular traditions of classifying natural regions.

Key concepts of landscape ecology are also pertinent to this endeavour of classifying natural regions, as framed within acknowledged principles of the structure and functioning of habitat mosaics (Forman 1995a,b). The questions and subjects of this study place special emphasis on islands and fragments of aquatic landforms. This distinction between island and fragment is critical, where one seeks to understand where and how biodiversity has come to be distributed in heterogeneous landscapes. The habitats dominating islands

and fragments have evolved within a matrix of more contiguous habitat. Here, equally great importance relates to the relative difference in the physical structure of habitats within an island or fragment compared to their surrounding matrix. Contrast of properties is the key variable in this respect. So is time - especially in this model of landscape structure - as to how long an island of floodplain or fragment of river has persisted in isolation (Watson 2002). Habitat structure and quality act on critical demographic variables such that a particular population (with respect to availability of key ecological resources) will either persist in a patch or go extinct. Compared to sink habitats, optimal conditions constitute source habitats, where populations persist from increasing over time (Dunning *et al.* 1992). Other key variables also relate to landscape structure, especially how permeable a habitat matrix is to particular organisms. This is governed by many factors with respect to individual behaviours and ecological dynamics. The life history and natural history of the particular species is of overwhelming importance in how organisms utilize habitat patches in the landscape (Addicott *et al.* 1987; Wiens *et al.* 1993; Wu *et al.* 2006).

Thus, the dambos of perennial grasslands, formed along drainage lines (described below), appear to be more permeable to dispersing lechwes compared to miombo savanna. So, it is feasible that lechwe antelopes can disperse along dambos that link larger floodplains. This process could therefore be critical to patterns of gene flow among what appear to be geographically isolated populations. The physical habitats of south-central African wetlands contrast starkly against the matrix of savanna in which they have evolved. Some wetlands may also constitute fragments of formerly larger landforms. This especially applies to rivers, following piracy events; although some wetlands can grow, almost exponentially, through time, through processes of accretion. The Congo and Zambezi rivers are excellent examples of the latter (Chapters 4 & 5).

2.5.2 Life as a Geological Layer and Wetland Archipelagos

The central adage of panbiogeography that conceptualizes “life as a geological layer” (Craw *et al.* 1999) manifests quite plainly in the strong structuring of aquatic biodiversity in wetlands. The physiographic history of south-central Africa’s wetlands, responsible for extant hydrographic patterns, has exercised overwhelming control over what aquatic biodiversity occurs where (Skelton 1994; Section 4.11). Here, the complementary importance of the three principal biogeographical processes of speciation, extinction and dispersal are starkly distinguished in aquatic landscapes (Crisci *et al.* 2003). Stenotopy is the obvious explanation: quite simply fishes and other organisms go extinct, unless they succeed in tracking the slightest of topological shifts in the matrix of their aquatic habitat most intimately. Since the evolutionary dynamics of wetlands and their biota have invariably been stitched so tightly together, patterns and processes of hydrographic history provide not

only a unitary, but also insightful, thread of explanation to decipher evolutionary history. It is fortuitous that the histories of aquatic biodiversity are closely entwined with landforms. Panbiogeographers apply the term geobiota to describe such entities (Craw *et al.* 1999).

It follows that our studies and understanding of wetland landscapes, and their biota, stand to gain valuable insights from classifications structured by patterns of evolutionary links between landforms and biota. Although the jurisdictions of Africa's freshwater ecoregions are indeed valuable to frame research and conservation activities; they ignore important facets of evolutionary history; so a logical rectification of this deficiency might reclassify the hydrography of the entire continent in a historical context. This would delimit drainage systems primarily in terms of how spatial patterns reflect shared history among landforms and biota. These patterns can be reconstructed by inter-relating pertinent aspects of geological history to the evolutionary tracks represented by speciation patterns in aquatic biota. It appears that natural centres of aquatic evolution (analogous to phytochoria) will be revealed by such a synthesis.

The datasets compiled in Chapter 4 reveal how distributions of aquatic biodiversity exhibit strong signals of geographical structure; especially where peaks of aquatic endemism are confined within hydrographic basins or smaller wetlands. The lakes in the East African rift valleys exemplify what such a classification can reveal; albeit partitions between assemblages have become blurred by more frequent dispersals among faunas within principal drainage systems across south-central Africa. Here geological dynamics have exercised more subtle influences, and geomorphological barriers may also be porous to the more dispersive of organisms. As importantly, in the past, each drainage basin has experienced links with its neighbours through rearrangements of rivers and their catchments. Nonetheless, congruence in biogeographical patterns among aquatic species often point to a common control on their origin. And where we are able to correlate and synthesize biogeographic patterns closely with geological history, revealing evolutionary insights can then follow. Unfortunately, such an endeavour is hamstrung by incomplete and fragmentary evidence. This lack of data especially handicaps a reclassification of all Africa's wetlands, and incomplete knowledge weakens both biotic and geological datasets. Moreover, it is a formidable task to collate, where feasible, the first order biogeographic and geological data scattered through a voluminous literature. This challenge structures the synthesis in Chapter 4, and is restricted to within south-central Africa.

2.5.3 The Katanga-Chambeshi Wetland Archipelago as a Study Area

Several large, shallow wetlands dominate the topography of the south-central African plateau, and comprise an archipelago with total area of at least 2.5 million km². Representatives of the *Kobus leche* complex exhibit a patchy distribution across this archipelago. Extensive drainage networks maintain these wetlands, within which seasonal floodplains (especially water meadows) provide optimal lechwe habitat. These wetlands appear to have constituted source habitat for lechwes during the Pleistocene, and perhaps through the late Neogene. The combined evidence now available reveals that the extent of this region corresponds closely to that of the Zambezi phytochorion (Cotterill 2005; Chapter 4).

A useful index of the availability and extent of lechwe habitat is represented by the patchwork of Zambezi grasslands that complement aquatic and semi-aquatic vegetation. These include seasonally inundated grasslands, termed valley grassland by Vesey-Fitzgerald (1963, 1970). As summarised above, historical evidence reveals that lechwe were not confined solely within demarcated floodplains, such as Bangweulu and the Kafue Flats. They also occurred along broad, shallow river valleys, notably in Angola and northern Zambia. As discussed above, this region should also include the Upper Kunene river and Owambo basin (including Etosha pan), based on previously overlooked evidence. (Not least, lechwe antelope occurred historically in the Upper Kunene system.) Furthermore, as detailed in Chapter 4, biogeographical affinities of fishes provide persuasive evidence to include the Etosha-Upper Kunene system into this Katanga-Chambeshi archipelago (Fig. 2.2).

Shared evolutionary history is the dominating criterion for this classification. Combined patterns in the geomorphic and biotic make-up of the Katanga-Chambeshi region points to a complex history of landscape evolution, initiated at least since the late Neogene. Alongside neo-tectonics and drainage changes, climatic fluctuations through the Plio-Pleistocene have repeatedly rearranged the topology of habitats within this archipelago. Their evolution has ensued on a comparatively stable, ancient land surface mantling the south-central African plateau (Cotterill 2004, 2005; Chapter 4). It is their shared evolutionary history, which justifies classifying all these islands and fragments of wetlands in one archipelago. Detailed justifications for delimiting the topology of the Katanga-Chambeshi region are reviewed in Chapter 4. The majority of these wetlands were formerly linked within the Palaeo-Chambeshi drainage system - represented today as the Upper Zambezi-Okavango, Upper Kafue, and the Upper Lualaba and Luapula (Congo) systems. Extant wetlands in northeast Botswana include the Okavango-Linyanti wetlands, but covered a much larger area, that included the Magkadikgadi basin (Figs 2.1 & 2.2).

2.5.4 Biodiversity of the Katanga-Chambeshi Region

The Katanga-Chambeshi region is bordered by semi-arid biomes of southern Africa to the south west; while its northern limits abut the mosaic of mesic savanna and the Guinean-Congolian forest belt. The mountainous escarpments and deep valleys of the middle Zambezi and Luangwa rifts contain the Katanga-Chambeshi region to the east and south (Cotterill 2004, 2005, 2006, Fig. 2.2). Mesic miombo savanna is closely associated with grassland, where dambos anastomose through miombo woodlands to cover much of the south-central African plateau (White 1983; Goudie 1999a; Von der Heyden 2004). This Palaeo-Chambeshi archipelago comprises no less than sixteen permanent wetlands of biogeographical significance to lechwes. Each is the major node in a drainage network, whose extant topologies formed quite recently in geological time. Key aspects of landscape evolution (especially since the Late Cenozoic), which characterize this Katanga-Chambeshi region, appear to date back to a grassland mosaic of Neogene origin.

So it is interesting that the extent of White's Zambezi phytochorion largely encircles the overall extent of the Katanga-Chambeshi region, whose wetland archipelago is recognized primarily on attributes of aquatic landforms. The nature and extent of Zambezi valley grasslands (Vesey Fitzgerald 1963, 1970) are probably the singular explanation for this relationship; and both natural regions reflect a strong geomorphological control with respect to a large component of floodplains. These regions of very large expanse also include parts of palaeo-lakes that formerly existed in the Etosha basin and Okavango-Kafue graben. The biogeographical unity of the Katanga-Chambeshi region is represented by a distinct congruence exhibited in fish assemblages. The affinities among suites of species reveal close historical links between wetlands that were fragmented recently. This region of shared affinities extends across Zambia, from Katanga: south to Botswana, west to the Cuanza and Kunene systems in Angola; and includes the Owambo basin (Fig. 2.2, Chapter 4).

The total richness of wetland plants in south-central Africa can only be guessed at. The incomplete evidence reveals that the flora of these floodplains and dambos is diverse; but herbaria collections are patchy because inventories are far from complete. The vegetation of most of the region's wetlands have not been collected thoroughly. The endemism and richness of wetland floras are difficult to compare and a high proportion of this knowledge exist only as unpublished reports in the "grey literature" generated by government and consultant reports (Timberlake *et al.* 2000). So it is not unlikely that at least some of the plants grazed by lechwes await formal taxonomic description. Timberlake *et al.* (2000) provisionally listed 736 plant species occurring within wetlands in the Zambezi basin; but this review excluded several major wetlands formerly

linked to the western section of this basin (Chapter 4). Available knowledge reveals two notable patterns in this wetland vegetation. One, species richness of floodplains distinctly exceeds that in the permanent swamps they border. Two, total species richness in wetlands on the south-central plateau is distinctly higher than those in the Middle and Lower Zambezi valleys.

At least 662 taxa of plants are recorded within the wetlands of the Upper Zambezi drainage system, while totals of 423 and 394 taxa are known from the Okavango and Chobe-Caprivi, respectively. Endemism of true aquatic plants appears to be low within these drainage systems. Two examples are *Eragrostis punctiglandulosa* restricted to the Kafue Flats and *Microchloa annua* in eastern Barotseland (Timberlake *et al.* 2000). It is important to compare this apparent low endemism, of true aquatic plants, against the 102 species of geoxylic plants (55 genera among 30 Families of angiosperms) restricted within Upper Zambezi grasslands and floodplains. These form “underground forests” in Barotseland and eastern Angola. Their common growth form is a convergent adaptation to anaerobic soil conditions that prevail in these seasonally flooded valleys (White 1976b, 1983). Species richness of orchids peaks in the dambos and grasslands of south-central Africa. This is exemplified in the speciose Disinae, with no less than 17 endemics (in a total flora of 45) are restricted to this poorly surveyed region (Williamson 1978, 1979; Linder 1983). These orchids are confined within wetland related vegetation types (mushitu forest, dambo and grasslands). They exemplify the Congo-Zambezi watershed centre of floristic endemism identified by Linder (2001).

White (1965) distinguished the Zambezi, Katangan and Barotse centres of endemism embraced in the Zambezi phytochorion. Endemism of the Barotse centre reflects almost closely on the evolutionary significance of the grasslands. The biogeographical significance of these grassy mosaics awaits deserving recognition. The underground forests are one indicator of the high endemism in Zambezi grasslands, and these extensive areas of edaphic grassland on Kalahari Sands attest to this evolutionary significance. Besides the *K. leche* complex, Puku, *Kobus vardoni*, and Crawshay’s waterbuck, *K. crawshayi*, are two other redecine antelopes endemic to the Katanga-Chambeshi region, and dependent on dambo grasslands and floodplains (Cotterill 2005). The ranges of Kinda baboon *Papio kindae* (Sarmiento 1997; Rogers *et al.* 2003) and the southern population of Sitatunga, *Tragelaphus spekei selousi* (see Manning 1982) is also centred within this portion of the African plateau.

2.6 CONCLUSIONS

2.6.1 Behavioural and Ecological Specializations of Lechwe Antelopes

The evidence reviewed in this chapter reveals that dense concentrations of lechwe antelopes formerly dominated the principal floodplains of south-central Africa. It is reasonable to assume that these large mammals strongly influenced the ecology of these floodplains in important respects. Recognition of their significance has yet to be given due respect in the studies and management of the wetlands of south-central Africa, especially considering widespread extirpations of these antelopes. By virtue of mammalian biomass, lechwes are important primary consumers in the floodplain ecosystems. The autecological processes propagated by individual lechwe are especially significant. The concept of ecological engineers (*sensu* Jones *et al.* 1994, 1997) aptly describes how lechwe antelopes dominate the ecology of African floodplains. Through cumulative effects, the behaviour of lechwe herds strongly modify the availability of resources to many other organisms in the same habitats. So far, the ecology of these dynamics has only been quantified in relation to the floodplain vegetation on the Kafue Flats; where it appears that fishes and waterbirds are the more conspicuous benefactors from lechwes foraging in water meadows. Adaptations in several plants strongly suggest coevolutionary responses to the spatial and temporal patterns, whereby lechwes impact on floodplain landscapes. This conclusion remains to be tested with replicated exclusion experiments that test quantitative comparisons. The challenge is to quantify ecological dynamics in terms of trophic interactions, alongside monitoring populations of interacting organisms.

Differences in patterns of social organization and breeding behaviour between populations of lechwes has been interpreted as adaptive responses to local ecological conditions. This explanation accounts for the divergence in mating systems between *K. kafuensis*, a lek breeder; compared to the mating systems of resource defence polygyny in *K. leche* and *K. smithemani*. Furthermore, the latter two populations exhibit important differences further reflecting adaptive responses to local ecological conditions. Considered overall, these contrasting patterns in mating systems and attributes of lechwe herds are most plausibly explained as a complex function of local adaptations by both sexes to ecological determinants. The principal determinants include dynamics of food supply, and predation, which are equally important in controlling spatial patterns in availability of breeding females to dominant males.

2.6.2 Evolution of Floodplains, Biogeography, and the Diversity of Lechwe Antelopes

As based on the phytochoria mapped by White (1983), it appears that the evolutionary and ecological significance of south-central Africa's Zambezian grasslands has not received deserving attention.

Reorientating priorities, to acknowledge their importance, reveals overlooked biotic targets worthy of unprecedented investments in both scientific study and conservation (Cotterill 2004, 2005). Allied with the

intricate history of landscape evolution, the high fidelity of lechwe antelopes for floodplains makes for interesting biogeographical patterns. Floodplains only exist under strict hydrological and topographic situations, which conveniently facilitates mapping where lechwe habitats exist today, and existed in the past.

Fortuitously, the valley grasslands, (mapped by Vesey-Fitzgerald 1970) together with more complete mapping of the Zambezi grasslands by White (1983), provide a convenient proxy delineating potential lechwe habitat. These patches form an archipelago of fragments and islands, presently or formerly linked. Distributions of Recent lechwe populations reveals they have populated ten principal wetlands, all maintained by the seasonal flooding of large drainage systems. As mapped in Fig. 2.2, these extend from the Upper Cuanza (1) and Owambo basins (2), which includes the Upper Kunene river, with all bordering the Atlantic watersheds; through to the Okavango and Chobe-Linyanti (3) in northeast Botswana. The latter network is closely linked with floodplains along rivers in southern Angola, principally the Cubango and Cuando drainage systems. They are separate from the Upper Zambezi and Barotse basin (and associated tributaries) that extend northwards to the Cameia depression (4). A separate complex of floodplains and swamps straddle the Upper Kafue catchment, including the Busanga and Lukanga Swamps (5), which are discrete from the Kafue Flats (6). The combined drainage of the Bangweulu-Upper Chambeshi system (7) lies south of the isolated Pambayshe Swamps (8) of the Luongo-Kalungwishi drainage systems. The Kashiobwe Flats form a distinct wetland linked around Lake Mweru to the latter's delta with the Kalungwishi and extending east to the Mweru-Wantipa system (9) where lechwes occurred historically. In Katanga, the Upemba Swamps (10) form a distinctly isolated wetland. The extant biodiversity of this wetland archipelago reflects a pronounced legacy of antecedent hydrographic patterns. It follows that reconstructing the evolutionary dynamics of this history, whereby drainage systems evolved their modern topologies, should reveal important controls on the origins and affinities of aquatic biodiversity in this archipelago. And here the evolutionary history of lechwes as an ecologically dominant species in floodplains assumes unprecedented importance. (Details of the Quaternary history of landscape evolution across this Katanga-Chambeshi region are reviewed in Chapter 4.) In two complementary respects, the concept of a wetland archipelago provides a useful heuristic framework for this study:

1. The biotic and geomorphological properties of each landform, and links among them, gain a revealing context, when framed within the history of an archipelago. As adequately as available data permit, the objective of Chapter 4 is to reconstruct the evolutionary dynamics of this archipelago, with close attention to past links and geomorphological events through the Plio-Pleistocene.

Furthermore, the relatively reliable dating that can be applied from archaeological evidence through the Quaternary (Chapter 5) refines timings of key events in the evolution of the Katanga-Chambeshi archipelago.

2. The geographical structuring of lechwe populations, which manifests in a distinct pattern across this archipelago, present targets to test with phylogeographic hypotheses. Their resolution should greatly aid deciphering the evolutionary history of these large mammals (Chapter 6). Equally, the detailed study of these patterns underpins a taxonomic review of the *K. leche* complex (Chapter 7). Finally, in the conclusion to this study (Chapter 8), I synthesize all these data in a multi-disciplinary treatment of pertinent evidence to reconstruct the evolutionary history of lechwes in south-central Africa.

2.6.3 Conservation Importance and Taxonomies of Lechwes

A thorough socio-economic survey of the optimal utilization of any wetland needs to recognize that its biodiversity constitutes the prize capital of the landscape. In this respect, the significance of lechwes in dominating the ecology of floodplains places great, belated significance on extirpations of their populations across south-central Africa. The life history attributes of lechwes allow these populations to sustain high harvest rates with respect to protein production from wetlands that are difficult to exploit directly by other means in cost-effective development programmes. The evidence that lechwe help maintain a high ecological productivity of floodplain fisheries is circumstantial, but deserving of priority research.

Any such study, and/or conservation planning, needs to improve our existing, incomplete knowledge of the ecology of these landscapes. There is much scope for studies to elucidate the ecology of lechwe antelopes in wetlands, with respect to their adaptations: and to understand how these large mammals interact in aquatic assemblages. These requirements emphasize the relevance of central objectives in this study seeking answers to evolutionary questions. They place the precedent on these interrelated questions:

1. With respect to microtaxonomic patterns, how have the lechwe populations of south-central Africa individuated through evolutionary scales of space and time?
2. Where and when did the species of lechwes evolve with respect to changes in the topology of the Katanga-Chambeshi wetland archipelago?

The findings of any such detailed study in evolutionary biology are influenced by many assumptions and factors. Those applied to the category of species in microtaxonomic classifications are of special significance in this study of relatively recent evolutionary events. So first I must first address vexing questions as to exactly what a species is, and how these entities can be characterized accurately and precisely. This is the objective of Chapter 3. This logically precedes the review to refine what is known about the evolutionary dynamics of the Katanga-Chambeshi region, focussing on antecedents of extant hydrographic patterns.

"Whatever its origin, this high-lying basin, for the most part deeply sand-covered, with its anomalous drainage system, constitutes the most striking feature in the physiographic structure of southern Africa."

Description by G. W. Lamplugh (1908: 166) of the Kalahari Basin that covers a vast portion of southern and central Africa.

CHAPTER 3



Red Lechwe, *Kobus leche*, Busanga Swamps, October 2002. Three males and young
Photograph: F. Cotterill



Black Lechwe, *Kobus smithemani*, Bangweulu depression. Adult males
Photograph: F. Cotterill



Male Puku, *Kobus vardoni*, Kasanka National Park, Bangweulu depression. October 1999
Photograph: F. Cotterill

Male Common Waterbuck, *Kobus ellipsiprymnus*, Moremi Game Reserve, Okavango Swamps, April 2001
Photograph: F. Cotterill



Female Crawshay's Waterbuck, *Kobus crawshayi*, Kafue National Park. October 2002.
Photograph: F. Cotterill



CHAPTER 3 CONCEPTS, PARTICULARS, AND THE INDIVIDUALITY OF SPECIES AND SPECIATION

"Biology concerns itself with diversity as such, and it is of fundamental theoretical significance that each organism is unique." M. T. Ghiselin (1971: 117)

"Anyone who finds the relevant distinction between spatiotemporally restrictedness and unrestrictedness that I am laboring to elucidate incomprehensible or biologically irrelevant is going to have a very difficult time in understanding biological phenomena" D. L. Hull (1987: 117)

3.1 INTRODUCTION

It is reasonable stipulation that a detailed study of a taxonomic problem should explain how the studied organisms have been classified, and equally, detail how microtaxonomic categories and entities have been treated. The trend in such contributions is to present some background and context to the species problem. Such reviews centre around definitions of opposing (and sometimes nested) species concepts to frame critical discussion, which compares their merits and weaknesses. Invariably, such reviews are challenged to critically assess a vast literature about species concepts and speciation. These reviews typically then conclude by justifying the investigator's choice of species concept(s) in the study.

This review is different. It has proved impossible to explain the evolution of lechwe antelopes, in deserving detail and explanation, without justifying the taxonomy employed to characterize their biodiversity. So I emphasize the philosophical basis as to why I characterize biodiversity the way I do. This taxonomic treatment is based on a spectrum of synthesized ideas: many reiterated previously. So this chapter frames the species problem within an ontology of biodiversity, which builds on the metaphysics of new evolutionary ontology that is Michael Ghiselin's Individuality Thesis (Ghiselin 1966, 1974, 1997, 2005a,b). It presents a summary of the nature of individuals and discuss how their properties influence the most fundamental aspects of biology. The tenets of this philosophy apply across natural history, and all the life sciences. They emphasize how the universal ubiquity of uniqueness has manifested in historically generated entities. What I term Darwin's Law neatly encapsulates these tenets. The state of affairs it describes confers irrevocable consequences on metaphysics and the historical sciences, not least biology. Darwin's Law proves a handy heuristic device to press home aspects of the argument as it develops through this chapter.

3.1.1 Scientific Concepts and the Species Problem

The growth in biological knowledge since the Enlightenment has drawn together empirical data about the biosphere with ideas formalized by philosophers of science. Scientists' descriptions and

experiments document patterns and mechanisms in properties of biodiversity, and the complexes where it occurs and has evolved. All this information is structured by concepts, of which a plethora have been explicated. Conceptual refinement is an integral process wherever the scope and quality of knowledge increases. Key epistemic functions of concepts include classification and categorization. They enable us to interlink and synthesize disparate information about natural entities. The origin, maturation, and equally rejection, of concepts to organize scientific information has proven critical to better understand complexities of the living world (Mayr 1982; Hull 2001; Sapp 2003).

The distinction between islands versus fragments (as argued by Watson 2002) is an example of how critical conceptual refinement can be when striving to quantify and understand natural patterns in biodiversity and earth systems (Chapter 2). Comparatively well established concepts include that of the gene, chromosome, ecosystem, lineage and population. Their maturation is exemplified by burgeoning attention to exons, transposons, ecosystem engineering, gene trees, and metapopulations, respectively. Their importance can be gauged by the large literatures structured around each of these concepts. For historians of science, each of these bodies of literature narrates the intricate development of a concept over many decades.

The finer detail, in fact precision, of concepts employed to classify biodiversity is most important; especially because systematics and taxonomy have several integrated functions as the fundamental biological sciences. Such classifying concepts delimit the categories that structure biological taxonomies. Concepts prescribe what natural entity is classified into which category. Genera are one example as the category for real world entities such as *Homo*; where these categories are conceptual constructs and so are fundamentally distinguished from the material entities they classify. Together, these concepts and taxonomies are critical to support the universal flow of names of organisms and associated information through science and society (Simpson 1961; Systematics Agenda 2000; Cotterill 1995, 2002a).

No concept in systematics, in fact all of comparative biology, is of more critical importance than that of the species. It is quintessential to the theory and practice of biological classification, and at all scales of biotic diversification (Simpson 1961; Mayr 1982, 1996, 1997; Sterelny & Griffiths 1999; Cracraft 2000). The fundamental epistemic role of species is derived from deep traditions, as humans have used the species concept since prehistoric times. This universal, albeit imprecise usage, forms a large portion of the vocabularies in all languages. These lexicons classify familiar, edible, noxious, and other organisms, which have attracted repeated attention sufficient to gain a name in that culture.

So it is somewhat surprising that a long standing debate revolves around the species category, quite possibly the oldest in several centuries of natural history. This debate ranks as one of the most controversial in contemporary science, and it has ramified across a large canvas of philosophical and biological enquiry (O'Hara 1993; Hey 2001). Some of the central issues at stake in this debate (e.g. trinomial classification and the relative importance of reproductive isolation) can be traced well back into the 19th century (Mayr 1982, 2001). The quintessential challenge at stake is refining a concept of the category of species universally applicable to describe, and classify, all the rich complexity of extinct and extant biodiversity. To underline a critical point - the species category is purely a concept; yet the species it classifies are real.

The species debate has intensified over the past two decades, through a period when novel issues have increased the complexities to be accommodated. These new catalysts include ideas in the philosophy of biology and theory of systematics, alongside rapid growth in the fields of molecular genetics and genomics. The latter continue to generate new data rapidly, which are revising established knowledge of species and speciation (Venter *et al.* 2003; Davis 2004; Ryder 2005). It is important to single out how tree-thinking has accompanied the growth of phylogenetic systematics, and further, injected novel vitality into the species debate (O'Hara 1993). Tree-thinkers conceptualize each segment of Darwin's Tree of Life as a unique part of a greater, interconnected whole. Burgeoning acceptance (tacitly and directly) of tree-thinking underlies the significant growth of phylogenetic systematics (O'Hara 1988, 1997) and allied developments in biogeography and historical ecology (Brooks 1985; Craw *et al.* 1999; Brooks & McLennan 2002). Pertinently, tree-thinking underlies advocacy of phylogenetic species concepts (PSCs), summarised in Table 3.1.

Adequate attention to the nature of the species problem would require book length treatment, and likely fill volumes should it treat its historical details exhaustively. Fortunately, several recent books have reviewed major aspects of the problem. These detail challenges species concepts face in characterizing biodiversity (Claridge *et al.* 1997), and several review the species problem within the context of understanding patterns and processes of speciation (Otte & Endler 1989; Howard & Berlocher 1998; Schilthuizen 2001). All discuss the problems of defining the species category and characterising biodiversity. Two recent multi-authored books (R. A Wilson 1999; Wheeler & Meier 2000) compare competing species concepts in detail. Neither has shied away from the varied philosophical tensions that underscore the species problem. New contributions routinely appear in peer reviewed periodicals. Certain journals have devoted entire parts to the debate: notably *Journal of Nematology* (1999) 31(2) and *Fish and Fisheries* (2002) 3(3).

3.1.2 Operationalism

This is a convenient stage to mention the operational imperative invoked by some scientists and philosophers as the most important (if not singular) criterion against which the scientific relevance of a concept stands or falls within science. The underlying motivation here is to remove theoretical error, such that one then only has to deal with empirical error. This can be a reasonable assumption and option, but only within strict limits of relevance. Hull (1968) demonstrated how operationalism becomes nonsensical when applied to “fuzzier” entities in nature; because it retards discovery of the real properties of nature in such situations. Operationalism flounders where the concept fails to quantify the totality of the material entities (or entity) that it purports to describe. A principal reason is that minimalist concepts follow on operational strictures. The latter tend to pejoratively simplify, distort and at worse trivialize properties of natural phenomena they purport to characterize.

The history of elaboration of the concept of the gene is an apt example of the strengths and weaknesses of operationalism (Hull 1968; Portin 1993). Operationalism has been invoked and applied repeatedly, under different guises in the species debate (Wiley 2002). In fact, operationalism currently dominates the species debate, as is clear in De Queiroz’s (2005) review. This problem catalyses a stance, fundamental to this review, to stand back from myopic concerns over operational strengths and weaknesses of species concepts. The larger metaphysical landscape has so much more to offer, not least in placing the philosophical poverty of radical operationalism into appropriate context.

3.1.3 The relevance of the species debate to this study

As recognized by Ansell (1972) and Grubb (1993, 2005), no less than 71 species of African Bovidae have evolved in a comparatively rapid, and spectacular, radiation (Chapter 4). The need to elucidate the real species diversity of antelopes awaits deserving attention (Cotterill 2003a, c) and recognition of this challenge follows belatedly on concerns by Ansell (1958a,b) who discussed Sable antelopes, *Hippotragus niger*, and Lechwes, *Kobus leche*, as exemplary taxonomic problems. Surprisingly, this problem extends to other large mammals. An arresting example of the “forgotten diversity” of African large mammals is the relatively recent recognition that the real diversity of extant Proboscidea in Africa comprises no less than two species, whose lineages reveal comparatively deep histories of evolutionary individuation as revealed by morphological (Grubb *et al.* 2000) and genetic evidence (Roca & O'Brien 2005; Roca *et al.* 2005).

With the notable exception of on going debates of how best to classify hominids and living primates (Groves 2001; Tattersall & Mowbray 2005), it appears that most mammalogists either avoid taking a

firm stance on a species concept, or follow the entrenched tradition and continue to rely on a polytypic, trinomial taxonomy. Vrba (1995) is a notable exception. Although Vrba (1995b) argued the merits of the Recognition Species Concept (Table 3.1), her actual descriptions and classifications of bovid species (e.g. Vrba 1995b) are not explicit as to which criteria were employed to delimit the species category.

A thorough review of the species debate, which attends to all its numerous historical and philosophical issues and problems, obviously lies beyond the terms of reference of this thesis. As the literature stands, scholarly treatment of even part of the debate necessitates complex patterns of citation, with lengthy bibliographies. Nonetheless, it really does matter how we go about delimiting and classifying populations that comprise phyla. Radically different taxonomies hinge on microtaxonomic decisions based on one's choice of species concept, and whether trinomials are employed. The Evolutionary Species Concept (ESC), originally introduced by Simpson (1951) structures this taxonomic reappraisal of the *Kobus leche* complex - as previously applied to characterize particular Chiroptera (Cotterill 2001a,b, 2002b), antelopes (Cotterill 2003a-c, 2005) and birds (Cotterill 2006).

My defense of the ESC is based on a more encompassing philosophy, which makes this chapter a conspectus structured on a philosophical argument. I present the metaphysical foundations which explain why the ESC provides the common currency to compile and compare information about biodiversity. Its conceptual scope extends to biogeographical narratives of deep history built on its core metaphysical strength of universal classification of biodiversity. Organisms of disparate evolutionary origins occupy one species category under the auspices of the ESC.

3.2 PHILOSOPHICAL FOUNDATIONS

3.2.1 Metaphysics

Metaphysics is the science that deals with reality at the most fundamental level; where ontology refines what and how things can exist. In this respect, concepts are the key tools used to create knowledge. Epistemology pertains to what is known, and what is potentially knowable. Epistemic principles and tools empower scientists to discover and classify knowledge. Any logically coherent attempt toward resolving the species problem has to reconcile with the separate, yet twinned, challenges entailed in ontology and epistemology. This entails refining an ontology of species together with grappling with the epistemic challenges attached to any activities whereby we discover and describe actual species in nature (Ghiselin 1997, 2002b; Mayden 1999, 2002; Wiley 2002). These two disciplines delimit, into

two complementary domains, all philosophical and scientific phenomena and activities, which relate to the nature of species and characterization of biodiversity.

The ontology must accommodate the nature of the species category into a conceptual framework, which succinctly accounts for all species (those real entities that have evolved) in all their multifarious complexities. The complementary epistemology should detail those robust, yet practicable, procedures that enable biologists to get on with the science of characterizing species into precise and accurate classifications (Ghiselin 1997). The solutions to these problems are grounded in metaphysics, but these efforts are framed by, and interface with, natural history. For the overall scope of living variety - in all the complex details of biodiversity - directly informs metaphysics with what it has to explain. The poorly appreciated richness of species is the reality that an ontology of the species category must explicate into a universal context. These real world complexities severely challenge the concepts and tools available to science to characterize biodiversity.

Some practicing scientists may object to how philosophy drives scientific research in such profound ways, and vice versa. It especially runs up against the tradition that sees science and philosophy as two distinctly segregated domains of intellectual activity and enquiry. Yet, more and more domains of research, despite their deep tradition as stolid subdisciplines of philosophy, have surrendered their core operations to the natural sciences. Epistemology and ethics are two. Metaphysics is yet another (Ghiselin 1997). The importance of these inter-dependencies between science and philosophy is illustrated by a recent study that sought to define the ontology of the category of the organism. Examples obtained from natural history were critical for J. Wilson (1999) to answer the twinned questions: “What is a living individual?”, and “What entities should a population biologist count when counting organisms?”. This study demonstrated how the explanatory ontology was severely tested by the variety of living examples thrown up by evolution. Paralleling, probably exceeding, the total complexity of evolved species, there are almost infinitely many different ways of being an organism. Several billions of years of evolution presents a bewildering complexity of organisms for an ontology to accommodate.

The orthodoxy of biology tends to recoil violently at the idea that metaphysics is science, let alone that might hold primal relations with science. The fact that the core science of biology, namely natural history, informs metaphysics might well strike stolid biologists as even absurd. The essay by Redhead (1995) provides a parallel to my position in how physics (especially quantum mechanics) informs metaphysics about the fundamentals of reality in the most revealing ways. Dissenters need to consider

definitive, scientifically credible reasons why biology should not inform philosophy about the nature of living reality; and as importantly, how the life sciences can even exist as legitimate academic pursuits if not informed by an ontology founded on a metaphysics couched in natural history.

Where and when philosophers permit their quests to be informed by biology, the consequences result in severe tests on the explanatory powers of metaphysics, where it is directly challenged to develop ontologies that accommodate all this real complexity (J. Wilson 1999). It would be most limiting to construct a metaphysics of life that attended solely to lechwe antelopes, within the parochial confines of mammalian natural history. The species concept used to classify these organisms might apply to other mammals, but probably be inapplicable to other vertebrates. Such a hypothetical exercise would struggle to masquerade as an exercise in comparative biology; for microtaxonomic units studied in one group of organisms must be comparable with all other similar entities. This means not only vertebrates, but all Metazoa and in fact all biodiversity.

And so it is with species. Metaphysics offers the only means to explain all manifestations of their complexities in terms of scientific credibility. This imposes significant limits and demands not only on ontology but equally epistemology. Some might find it paradoxical that these demands actually delimit (quite severely as it turns out) the spectrum of philosophical solutions that can be brought to bear on the species problem. For it turns out that many of the time honoured categories of typological classifications are not just irrelevant but grossly misrepresent realities. If they are to be credible, any species concept must explicate objectively the quirky properties of the living world, and equally embrace the peculiar conditions differentiating the species category from all other categories of living complexity. Thus, concepts of the species category must reconcile with all the multifarious contingencies and complexities of biodiversity manifested in evolutionary history.

3.2.2 Individuals, Organisms and Species

The word individual has overlapping, but different, meanings in philosophy and popular usage. Biologists usually equate it with an organism. In traditional usage by philosophers since Aristotle, forming in fact the philosophical consensus, the term is used in a more abstract context in metaphysics, referring to all spatio-temporally bounded particulars. As particulars, individuals contrast with universal properties of classes. The principle of individuation refers to the difference of an entity, its indivisibility, impredicability, and its spatio-temporal location (Audi 1999: 424-425, 562-566). The meaning of individual has an even more explicit meaning under the philosophy of absolute realism applied in this thesis; where “Absolute realism holds that what is true or false has absolutely nothing to do with what

anybody knows or opines.” (Ghiselin 1997: 301) Individuals are construed as distinctly bounded, autonomous entities, that exhibit cohesion amongst their parts. They appear, persist and die. Individuals are absolutely concrete, and so contrast starkly against classes (universals) which take on an abstractness. “Individuals are incorporated in other individuals, whereas classes are included in other classes” It is impossible for classes to participate in processes, but individuals are able to (Ghiselin 1997: 302). This distinction is not just fundamental but critical for living complexes to exist. Organic evolution only involves individuals. Only individuals can evolve and engage in processes, and be changed by processes (Ghiselin 2002b).

The usage of individual by ecologists and evolutionary biologists has nearly always coincided with the singular organism (Huxley 1932; Medawar 1981). Santelices (1999, 2004) distinguished between individual organisms on three criteria of genetic uniqueness, genetic homogeneity and autonomy. And the criterion of genetic distinctiveness receives increasing attention (Gibson & Dworkin 2004; Pineda-Krch & Lehtila 2004a,b). The subject of spatio-temporal boundedness of organisms has also applied a physiological approach (Turner 2000, 2003, 2004), which extends Dawkin’s (1978) concept of the extended phenotype. The spatio-temporal limits that exist around living organisms is the subject of a vigorous debate in the philosophy and biology of evolution (Miller 2003; Laland 2004; Dawkins 2004).

3.2.3 The Individuality Thesis

This philosophical stance considers species as real entities and fundamental units of biodiversity, following arguments developed previously (Frost & Kluge 1994; Wiley & Mayden 2000; Mayden 1999, 2002). An essay by Jordan (1905) seems to have been the first attempt to emphasize the reality of species (Mayr 1955). The argument (that species are real entities in the natural world) was emphatically articulated by Dobzhansky (1937). Fundamentally, this solution to characterizing the species and the species category acknowledges that biology is an historical science (Mayr 1982, 1996, 2004). As importantly, Mayr tacitly recognized an ontology founded on the Individuality Thesis. Its axiom is that all real world entities are either classes or individuals. Unlike classes, individuals lack defining properties, and above all do not exhibit instances. Boundaries around an individual are restricted in space and time. An individual can incorporate other individuals; thus as an individual, a species, *Homo sapiens* for example, incorporates parts - organisms (Ghiselin 1974, 1997; Baum 1998). Thorough treatment of the Individuality Thesis is beyond the ambit of this study; and its detailed explication has been assembled by Ghiselin (1966, 1971, 1974, 1997, 2002a,b, 2005a,b), Hull (1987, 1988), Wiggins (1980), and Williams (1985, 1989). (In parallel, if not overlapping geology (Frodeman 1995), it is

poorly appreciated that biology is equally an hermeneutic science with respect to how investigators interpret signs (traits and characters) in historically derived biotic complexes.)

It is important to emphasize how species contrast with natural kinds, where a natural kind is a class containing two or more individuals (Baum 1998). The foundations and implications of the individuality thesis are implicit in Darwin's philosophy of biology, and underpin the theory of evolution. Species are lineages comprised of parts (organisms) that exhibit cohesiveness. Individuals are spatiotemporally bounded entities whose parts exhibit cohesion. Thus individuals, but not classes, can participate in natural processes and are self-replicating (Mayden 2002).

An individual invariably exhibits turnover of its parts, such that their states are irreversible. Baum (1998) employed the instructive analogy of the classical problem of Theseus' Ship, which experiences a continuing history of repair, with planks and other parts being discarded and replaced with new. It is instructive to contrast this continual turnover of parts through the individual, with reusing the same parts to build a different ship. This new ship slowly assembled from these same parts would not constitute the same ship. The reason is a break in cohesiveness among the discarded parts. This analogy becomes tricky to apply to the lifelines of some organisms (especially parasites) with life histories punctuated by very different life forms. Its resolution has received detailed attention elsewhere (J. Wilson 1999).

Despite the process of descent with modification, with the losses and replacement of organisms, persistence of anastomosing (tokogenic) threads within a population manifests into an individuated lineage. Such a lineage, organism or species, exists within a unique spatio-temporal domain delimited by its birth and death (J. Wilson 1999; Mayden 2002). Biologists are challenged to discover and characterize individuated lineages. (Parenthetically, it is important to note, as detailed further below, this fact places those who delimit reproductive isolation as the *sine qua non* of speciation (e.g. Coyne & Orr 2004) in a philosophical quandary.) The ontological limits on the species category need further explication. It is instructive to reflect on how the nature of species relates to biodiversity overall. So, I now present a larger ontology of all biodiversity structured by the Individuality Thesis (Cotterill 2002a, 2003b).

3.2.4 Uniqueness, Variation and Variety in Living Complexes

This philosophical discussion first needs to delimit the meaning of two terms so often loosely applied - namely variation and variety. Here, I employ the concept of variety to refine an ontology which distinguishes variation from diversity. The term, variation, describes the emergent properties among two

or more unique living entities, which share at least one immediate ancestor in the histories of their individuation. Variation is a most familiar attribute of living entities. Co-occurrences of unique biological entities, sharing recent ancestry in a population manifests in variation (Darwin 1859; Lewontin 1974). Levins and Lewontin (1985), Rose (1997, 2005) and Lewontin (2000) have emphasized this property of life. Here, the quintessential phenomenon to reconcile with is the circumstance that any two such closely related entities, no matter how identical, have only to differ in one detail to be unique. The inevitable consequence is variety: either variation or diversity. These are more traditionally treated as continuous versus discontinuous variation (e.g. Dobzhansky 1937). The delimiter between variation and diversity is principally scale dependent; but in either case we are dealing with spatio-temporally delimited entities.

The term 'population-thinking' conceptualizes the phenomenon of continuous variation in living entities; "We call the concept which emphasizes uniqueness of each individual *population thinking*" (Mayr 1988: 224, italics his). It also remains to be widely acknowledged that the spread of population-thinking through NeoDarwinian biology followed on two protagonists, not just one - George Gaylord Simpson as well as Ernst Mayr. It is not widely recognized that Simpson (1940) established the theoretical platform, and equally the quantitative methods of population-thinking. He argued that studies of species should quantify the entire variation of samples available to taxonomists; and employ statistics of their variation as proxy estimates of that of sampled populations. This groundshift in how biodiversity has come to be studied is now recognized as no less than revolutionary compared to the typological tradition that characterized all previous philosophies and studies. It was rapidly adopted through the 1950s as a keystone of the Neo-Darwinian Synthesis. The concept is implicit in Ernst Mayr's copious writings about taxonomy and species from 1940, but was only named population-thinking in 1955. Thereafter, Mayr (1959) emphasized how it set biology apart from the physical sciences (Chung 2003). Mayr only placed the label of population-thinking on this revolution nearly two decades after Simpson's seminal paper (Laporte 2000). In fact, Charles Darwin had initiated this revolution more than a century earlier. It was Darwin's scrutiny of individuals, and equally appreciation of historical causation, that proved critical to derive and develop his philosophy that structures all 22 of his books (Ghiselin 1971, 1984; Lewontin 1983; Mayr 1991; O'Hara 1997). Its revolutionary discoveries cannot be overemphasized, especially as it persistently misunderstood:

"To see what a change has taken place, let us have recourse to a metaphor, and compare the Darwinian Revolution with that brought about by Copernicus. The great astronomical revolutionary had changed the positions of two heavenly bodies, so that the sun had moved from a peripheral to a central position. Darwin effected a very similar revolution, in that he

reversed the positions of individuals and groups. His theory treated the actions of individual organisms as the cause of what was observed at higher levels." (Ghiselin 1971: 122)

It is differences, not likenesses, between individuals that are of great theoretical interest. Instead of asking how an organism generates descendants of the same kind, the Darwinian investigator of inter-generational descent asks how offspring differ from the parent. This distinction radically influences what kinds of groups arise from the particular histories of individuals. One is left to grope for analogies to relate the profoundness of the Darwinian Revolution into familiar terms of reference. After 1859, biology had to be done in a language that was not merely new, but radically different from any other (Ghiselin 1971). Remarkably, the grammar and syntax of Darwinism has still to overturn that entrenched in large realms of science, including life sciences such as ecology, medicine and molecular biology:

“Darwin invented a new way of thinking about evolutionary problems, and it was this that gave him his prowess in general biology. Not so the vast majority of those who came after him. As a rule, they took up only the most simple-minded aspects of Darwinism, and their ideas about it were the most crudest form of travesty.” (Ghiselin 1971: 130)

The variation recognized by population-thinkers is an historical product, with the organisms comprising a population united by their relatively recent history of reticulate descent (tokogeny, *sensu* Hennig 1966). A familiar manifestation of uniqueness manifests through the lifeline of an organism, through its ontogeny; as cell lineages develop and diverge, and they differentiate into different organs, and other tissues and morphologies (Rose 1997, 2005). Thus, even siblings with identical genotypes are unique, because their phenotypes differ as a consequence of individual lifelines. Singularities of uniqueness among organisms imparts a real and dynamic variation to a population:

“This uniqueness is true not only for individuals but even for stages in the life cycle of any individual, and for aggregations of individuals whether they be demes, species, or plant and animal associations. Considering the large number of genes that are either turned on or off in a given cell, it is quite possible that not even any two cells in the body are completely identical. This uniqueness of biological individuals means that we must approach groups of biological entities in a very different spirit from the way we deal with groups of identical inorganic entities. This is the basic meaning of population thinking.” (Mayr 1982:46).

Burgeoning growth in genomic databases of the individuals comprising closely related populations, namely *Homo sapiens*, reveals the genetic differences between any two individual humans to be far greater than conventionally believed (Gibson & Dworkin 2004; Pineda-Krch & Lehtila 2004a,b). An abundance of single nucleotide polymorphisms (SNPs) and structural rearrangements at small scales across chromosomes are being documented (Feuk *et al.* 2006). The SNPs and other differences amongst organisms appear to have important influences in evolutionary processes. The picture

emerging from genomics about differences between genomes of closely related organisms points to a configuration of variation verging on the infinite (Rose 2005).

3.2.5 Diversity: Tree-Thinking, and Biodiversity

Comparative biologists almost take the lineage concept for granted. This iconographic has a long tradition of usage to visualize the entities into which parts have been organized by inter-generational descent. Lineages graphically represent the passage of processes entailed in inter-generational descent, in which interactors and replicators occupy focal roles (Hull 1980). Equally, the stages in the lifeline of an organism also depict what is a continuous lineage. A consequence of historical processes has been the formation of particular groups incorporating unique parts; and the properties, and equally the trajectories, of these groups reflects directly on what happened to ancestral parts. So, thanks to evolutionary processes, uniqueness in living systems has manifested across larger, in fact immense, domains of space and time. This variety is represented in the diversity of species and higher phyla. Patterns of discontinuous variation dominate living variety at this hierarchical level (Fig. 3.1).

Complementing the concept of population-thinking, ‘tree-thinking’ (O’Hara 1988, 1997) encapsulates an overarching concept describing how individuals have been organized by evolution into the diversity of species and larger, more inclusive phyla. The Tree of Life is the time honoured iconographic rendition of this pattern. Tree-thinking underlies the philosophies and methods of phylogenetic systematics, which implicitly recognizes each species and clade as unique parts of a singular Tree of Life. This variety of life is a complex assemblage of all the historical products of evolution. Cotterill (2002a, 2003b) argued that Dobzhansky (1973: 125) did not go far enough when he stated that “Nothing in biology makes sense except in the light of evolution” (also see Ayala 1977). More accurately, “Nothing in biology makes sense except in the light of history” (Rose 1997).

Popular definitions of biodiversity compartmentalize the variety of life into structural, compositional and functional components. This perspective in neontology has proceeded into arenas of epistemic operations where many investigators have lost sight of what individuals they are actually studying. So much the worse for neontology (Cotterill 2002a). These weaknesses reveal a tension between a holological versus mereological view on the composition of biodiversity. This dichotomy has traditionally delimited ecology (Hutchinson 1978) with all the established traditions and theories of systems versus populational researches. The Individualistic philosophy advocated in this study is

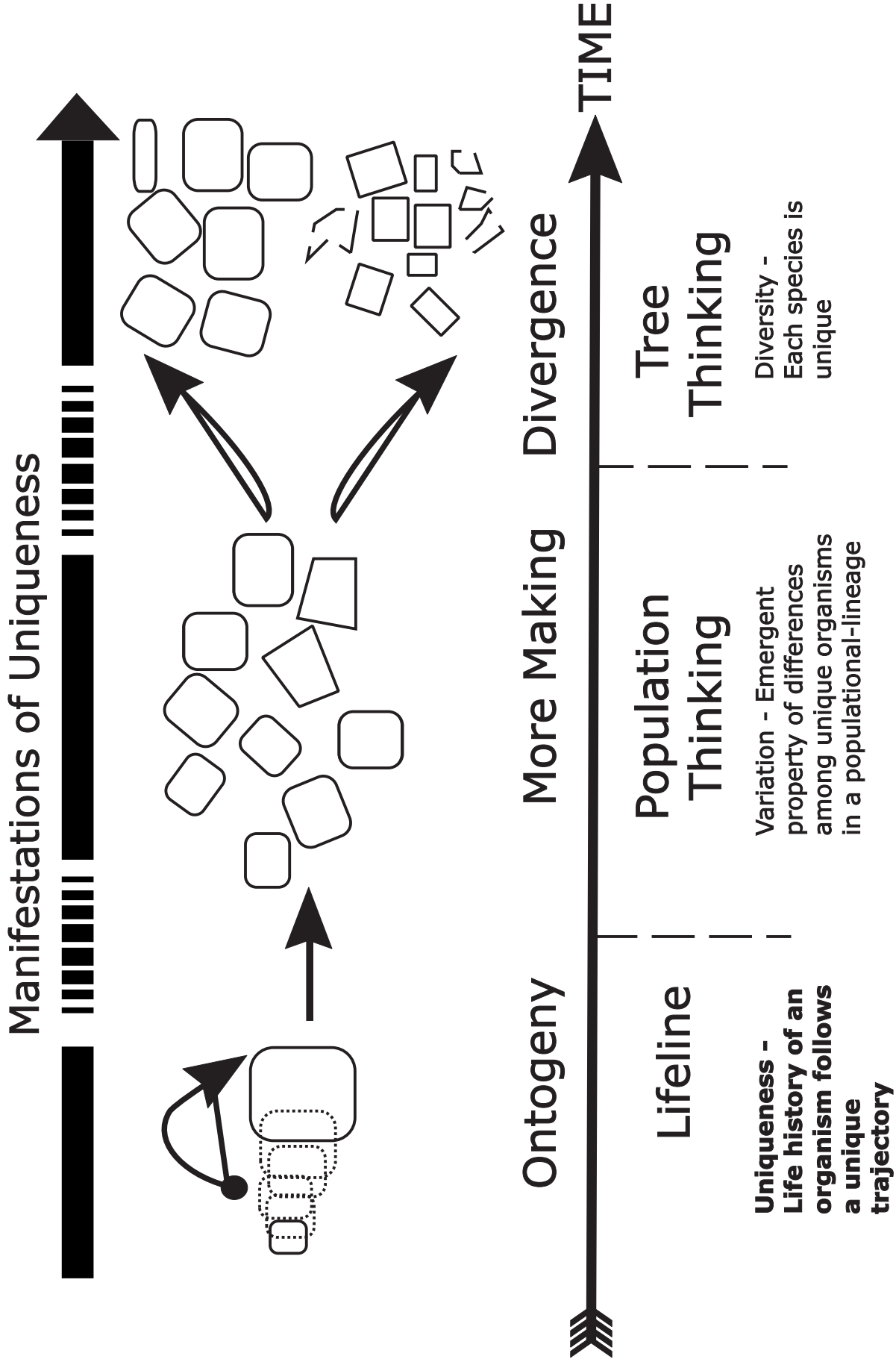


Figure 3.1. Depiction of the hierarchical structure of biodiversity to which the complementary concepts of life history, variation and diversity apply. The heuristic labels of Lifeline, Population-thinking and Tree-Thinking encapsulate the concepts and methodologies employed in these respective research arenas. Modified from Cotterill (2002a).

intrinsically mereological, in detailing how historical associations among parts (organisms) manifest in a larger entity (species): with all these spatio-temporally contained entities being individuals, which are components of biodiversity. These individuals manifest in the diversity of life. At best, holological classifications of biotic complexes provide heuristic renditions of interacting individuals in physical landscapes. At worst, artificial entities in human perceived systems, such as trophic units, are treated as real evolutionary units.

3.3 DARWIN'S LAW

Biological uniqueness manifests universally through living complexes. I cannot imagine a singular exception to this pattern. This ubiquity manifests throughout the biosphere. Its hierarchical structuring manifests in a fundamental organization. It is equally interesting that variety (arising from uniqueness), has become packaged within certain individuals, notably species and clades. These properties of biodiversity prescribe peculiar constraints on how biologists can conceptualize and characterize variety. Moreover, the universal occurrence of these phenomena constitute a scientific law, which I term Darwin's Law:

All living entities are unique; so inherent differences between two or more entities manifests in the biological variety representing in lineages. Uniqueness characterizes the genome and phenotype of an organism through its life history; as it manifests in the dynamic variation of populations, and is expressed in the diversity of species, and the clades into which species are incorporated. This ubiquity of uniqueness is universal throughout the living world. It determines fundamentally the properties of all individuals, including organisms, species and all larger spatio-temporally bounded entities that incorporate the former. This intrinsic creation of variety at all levels of life (biodiversity *in toto*) is an inherent consequence of historical processes. Structured through complementary hierarchical levels, threads of accumulated history have structured unique individuals into biodiversity.

Judged against the nomic criteria identified by Cooper (1998) for generalizations about biological phenomena, Darwin's Law possesses very high epistemic resiliency and robustness. Even more remarkable, it exhibits a universal scope of explanation wherever scientists engage with any manifestation of an individual in the biosphere. If there is a fundamental particle in this ontology, it is the notion of a unique entity. Our reconciling with this ontology framed by Darwin's law is fundamental to solve the species problem, because it reveals exactly what entities biologists are challenged to characterize as species.

A major benefit is that Darwin's Law directly delimits what biodiversity (i.e. individuals) can occupy the species category (Cotterill 2002a, 2003b, Fig. 3.1). Hereafter, the far reaching ramifications of Darwin's Law are invoked repeatedly - directly and heuristically - to emphasize ontologically loaded

precedents that refine and delimit what species are. The species category includes those individuals whose lineages comprise the largest reticulating (i.e. tokogenic) entities. The fact that lineages are not reducible to tokogenetic relationships (Wiley 2002) follows from this exhibition of biological uniqueness at higher levels. The distinction by Baum (1998) between natural kinds of species differentiated by causal versus historical connections gives us two complementary ways to look at the same individual. They are two different concepts to configure properties of the historical entities created by interacting organisms, in terms of interfacing of their cohesive connectivity. Thus synchronic (time delimited) species concepts delimit populations, in contrast to diachronic (time extended) concepts that emphasize temporal dimensions of lineages. Independent of overzealous prescription to either view, these are reciprocal views of the same species.

This ubiquitous uniqueness of living entities (Simpson 1963b; Montalenti 1974) is a function of their history (Hull 1975). And it follows that the hierarchical structuring of living variety into variable populations and diverse species and taxa, is a fundamental property of life. Framed by Darwin's Law, the species category encompasses those unique individuals which exist as lineages (Cotterill 2003b). This follows Wiley (1978, 2002) who recognized that these individuals are identical to those recognized by Simpson (1951) and Hennig (1966). Species are those segments of lineages that have persisted between critical events; and whose unique topologies reflect their respective evolutionary histories (Adams 1998, 2001; De Queiroz 1998, 1999; Wiley & Mayden 2000). A major factor influencing the veracity of our knowledge about biodiversity hinges on the accuracy and precision with how we dissect its living variety according to intrinsic natural patterns. Concepts have fundamental influences on the accuracy and precision of resultant knowledge. Our cognisance of these phenomena frames and underpins any serious attempt to conceptualize and characterize species (Section 3.9, Figs 3.1 & 3.2).

Numerous investigators have applied mathematical logic to try and define and model aspects of individuality in living systems (for example, Michod 1999). These attempts are challenged by onerous complexity, especially if they are to depict the complexity of an organism's genome in mathematical logic with requisite thoroughness. We can do well to reconcile with this, and allied challenges facing attempts in developmental biology and genetics to decipher the genomic complexities that contribute to the uniqueness of an organism. They are coupled with the behavioural, ecological, and evolutionary dynamics of populations (Lewontin 1999, 2000, 2002). The purely conceptual foundations of Darwin's Law, presented above, provides a way around these daunting empirical challenges.

I conclude that it will prove most difficult to articulate a species concept (and equally study biological diversity) if one employs ontological credentials outside of the metaphysical framework prescribed by Darwin's Law. The advocates of any such attempt are challenged to explicate how such a philosophical construct possesses the requisite metaphysical, and thus scientific integrity, they might credit it with. Theoretically, one can invoke a heuristic example where the discovery of a group of identical organisms would refute the ubiquity of uniqueness. Despite sparse knowledge of the biosphere, what biology has discovered, and continues to discover, about the staggering variety of life reinforces the universality of Darwin's Law.

The scholarly argument by Stamos (2003) that species are relations - not individuals - did not address critical arguments by Ghiselin (1997), Baum (1998), and J. Wilson (1999) that underpin and structure the ontology of uniqueness, encapsulated in Darwin's Law. Should species indeed be relations, then aspects of this study might need revision. Yet, this 'species as relations' thesis conforms closely to the individuality thesis because both ontologies place a primacy role on how causal relations among organisms have manifested through history into larger-scale structures in the form of populational lineages. Stamos (2003) ignored the ubiquity of uniqueness exhibited among species and their parts, nevertheless his ontological parallels that established in Chapter 3. Thus, his argument that species are relations - not individuals - would not change this taxonomic treatment, analysis or conclusions, and neither the biogeographical analyses (Chapters 4-7).

3.4 SPECIES AS INDIVIDUALS AND THE INDIVIDUATION OF SPECIES

3.4.1 Biological Diversification and Speciation

Many different processes can cause the individuation of novelty in the biosphere, and the origin of new species lineages are prominent products of this evolutionary history (J. Wilson 1999; Mayden 2002; Van Veller *et al.* 2003). There are three broad categories of speciation. One is reductive where hybridization of two, and even more, lineages fuse into a new lineage. An example is the origin of particular Darwin's finches in the Galápagos Archipelago (Grant & Grant 1996, 1998, 2002). Phyletic speciation is a second. This is also termed anagenesis, which entails gradual progression, whereby one lineage attains a distinct individuality. The third category is additive (also termed vicariant, or cladogenic) speciation in which the number of lineages increases after the speciation event. (Lynch 1989; Chesser & Zink 1994; Brooks & McLennan 1999). These perspectives on additive speciation owe a great deal to Darwin's Principle of Divergence (Mayr 1992), and underpins a key pattern integral to additive speciation events where one population evolves into two or more daughter populations.

Theoretically, a sympatric or allopatric context can apply to a speciation event in each of these three modes. The exception is anagenesis where lineage fission, and thus allopatry, is illogical. A fundamental difference distinguishes two modes of allopatric speciation. These two broad patterns reflect whether speciation entailed vicariance of the ancestral habitat, or alternatively a budding off of a founder population from the larger parent population (Mayr 1963, 2001). These two patterns of allopatric speciation are labeled dichopatric (secondary) versus peripatric (primary) speciation, respectively. Peripatry is also described as the peripheral isolates model (Cracraft 1984; Lynch 1989). Peripatric speciation is represented by two populations which exhibit abutting and sometimes overlapping ranges; while the extant populations in most dichopatric species manifest in geographically separated distributions (Mayr 1963, 2001; Snow 1981; Lynch 1989; Wiens 2004; Fitzpatrick & Turelli 2006).

Empirical studies of speciation patterns in selected groups of vertebrates have demonstrated that the incidence of dichopatric speciation, resulting from vicariance, significantly exceeds speciation events due to sympatric and peripatric processes (Lynch 1989; Chesser & Zink 1994). In the second part of Chapter 4, I pay close attention to the fragmented distributions exhibited among complexes of closely related species of vertebrates across south-central Africa's wetland archipelago. These isolates appear to reflect vicariance driven by drainage evolution in many fishes (Bell-Cross 1982; Skelton 1994) and particular birds (Cotterill 2004, 2006), reptiles (Broadley & Cotterill 2004) and mammals (Cotterill 2003a,b, 2005). Furthermore, an important function of the phylogeographic part of this study (Chapter 6) is to test whether the isolation of lechwe antelopes today does indeed reflect a vicariant history, or whether other demographic events have influenced their evolutionary histories - pertinently peripatry.

3.4.2 When does an individual begin to exist?

The entirety of species extends to no more than the sum of their parts and the collective interactions of these organisms. We are challenged to envision how historical entities individuate over evolutionary scales of space and time. Species are the units produced by evolutionary processes. This means species do nothing; they are effects in contrast to effectors (Cracraft 1989). "Species are much like developmental pathways within the ontogeny of individual organisms: both are effects rather than effectors. They are epiphenomena, developed, or evolved - in the true historical sense of the term - from lower-level processes. Both are historical entities or 'by-products'." (Cracraft 1989: 48).

Darwin's Law can be brought to bear on niggling uncertainties integral to studying and understanding speciation. When, ontologically speaking, does a species begin its existence as a spatio-temporarily bounded individual? This ontological problem shares many parallels with a debate carrying far reaching

ethical concerns: “When does a human being begin to exist?” (Smith & Brogaard 2003). The question common to any speciation event is when does the lineage assume ontological independence, and thus individuality? Our best hope of obtaining answers to this problem lies in two arenas of philosophy. One entails answers to ontological problems which ask how historical processes generate uniqueness. The second arena is epistemological, entailing the challenges of how such entities can be discerned. These issues are critical ingredients in the question “What is speciation?” This subject is a little easier to delimit than the concept of the species category; but it contains some intractable nuggets which resist unequivocal definition. As already emphasized the approach, in this thesis, is that speciation entails the individuation of a lineage. A young lineage initiates its existence through ramifying processes of tokogeny from the parent species. The genetic and thus phenotypic attributes of its organisms are invariably augmented from the parent lineage for some time after a lineage assumes its independent topology in time and space (Morjan & Rieseberg 2004). Whether occurring gradually or episodically, persistent tokogenic flow (termed Mayr’s Brake, Sterelny 1999) is considered significant in retarding the individuation of such demes.

The Greek myth of Theseus’ Ship instructively reveals a key process common to speciation. It provides an analogy of the situation, where organisms from a population are relocated into a new habitat. Here, their more-making activities manifest in a new lineage. This breakdown in cohesiveness in the parent lineage, and its establishment in a novel context involves two individuals. With respect to the lens of history, what matters is how long it persists. Evolutionary biologists are fond of asserting that the existence of such a lineage can be discerned after its persistence has manifested in a separate evolutionary history. It is relevant to acknowledge that subsequent dual exchange of organisms between the parent and daughter lineages does not obviate their respective ontological independence. Nevertheless, the fate of the majority of such young demes formed in real landscapes is phenomenological extinction. Either all parts die out, or they disperse into another lineage (usually that of the parent). Thus the circumstances of the birth of the new lineage, with respect to geography, constitutes the critical controls on where and how new species evolve. Where habitat vicariance (for example scission of a drainage system) creates more than one new dichopatric lineage, the ontological circumstances pertaining to individuations of these daughter lineages are unequivocal, subject to how inductive drag in geomorphological dynamics prolongs gene flow.

A considerable volume of writings in evolutionary biology represent the event of speciation as lineage scission, effecting additive speciation. Here, investigators are often challenged to distinguish the individuated lineage from the parent (stem) and/or sibling lineage. It seems be Hennig (1966) who

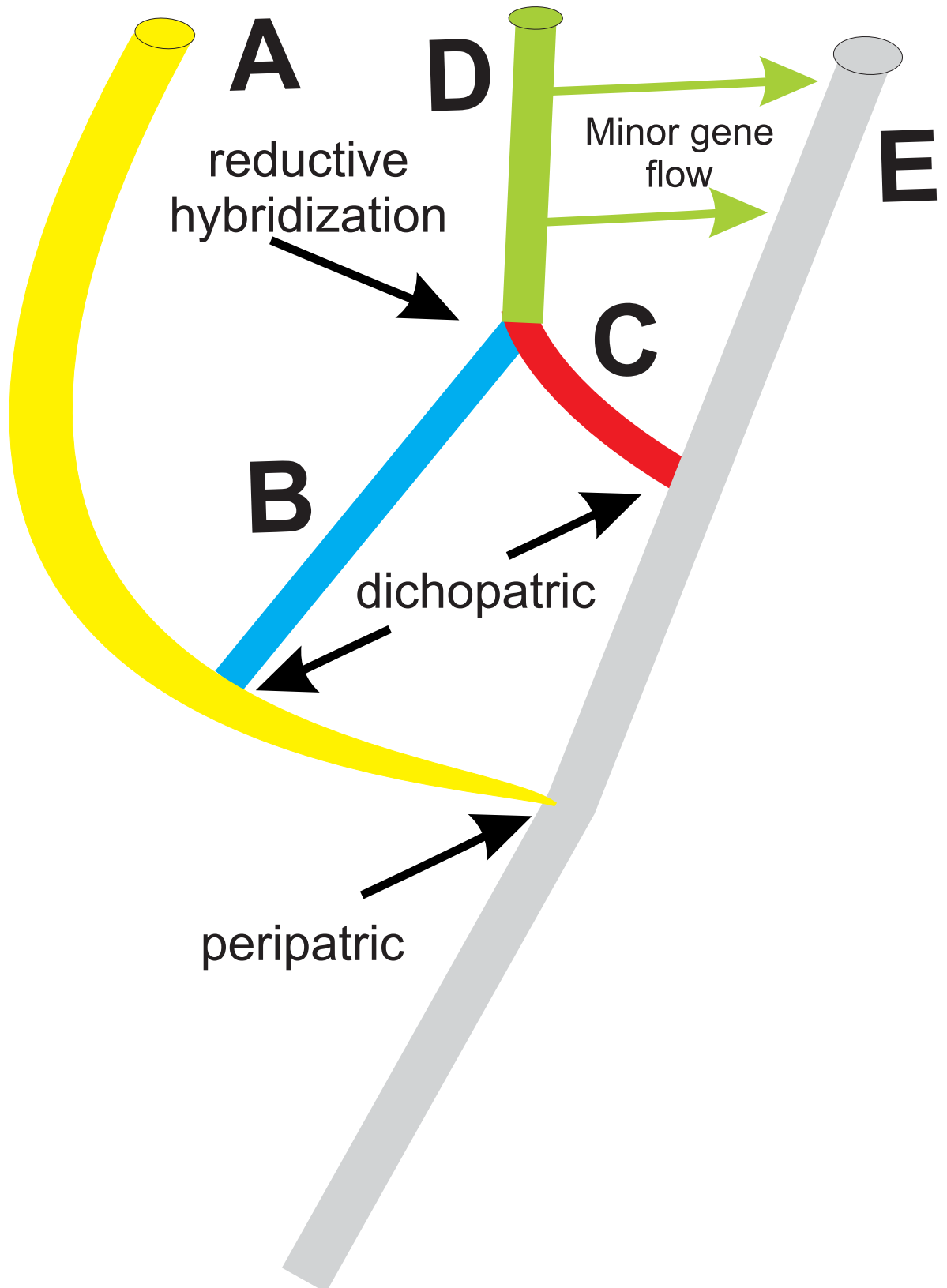


Figure 3.2. Graphical depiction of how lineages individuate through cladogenesis, with respect to allopatric and peripatric speciation events.

inaugurated the idea that ancestral species cannot persist after giving rise to one or more individuated lineages. This dogmatic notion has proved hard to expunge, especially from certain arenas of cladistic philosophy. Its credibility is rubbished by the fact that peripatric speciation in no way detracts from the individuality of the parent lineage, which persists despite losing some of its parts (organisms) which found an independent lineage (Fig. 3.2). It has become an established tradition to retreat from the challenge of trying to characterize individuation (where it is even articulated as such) and seek the essence of speciation. The phenomenon of reproductive isolation is probably the most popular; but before any further elaboration, it is necessary to deal with the notions that demographic processes and, and even aspects of the speciation process can be reversible.

Empirical evidence (e.g. Otte & Endler 1989; Berlocher & Endler 1998; Coyne & Orr 2004) reveals that speciation can occur through many different mechanisms, such that a plurality of categories could be built to classify the different sets of mechanisms. It is a fundamental truism to state that the individuation of a new lineage is a unique event. Such instances of the individuation of uniqueness follows Darwin's Law. Moreover, circumstances of individuation will obviously be unique, where and when a new lineage evolves in space and time. So it is not surprising that a pluralism of species criteria have been generated by biologists to try and characterize this diversity (Mayden 1997; Sluys & Hazevoet 1999). The fact that species are individuals means that biologists have to reconcile with "...the parallel individuation of groups of organisms by multiple biological processes." (Baum 1998: 647). Before taking this subject further, it is pertinent to discuss the notions of reversibility where they concern individuals.

3.4.3 Uniqueness, Irreversibility and Future Predictions

Recognition of pluralism is all one way. Speciation is an irreversible process, following Darwin's Law, and further given that "Nothing in biology makes sense except in the light of history" (Rose, 1997). Misinterpretations of this metaphysical constraint often appear under different guises in the primary literature. Masters & Rayner (1996), for example, concluded: "Species are the evolutionary ratchet. They fix irreversibly the products of *reversible* processes at lower levels of organismal hierarchy, and in so doing, generate the fundamental components of macroevolutionary pattern" (Masters & Rayner 1996: 225, *italics* mine). Similarly, Jolly (1993) distinguished the reversible phenostructure from zygostructure of African baboons, *Papio* spp. A parallel argument by Brooks & McClennan (1999: 130-131) distinguish micro-species from macro-species; and the former are considered ephemeral whilst the latter are persistent entities. Within the framework of Darwin's Law, it is nonsensical to argue that reversible processes occur within the anastomosing lineage of an evolving individual. Equally, the

recent suggestion that the “same” species of fishes can evolve repeatedly in different places and times (Turner 2002) is philosophically flawed. Baum’s (1998) treatment of the properties of individuated lineages refutes such explanations. All such notions that reversible processes exist in the living world are most tricky to accommodate under the aegis of the Individuality Thesis, and an ontology of biology founded on Darwin’s Law.

O’Hara (1993) correctly attributed a major part of the species problem to that of the incommensurable scales of enquiry across which studied lineages are compared. But he should know better than to have invoked the problem of narrative predicates. For evolutionary biologists are not in the business of predicting what the future stakes of entities; for this entails so much crystal ball gazing. It lies outside the edict of science to predict what the future holds for any lineage through the evolutionary scales of space and time. The theatre of enquiry for systematics is restricted to reconstructing key events by recovering historical narratives of the evolutionary chronicle (*sensu* O’Hara 1988). Any of our attempts to predict future behaviour of individuals are inherently speculative. A wealth of these events entailed the individuation of species to form many different natural kinds, each of which comprises the species category. This sets the stage to take this review forward, and discuss how we characterize species. Philosophers have thought a great deal about what defines robust knowledge of historical phenomena; and these philosophies of history have much to offer evolutionary biology, because we are studying processes and products of deep evolutionary history.

3.5 DISCOVERING INDIVIDUALS

3.5.1 The Evolutionary Chronicle and Historical Narratives

Building on Hull’s (1975) thesis that individuals are the central subjects of historical narratives, O’Hara (1988) applied this philosophy to systematics to conclude that evolutionary biologists are tasked with estimating events within the evolutionary chronicle. Moreover, the scale of enquiry in characterizing species is distinctly scale dependent (O’Hara 1993). Among several similar philosophies of history, that of Danto (1985) can be singled out. This distinguished between the ontological complexes generated by historical processes, and the activities engaged in by historians seeking to reconstruct characters and events. In all their ramifications, the complexity of past entities and events verges toward the infinite. Thus, the best efforts of historians can only estimate the nature of this historical chronicle. Similar conclusions were reached by Stanford (1986). This situation aptly applies to comparative biology.

Table 3.1. Summary of principal concepts of the species category, including the concepts of ESU and subspecies. This classification is a subset of the concepts summarized by Mayden (1997), with concepts listed in alphabetical order (although the subspecies and superspecies concepts are traditionally applied in combination with the BSC). One might argue that ESUs lie outside of this classification, but ultimately are proposed alternatives to traditional approaches to trinomials in microtaxonomy, which have applied concepts of subspecies, varieties and races.

Concept	Definition
Biological Species Concept (BSC)	<p>“A biological species is an inclusive Mendelian population; it is integrated by the bonds of sexual reproduction and parentage.” (Dobzhansky 1970: 354)</p> <p>“A species is a group of interbreeding natural groups that is reproductively isolated from other such groups.” (Mayr & Ashlock 1991: 26).</p>
Cohesion Species Concept (CSC)	<p>“...the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms.” (Templeton 1989: 12)</p> <p>“..the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability.” (Templeton 1989: 25)</p>
Evolutionary Significant Unit (ESU)	<p>"...a population (or group of populations) that 1) is substantially reproductively isolated from other conspecific population units, and 2) represents an important component in the evolutionary legacy of species" (Waples 1991)</p> <p>“ESUs should be reciprocally monophyletic for mtDNA alleles and show significant divergence of allele frequencies at nuclear loci.” (Moritz 1994: 373)</p> <p>“A lineage demonstrating highly restricted gene flow from other such lineages within the higher organizational level (lineage) of a species” (Fraser & Bernatchez 2001: 2742)</p>
Evolutionary Species Concept (ESC)	<p>"A species is a single lineage of ancestral-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." (Wiley 1978: 18).</p> <p>“...a lineage, comprised of organisms, whose history of individuation has manifested in its unique evolutionary trajectory through space and time.” (Cotterill 2005: 115)</p>
General Lineage Concept (GLC)	<p>“In short, species are segments of population-level lineages. This definition provides a very general conceptualization of the species category in that it explains the basic nature of species without specifying either the causal processes responsible for their existence or the operational criteria used to recognize them in practice.”</p> <p>De Queiroz (1999: 53)</p>
Genetic Species Concept (GSC)	<p>“...population subdivisions concordantly identified by multiple independent genetic traits should constitute the population units worthy of recognition as phylogenetic taxa” Avise and Ball (1990: 52)</p>
Phylogenetic Species Concept Diagnosable Version (PSC1)	<p>"the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983: 170).</p>

Table 3.1 cont...../

Phylogenetic Species Concept Monophyly Version (PSC2)	“...a geographically constrained group of individuals with some unique apomorphous character, is the unit of evolutionary significance (Rosen 1978: 176). Equates with ISC (Internodal Species Concept) of Kornet (1993) termed the CSC by Brooks & McLennan (1999)
Phylogenetic Species Concept Diagnosable/Monophyly Version (PSC3)	“...the smallest diagnosable cluster of individual organisms forming a monophyletic group within which there is a parental pattern of ancestry and descent” (McKittrick & Zink 1988, defined by Mayden 1997: 407). This version of the PSC was termed the PSC2 by Brooks & McLennan (1999)
Recognition Species Concept (RSC)	“...the most inclusive population of individual biparental organisms that share a common fertilization system” (Paterson 1985: 25)
Subspecies	“an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species” (Mayr 1969: 41).
Superspecies	“A superspecies is a monophyletic group of closely related and largely or entirely allopatric species that are too distinct to be included in a single species or that demonstrate their reproductive isolation in a zone of contact..” (Mayr & Ashlock 1991: 430)

A logical position with which to begin a review of different ways to discover species is with the phenomenon of reproductive isolation. This has received and continues to receive considerable attention by students of speciation; for it is commonly believed to be the defining property of the species category. This tradition has deep roots in systematics, especially among vertebrate taxonomists.

3.5.2 How Do We Characterize Reproductive Isolation? The Biological Species Concept (BSC)

The BSC deserves some attention, because of a persisting paradox; its epistemic and ontological weaknesses contrast starkly against its persistent popularity in certain zoological classifications. Definitions of the BSC have changed subtly and repeatedly since the first proposed by Dobzhansky (1937) and Mayr (1940). It is as important to acknowledge that the BSC has been defined in several different ways. These concepts all focus on reproductive isolation, but differ in subtle yet important details in how they interpret the latter (Beurton 2002; Chung 2003). In retrospect, an informative way to read Ernst Mayr’s voluminous writings about the species problem, is to acknowledge how it testifies to one long argument. They chronicle how a remarkable mind grappled through many decades with the slippery challenges of characterizing the heterogeneity of individuals as natural kinds. Mayr (1957, 1982) showed how precursors of the BSC can be traced far back into the 19th century, and in fact even earlier. Precursors of the BSC, championing the criterion of reproductive isolation, can be traced back to 1750. Beginning in the 1890s, the idea was formalized first in Karl Jordan’s arguments and practices

of taxonomy (Mayr 1955; Johnson 2005). Before Dobzhansky (1937) first articulated a BSC, the concept of reproductive isolation was implicit in Fisher's (1930) emphasis on genetic attributes of species.

Despite its acute weaknesses, the BSC continues to feature prominently in published taxonomic literature and biological textbooks. This employment is either salient, with it still structuring obsolescent taxonomies (awaiting revision), or from direct support in current literature. The BSC's dominance of a large body of published zoological knowledge is especially problematic where it is applied to manage biodiversity. This can confer unfortunate repercussions on the veracity of scientific information employed to structure and support management policies and environmental legislation (Mayden 1997; 1999, 2002). The BSC especially persists in mammalogy (Corbet 1997; Cotterill 2002a, 2003a-c, 2005). Not least, the BSC still dominates classifications of antelopes (Ansell 1972).

Between 1955 and 1975, modifications of NeoDarwinism focused on melding genetics with ecology, at the expense of palaeontology. Most critically, this neontological focus eclipsed considerations of the primacy of history from evolutionary biology. Adherence to the BSC solidified through this period. Attention to historical attributes of populations had to wait until the late 1970s, and still remains incompletely recognized (Kingsland 1995; Brooks & McClennan 1999, 2002). The extreme idea (summarized by Coyne & Orr 2004) that speciation entails the formation of a reproductively isolated population does indeed have a devout adherence of patrons in contemporary biology. Distorted applications of this criterion injects tricky problems into subsequent operations seeking to diagnose species. Extreme focus on reproductive isolation (at the expense of other properties of the species category) has manifested into a fixation, which assumes all the attributes of typological thinking (Mallet *et al.* 1998).

“Given the tremendous number of constraints of the BSC, this concept would also only account for a trivial amount of diversity, and is likely the worst concept that any area of biology should adopt.” (Mayden 2002: 177). The criticisms and defense by Avise (2000b), for example, reveal how defendants of the BSC fail to grasp the philosophical problems at stake between utterly disparate world views, diametrically apposed in their metaphysics. What sets these apart is their metaphysics. The Individuality Thesis cannot be bettered as an overarching explanation for the historically derived properties of the complexities of biodiversity. Darwin's Law places strict constraints on how we can, and cannot, conceptualize natural kinds.

More fundamentally, severe problems, with how reproductive isolation manifests with respect to causative agencies, conflict with what has been long understood in evolutionary biology about the levels (organism versus population) at which selection acts. Reproductive isolation is an effect not a force at the level of biological organization where it manifests among species (*contra* Morjan & Rieseberg 2004). Above all the ontology of uniqueness prescribes that it is lineages that individuate and become species, as a consequence of their unique evolutionary histories. So why should isolating mechanisms evolve to reinforce reproductive isolation in allopatric populations?

The concept of a Specific Mate Recognition System (Paterson 1985) pertains directly to these overlapping questions. Paterson (1978, 1982, 1985, 1986) and others (Eldredge 1985, 1995a; Hughes & Lambert 1989; Lambert & Spencer 1995; Masters & Rayner 1996; Lieberman 1992) emphasize the key conceptual and mechanistic distinctions between the BSC and RSC. Few, if any, phenotypic traits of an organism evolve for the good of the species. This was most infamously argued by Williams (1966). Advocates of the RSC argue that the SMRS constitutes a complex of adaptations which share the function of effective syngamy. Reproductive isolation of the lineage is an effect of the evolution of these adaptations. This distinction means that the BSC and RSC could not differ more fundamentally. So it is interesting how a widely acknowledged axiom of evolutionary biology - G. C. William's causes versus effects - remains virtually excluded from studies of speciation. The reasons for this psychosis remains obscure. It is unfortunate that Williams does not appear to be widely read; or has been insufficiently understood by those who dismiss the RSC as a synonym of the BSC.

Treating the evolution of reproductive isolation as a function of isolating mechanisms conflates cause with effect. So it remains remarkable that this critical weakness entailed in notions of speciation by reinforcement is persistently ignored (e.g. Mayr 1982, 2001; Mayden 1997; Coyne & Orr 2004). This is even more remarkable because reproductive isolation is a most challenging criterion to operationalize. This especially applies to extinct biota. For example, Barnosky (2005) analysed how speciation rates in mammals related to changing Quaternary environments. Unfortunately, the criterion of reproductive isolation (as opposed to cladogenesis), was applied to delimit species, and this created many Type II errors. Thus, the database grossly underestimates when and where species evolved.

Perhaps even more problematic with the myopic attention focused on reproductive isolation in studies of speciation is its philosophical poverty - a poverty magnified when considered against the rich complexity of the ontology challenging evolutionary biologists' enquiries. Speciation has come to be recognized as the individuation of a lineage (Wiley 1978, 2002; Section 3.4). It is therefore not

surprising that a species exhibits changes through its life history, as the individual evolves through time and space (Harrison 1998). Thus, the obsession with treating reproductive isolation, as the operational *sine qua none* of species and speciation, needs to return to the philosophical underpinnings of Darwin's Law, and research reproductive isolation accordingly. A reorientation of this research program needs to recognize which individuals are most commonly selected by ecological and evolutionary processes. Philosophical misinterpretations in the reproductive isolationist school await wider recognition.

3.5.3 The Recognition Species Concept: A Metaphysically Coherent Explanation of Reproductive Isolation

Besides this critical distinction between adaptation and effect (Williams 1966), the likelihood of isolating mechanisms evolving is slim. This is because "Reproductive systems aren't about keeping members of other species away so much as they are about finding mates and reproducing successfully." (Eldredge 1995a: 115). The study of reproductive isolation would benefit a great deal from a more coherent philosophical understanding of what precisely investigators are seeking to delimit. These are the individuals organized into an ontology of uniqueness encapsulated in Darwin's Law. The RSC articulates a philosophically coherent explanation of how reproductive isolation evolves. It is reasonable to envisage that adaptations evolve to enhance effective syngamy in an allopatric lineage. Together, these would manifest as a SMRS in a species' life history (Cotterill 2002b, 2003b).

Several processes have been invoked to enhance cohesion in a lineage. The SMRS is likely the dominant agency at least in sexually reproducing organisms (Brooks & McLennan 1999).

Unfortunately, Sterelny (1999) misconstrued the RSC, and concluded it to be just another version of the BSC. This example is no isolated incident. It is equally unfortunate that Paterson (1985) emphasized that speciation is synonymous with the origin of a new SMRS in a population. This is yet another example of failing to equate speciation with the event of lineage individuation, and being misled by an operational criterion. Vrba (1995b) was more correct in her characterization of the SMRS as a complex emergent property of a particular lineage system. Eldredge (1995a 138) espoused a similar view that the SMRS is a true species-level property.

Nevertheless, studies of reproductive isolation are quintessential to characterize sympatric species. The ontological questions pertain to what attributes of the individuation of lineages represent reproductive isolation. These questions direct subsequent epistemic operations. Bush (1993, 1994) emphasized that speciation entails divergence of two lineages along independent evolutionary paths. This can culminate in reproductive isolation, but is often preceded by gene flow between the lineages.

The conceptual scope of the RSC, and more specifically the SMRS focuses searches for genetic mechanisms associated with speciation. Here lies a subtle, yet stark, distinction between such operations under the aegis of the RSC compared to the BSC. The emphasis on elucidating the “genes responsible for selection” under the rubric of the BSC generates a philosophically misguided research programme, unless structured under the ontology of the RSC. Wu (2001) revealed that speciation in *Drosophila* appears to be closely associated with rapid divergence in protein-coding genes, whose positive selection is a consequence of mate choice. Here, an example of genetic attributes of the SMRS are positively selected genes encoding reproductive proteins in acrosomes of spermatozoa and/or the zona pellucida of ova. Protamines and zona pellucida glycoproteins are respective examples. Their ontological status and mechanistic functions are traditionally discussed under the conceptual guise of the BSC as causing reproductive isolation (Swanson & Vacquier 2002; Wu & Ting 2004). They can be more logically viewed as components of a SMRS. These operations entail the comparison of sampled populations of organisms to test whether they represent one or more individuated lineages.

This would mean that sexual selection has played an important role in divergence at the genetic level. Many of these genes encode reproductive proteins (Wu 2001). Thus, a new SMRS could in fact evolve rapidly in response to sexual selection. This in turn would manifest in relatively rapid individuation of a lineage in allopatry. Cichlid fishes exhibit remarkable examples of this phenomenon in all the spectacular diversity formed in explosive speciation events. I return to this subject later in this thesis (Chapter 7) when discussing the evolution of particular antelopes.

3.5.4 Speciation discerned by Evidence of Character Transformation in Lineages

As a product of a speciation event, a lineage has individuated along its unique evolutionary trajectory. How can we discover such lineages? In practice, populations are compared to evaluate their differences. This is where it gets controversial, with respect to exactly what evidence is applicable and sufficient to diagnose such individuated lineages accurately. Phylogenetic Species Concepts (PSCs) hold centre stage in these activities, with attendant controversies.

Baum and Donoghue (1995) classified PSCs into two classes (character versus lineage based). Their epistemic rationales differ fundamentally. These arguments for certain of the PSCs as an optimal solution to discover lineages that exhibit evidence for independent evolutionary histories (i.e. evolutionary species) are epistemologically sound. The problems are associated with certain weaknesses in the different PSCs with respect to what they discover. As discussed by Doyle (1992), this conflict is also seen in the incongruities between sorting and individuation of gene trees within populational

lineages. In consequence, what entities biologists “individuate” can differ greatly depending on which PSC is used. The singular problems are the lack of guidelines (inherent in the ontological scope of the concepts’ similar definitions) as to how to frame and focus discovery operations.

3.5.4 Phylogenetic Species Concepts and the Obsessed Operationalists

Based on the strict criterion that a species be delimited solely by character transformation in an evolved lineage, Wheeler & Platnick (2000) argued that species can only be diagnosed precisely, if at least one apomorphic trait has fixated in the lineage. Furthermore, they stipulate that this fixation must manifest in extinction of the plesiomorphic character state. This reveals how certain PSCs prescribe the ontological existence of an important suite of lineages; these being those that have budded off the parent individual. Notoriously, these include the stem species envisaged by cladists as going extinct after speciation (as argued by Hennig 1966 and Frost & Kluge 1994). Fortunately, such species (whose existence we might otherwise miss if using the PSC3 only) can be diagnosed using Kornet’s ISC (PSC2). The latter strategy is most conservative as it requires evidence for both lineage splitting and character evolution to diagnose a species (Brooks & McLennan 1999; Table 3.1).

A burgeoning arena of research in evolutionary biology applies genetic evidence to discover individuated lineages. There is a subtle distinction here, where estimates of gene trees are approximated to reflect the scission of the organismal lineages in which their alleles and/or haplotypes have evolved. An important contribution from phylogeography, it has applied genetic, or better termed genealogical, criteria to the species debate; where the Genetic Species Concept (GSC) and its variants has been promoted in this role. It has already been applied somewhat overzealously. *Avise et al.* (1999) concluded that the relative degree of divergence in neutrally evolving genetic markers provides a useful criterion to diagnose whether or not a lineage is a species. A singular handicap of this idea is its subjectivity, with respect to how much divergence distinguishes a species. Thus, several thousand species of cichlid fishes, comprising the respective species flocks of Africa’s Great Lakes, would scarcely qualify as intra-specific phylogroups (Hendry *et al.* 2000).

This example of cichlid fishes also exemplifies weaknesses in yet another operational solution applied to characterize species. Templeton (2001) proposed testing whether or not lineages form cohesive species against the criterion of whether relationships among neutral genetic markers have coalesced into clades. Yet the clades comprising Africa’s speciose cichlid flocks are characterized by shared ancestral polymorphisms. This is a familiar problem in a different guise. It scarcely differs from the problems with the Genetic Species Concept, where “... species are only those things that differ from one another

by a set genetic distance. Who determines the genes or proteins to be examined? Or, better yet, who gets to determine the magic distance at which species diverge?"(Mayden 2002: 177). The limitations of this mind set have been discussed in detail by Ferguson (2002), who concludes that the concept is too theory bound to be applied to characterize biodiversity objectively. The criterion of unequivocal lineage sorting also underpins Nested Clade Analysis that is very much in vogue in phylogeography (Templeton 2001, 2004). Knowles & Maddison (2002) and Dolman & Moritz (2006) argued that coalescent Bayesian models, which estimate demographic parameters, cope better with the heterogeneous patterns whereby genetic characters have become distributed across interrelated populations through complex histories entailing many demographic processes. Discussion of this tension in phylogeographic theory will be deferred until later (Chapters 6-8).

Rigorous adherence to the criterion that only one or more synapomorphies can diagnose a lineage's "speciesness" ignores many instances of actively speciating lineages. Although their constituent organisms may lack synapomorphic characters, they are still parts of an individuated lineage. Thus a wealth of data (behavioural, genetic, morphological) is rendered unavailable to a biologist who adheres strictly to the criteria of Nixon & Wheeler (1990). Yet, ironically, such data can be employed to discern individuated species! This criterion only employs a synapomorphic criterion to delimit species; and it is in fact more flexible than other versions of the PSC prescribing adherence to strict monophyly to characterize species (Mishler & Theriot 2000). When considered in terms of fundamental foundations of the ontology of species, discovery operations founded solely on the PSC are severely delimited as to what parts of *species* are characterized [*italics mine*]. PSCs can miss an important category of individuated lineages, because the latter fail to meet artificial qualifications prescribing what qualifies as a species. This deficiency is expressed in epistemic errors where young (recently evolved) species are ignored, because constituent organisms lack diagnostic characters, as selected by the investigator. So we see, yet again, obsessive adherence to operationalism (*sensu* Hull 1968) hamstringing systematics. Application of the operationalist approach to defining species has reached its extreme in the proposed multi-faceted concept of a species, defined as "...if it walks like a duck, quacks like a duck, has webbed feet like a duck', it must indeed be a duck.'" (Crowe 1999: 1492).

Recent proponents of the superiority of PSCs (Martin 1996; Zink 1996a,b; Cracraft 1997) argue that the PSC1 (Cracraft 1983) is the species concept of choice to characterize vertebrate biodiversity objectively; with synapomorphic characters employed, as advocated by Nixon & Wheeler (1990), to diagnose individuated lineages. Conversely, advocating the RSC, Vrba (1995b) argued against the PSC1 because there exists no lower limit to applying *ad absurdum* its criterion of "the smallest diagnosable cluster of

individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983: 170). So one might then logically pursue this to minute topological scales, where maternal or patriarchal lineages - even a single organism or cell line - could logically form such units of smallest diagnosability (Vrba 1995b). Brower (1999) presented operational procedures to minimize this problem. And it is convenient that Darwin's Law takes care of this problem in less operational terms. Quite simply, only a species lineage can qualify as a species. Genealogical and cellular lineages very obviously cannot, and neither can those created among families and demes. Equally, as with other operational concepts of the species category, Darwin's Law structures the respective strengths and weaknesses of PSCs; which is especially important where we are challenged to characterize cryptic (and/or young species) which are so often difficult to discover.

3.6 A GUIDE TO CONCEPTUALIZE INDIVIDUAL SPECIES AS COMPRISING ONE NATURAL KIND

3.6.1 Evolutionary Species Concept (ESC)

It is instructive to acknowledge that "[s]pecies are simply populations that retain their historical individuality in time, irrespective of the underlying cause(s) of their cohesiveness or of what is happening at the margins of their distributions." (Tattersall 2003: 665). So far this essay has argued that students of biodiversity have a toolkit comprising several quite different criteria to discover individuated lineages. This epistemic toolbox allows complementary discovery operations. Overall, the structure of biodiversity prescribes overlapping zones within which each concept is applicable to discern species. Their applicability is restricted to the study of only those individuals that occupy the species category as delimited by Darwin's Law. It follows from these ontological conditions, underwriting tough epistemic constraints, that the ESC is the best guide yet defined to direct our discovery operations.

There is a strong argument, marshaling philosophical reasons together with biological data, why the ESC is the only concept that comes anywhere meeting any modicum of the disparate demands on a universal species concept (amongst those listed Table 3.1). The detailed arguments (Adams 1998, 2001; Brooks & McLennan 1999, 2002; Cotterill 2002b, 2003a,b, 2005; Mayden 1999, 2002; Miller 2001; Wiley 1978, 2002; Wiley & Mayden 2000) have converged on what is a consilient solution to the species problem (Cotterill 2003b). It is also useful that the ESC does, in fact, avoid major issues in the species problem discussed at length by Hey (2001).

Some terms of phrase in the terminology, in various overlapping definitions of the ESC, deserve a little explication, particularly as some writers have denigrated the scientific applicability of the ESC. These

criticisms pick at semantic weaknesses perceived in the definition. One recurrent issue is “unitary role”; which pertains to the individuality of the evolved lineage. Yet another is “evolutionary tendencies and fate”. This is a semantic variant of what I term independent history. It is inherently retrospective, and so stands firmly under the edict of comparative biology, and especially systematics, being to estimate the evolutionary chronicle (*sensu* O’Hara 1988).

A recurring argument (e.g. Wheeler & Meier 2000; Tattersall & Mowbray 2005) condemns the ESC as not operational. As discussed above, concerns about operationalism persists as a distinct virulence in the species debate. Wiley & Mayden (2000: 75) concluded that the inapplicability perceived as a weakness of the ESC is actually its strength. Surrogate species concepts serve as criteria to diagnose individuated lineages. "Only the ESC is acceptable as a guide to discovering diversity referable to biological species as Individuals; all other concepts require a predetermined type of divergence or process." (Mayden 2002: 181). Aspects of species’ histories can be discovered, provided evidence for lineages’ individuations exists in extant and/or extinct populations (following Brooks and McLennan, 1999; Wiley & Mayden, 2000; Miller, 2001; Mayden 1999, 2002).

3.6.2 The ESC and the Consilient Solution

The broad conceptual scope of the ESC not only accommodates the heterogeneous properties of the species category, but it guides our discoveries of species; if one employs the appropriate methodology (see Cotterill 2001a,b, 2002b for explication in applications to Chiroptera). The Consilient Solution (Cotterill 2003a,b) is founded on ontological and epistemological arguments in phylogenetic systematics (Frost *et al.* 1992; Frost & Kluge 1994; Ghiselin 1997) that species are historical individuals (Kluge 1990). The core of this solution is that the ESC provides the ontological guide for epistemic operations to discover and classify species into a common category. Emphasizing that species are genealogical lineages, Hull (1987) pointed out that the agreement among different concepts (latterly recognized as secondary species concepts) constitutes consilient support (*sensu* Whewell 1840) that they are discovering the same individuals.

It is interesting to identify what factors and ideas structure this solution to the species problem. In fact, several ingredients comprise this multifaceted, solution, which are all enabled by the combination of functions of the ESC. The latter both conceptualizes the species category and facilitates our discoveries of species by classifying epistemic criteria (Cotterill 2003b). A key catalyst has been a persistent tension in the species debate first pointed out by Mayr (1957), then largely forgotten for nearly four decades. Mayr emphasized, presciently as it turns out, that several criteria are applicable to the species category.

So the different concepts proposed are actually complementary criteria. Latterly, Mayden (1997) distinguished primary from secondary concepts of the species category. A very similar distinction was drawn by De Queiroz (1998, 1999) is defining all species concepts as constituting complementary criteria of the species category. Ironically, the General Lineage Concept (GLC) proposed by De Queiroz (Table 3.1) turns out to be a synonym of the ESC published several decades earlier (Mayden 2002; Wiley 2002; Cotterill 2003b). De Queiroz (1998, 1999) did not distinguish a fundamental difference between theoretical and operational species. His General Lineage Concept (GLC) treats all species concepts as forming a “spectrum of emphasis” on complementary properties of the species category. So Wiley (2002) has concluded that the GLC is a surrogate of the ESC. This appears to be yet another example of conflating ontology with epistemology in an obsession with operationalism.

3.6.3 How many Kinds of Species Exist?

The conclusion that ESC is only a time-extended version of the BSC, underlies advocacy of the latter as a primary species concept (Ghiselin 1997: 112). This main reason is that Ghiselin (2002b) has argued that populations which are either ecologically adapted, allopatrically isolated, or reproductively isolated represent three different natural kinds. He further argues that only the latter fulfill what he considered to be real species! Thus, he does not recognize that asexually reproducing organisms can be parts of a species! I argue that excluding the first two categories restricts the species category artificially. It further highlights an interesting contradiction. Not least, it ignores that lineages can exhibit heterogeneity in how their parts have become evolutionarily specialized. Thus, a species lineage - basically the same individual - can exhibit allopatry, with its organisms exhibiting peculiar ecological adaptations. A unique SMRS might, or might not have evolved in such a lineage. And many species, although deeply divergent in allopatry, may not be reproductively isolated. These attributes all manifest in the same lineage. Many individuals (individuated lineages) can fulfill all three conditions simultaneously; which can be discerned by the PSC1 and RSC as complementary criteria, not concepts, of the species category. The problems with the PSC and RSC arise from an operational overzealousness: a failure to recognize the larger ontological scope of the species category occupied by species.

I conclude that a singular ontological category delimits systematists' discovery operations. We need to marshal all relevant evidence within its conceptual framework, and get on with the business of characterizing biodiversity. Multiple evidence translates into a multifarity of discovery methods, in the form of a rich epistemic armoury. Taking Ghiselin's argument seriously - that only reproductively isolated lineages are species - is too operationally constrained to be considered a serious paradigm around which to structure evolutionary biology. A heterogeneous spectrum of species have evolved in

the biosphere through multifarious processes, which occupy the attentions of students of speciation. It will be even more difficult to delimit which of these populations solely represent reproductively isolated species.

Yet again, this weakness further exemplifies an obsession with operationalism which, as Wiley (2002) reminds us, returns to bedevil all scientific disciplines from time to time (Hull 1968), and especially applies to the species debate (Adams 2001). Classifications built with the ESC are untroubled by either niggles. As Wiley concluded:

"The ESC will undoubtedly be refined, but we should not lose sight of the fact that it is the only concept that ties together Hennig's phylogenetics and the various processes of speciation. It is a natural kind concept that links process and pattern." (Wiley 2002: 168).

3.6.4 Mayden's Discovery Nets

While one criterion is sufficient to diagnose the existence of an individual lineage, we can employ multiple criteria in our discovery operations. In the latter case, the resultant discovery is reinforced through consilience; where separately derived colligations of facts reveal that the same individual exists. As a first order explanation, the ESC is the most consilient explanation of the species category, because of its unmatched explanatory scope, which unifies all second order concepts. Thus, existing alone, genetic, morphological, and behavioural data may reveal an individuated species. These can be conceptualized by the PSC and RSC. The GSC can be employed as a conceptual guide to discern genetic signatures of a lineage's individuality. Equally, the RSC could employ behavioural, morphological and genetic data, where each pertains to adaptations evolved for effective syngamy, and thus attributes of the SMRS.

Mayden (2002) has argued that this role of the ESC in unifying knowledge of species provides biology with the best means currently available to obviate placing a glass ceiling on characterizations of biodiversity (Fig. 3.3). Mayden (2002) emphasized the equivalency versus the complementarity of species criteria. Here, each secondary species concept can be imagined to form a net, with which we can characterize biodiversity. Obviously, each has finite dimensions, and also distinct gaps in its epistemic capabilities. Thus, if applied in isolation misses certain species, because of inherent operational limitations (Mayden 1999). These discovery nets differ in overall size and also dimensions of internal mesh size. Their operational limitations translate into inherent design faults - their "epistemic holes" - through which certain species will then escape biologists' attention. The RSC, for example, will nearly

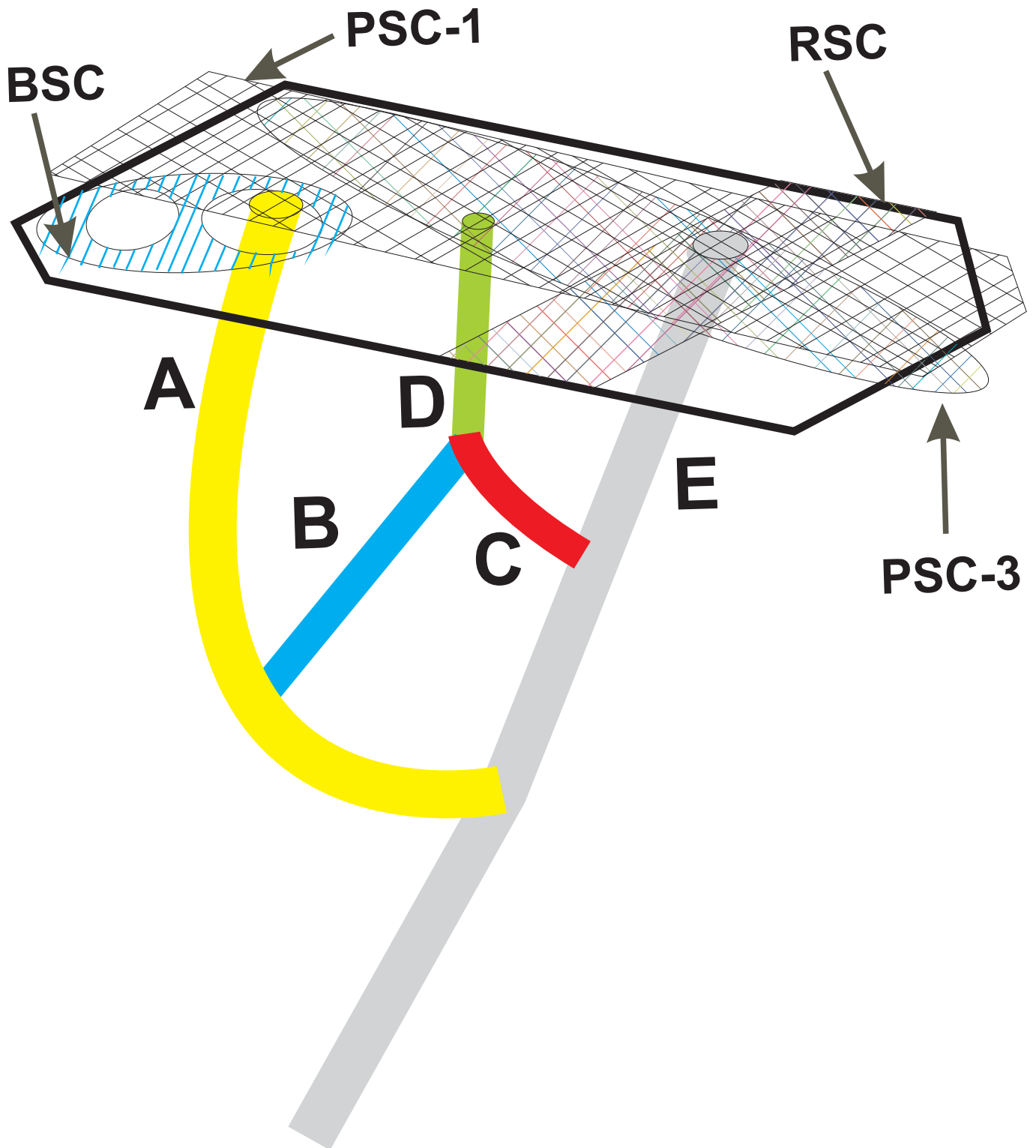


Figure 3.3. Graphical depiction of operational applicability of species criteria (secondary species concepts). The equivalency and complementarity of species criteria form a framework (termed *Mayden's Nets*, following Mayden 2002) which capture complementary (and more rarely equivalent) aspects of the species. Where operationalism overrules the limits of just one species criteria and renders it a lone epistemic tool used by taxonomists, then significant biodiversity will be ignored; where such a concept, notoriously a PSC1 or the BSC, is relied on solely to characterize biodiversity.

always miss recently individuated lineages. It is most fortunate for systematics, and thus all biology, that the ESC brings Mayden's Nets into coherent context to discover species. Overlapping our epistemic nets minimizes risks of ignoring existence of less obvious species (Fig. 3.3). Taylor *et al.* (2000) applied this consilient solution to the Fungi, where they deliberately avoid using the term "Concept", but employ that of operational criteria. They concluded that the PSC and GSC are optimal tools to diagnose the existence of fungal species. Paul (2002) has argued for the same approach to diagnose species of parasites, as did Brooks & Hoberg (2000).

The universal scope of the ESC renders all others as subordinate criteria, which can characterize either subsets of particular lineages, and/or a common stage in the trajectory of lineages through evolutionary time and space. As different architectural and engineering plans reveal complementary individualities of a building, species criteria work analogously to characterize species lineages. Other criteria hold genuinely complementary functions, whose abilities to characterize certain properties of lineages do not overlap. Thus the PSC of Cracraft (1983) diagnoses the existence of divergent lineages; while the RSC (Paterson 1985) reveals the population has evolved an SMRS. In the latter lineages, cohesiveness has manifested in exclusivity (Cotterill 2002b, 2003b). This is a most pertinent criteria, because it has proved very challenging to distinguish of unequivocal lineages within the *Kobus leche* complex within the framework of evolutionary rates of available genetic markers (Chapters 6 & 7).

3.6.5 Resurrection of Hypodigms

It is useful to revive yet another important concept developed by George Gaylord Simpson; especially as a handy concept is needed to universally describe the total evidence employed by any species criterion, within the theatre where all discovery operations occur. The hypodigm is this concept. It traditionally describes the total sample of organisms available to the taxonomist to characterize a taxon (Simpson 1940; Newell 1949). Most pertinently, the hypodigm can be applied by quantifying measured variation statistically. Measurements of such variation might be attributes of reproductive proteins, phylogeographic patterns, or morphological characters. In this study of antelope populations, they constitute cranial characters, and patterns of pelage. Equally, the same characters can be employed under the aegis of species criteria, such as a PSC and the RSC. The hypodigm informs us how reliable are these discovery operations with respect to how representatively variation has been sampled in the lineages compared.

Disagreements amongst taxonomists are not infrequently based on comparisons of different hypodigms of the same taxon (Mayr & Ashlock 1991). The ability of a hypodigm to reveal aspects of an individual

(species) is a function of the variation encapsulated in its sample. The parts of a hypodigm reveal particular facets of the parent individual; thus the hypodigm provides us with a window into the history of the lineage. Not merely just a label, nor just a set, the hypodigm encapsulates the processes whereby properties of sampled organisms are compared to the larger population.

3.7 SUBSPECIES AND EVOLUTIONARY SIGNIFICANT UNITS (ESUs)

“Statistically, this corresponds to a 90% joint nonoverlap, so metrical features can be tested by the coefficient of difference (C.D.), which is the sum of the standard deviations divided by the difference between the means (Mayr 1969). If $C.D. > 1.28$, the 90% joint overlap requirement is fulfilled, and in theory two subspecies can be recognized.” (Groves 2001: 36).

As framed by Darwin’s Law, this primacy of the Individuality Thesis also sweeps aside notions that species can be divided objectively into universally equivalent subcategories. Searches for categories discernable within that of the species has occupied a persistent debate in taxonomy since at least the 1860s (Mayr 1982, Johnson 2005). It has spilled over into conservation biology with concern over populations that we can categorize objectively. The practical relevance of the subspecies category was first debated in ornithology (Mayr 1982). Its revisiting by Wilson and Brown (1953) kindled a debate that persisted through the pages of *Systematic Zoology* for several years (Mayr & Ashlock 1991). This controversy entails two distinct problems. One is whether to treat the subspecies as a discrete taxonomic unit like species (albeit of lower taxonomic rank). Two, more fundamentally, we have to face ontological realities, and ask whether a distinct population is taxonomically distinct, and overcome philosophical problems of how to relate such an entity to that of an species (Mayr 1982).

A geographically isolated population can represent one of two entities; either a young (recently diverged) species, or a geographical isolate in a widely distributed species. Recently divergent segments can be conveniently labeled ‘Neospecies’, should one wish to distinguish such recently evolved entities as a natural kind (Cotterill 2003b). It will prove challenging to separate such categories from other hard to distinguish species, notably cryptic species. One contemporary approach to classify what can be called neospecies is to invoke the Evolutionary Significant Unit (ESU), as a supposedly better category than subspecies. The concept of an ESU was originally invoked as a heuristic guide to classify populations on the criterion of one (and sometimes more than one) genetic marker that have coalesced into reciprocal monophyletic lineages (Ryder 1986; Moritz 1994; Barrowclough & Flesness 1996). More recently, practicing biologists have invoked less stringent (and thus less prescriptive) genetic, and also ecological and behavioural, criteria to delimit distinct populations into ESUs (Grant 1995; Crandall *et al.* 2000; DeWeerd 2002).

Cracraft (1997) concluded that the concept of an ESU should be abandoned because its objectivity is precluded. Moreover, the populational entities that ESUs seek to characterize can be discovered by the PSC1, if they are indeed segments of individuated lineages (Cracraft 1997). Recently, Kizirian & Donnelly (2004) argued convincingly that the criterion of reciprocal monophyly (originally advanced to delimit ESUs) is not only very difficult to apply unambiguously; but ironically, it ignores the very diversity systematists seek to classify. This is especially where lineages judged to be paraphyletic are treated as conspecific. Yet again, an epistemic weakness manifests under the ogre of operationalism. Hughes *et al.* (2005) discovered botanical examples of recently evolved species of *Streptocarpus*, which constitute paraphyletic entities on genetic criteria. Framed by Darwin's law, these are individuated species (Chapter 7).

The ESU debate has muddled along independently, ignoring serious metaphysical criteria that structure the Consilient Solution, centred on the ESC. Much of the debate stems from the underlying species concept on which a pet notion of the ESU is derived (Roe & Lydeard 1998); and this aspect of the ESU debate culminated with Fraser & Bernatchez (2001: 2746) concluding that the unifying ESU "...should ideally operate under a unifying species concept." In this case they chose the GLC (De Queiroz 1998, 1999), which is a synonym of the ESC (Cotterill 2003b). (Parenthetically, I conclude that strictures of Darwin's Law, especially the goal of discerning unique lineages resulting from evolutionary history, rubbish the notion of Adaptive Evolutionary Conservation, which defines ESUs by participatory consensus toward a "Flexible; integrative; broadened taxonomic spectrum" (Fraser & Bernatchez 2001: 2745).). Moreover, the deep history of evolution runs counter to notions of deconstructive philosophies. Conservation stands to benefit more from knowledge framed by evolutionary history, and far less from politically correct ideas generated in participatory workshops. "If value judgements have to be made, let us hope they are the values of earnest seekers after truth, rather than those of academic politicians." (Ghiselin 2002b: 152).

The reasons for this lack of scientific credibility of the concept of the subspecies and ESUs are relatively straightforward. The voluminous rhetoric aside, all recently proposed ESUs do not escape crippling weaknesses that afflict the concept of a subspecies, with its various operational definitions such as Amadon's (1949) "seventy-five percent rule". These are all subjective criteria that obscure evolutionary history by failing to classify real products of evolution. Only in an artificial classification can we treat young segments of individuated lineages as distinct ontological entities. We can delimit segments of species lineages to create as many different kinds (categories) for as many criteria as we might choose to employ. Taxonomic chaos follows on such subjective treatment of bits and pieces of

individuals. Ultimately, conservation biology is weakened, because these so-called conservation targets lack ontological credibility.

The family of concepts associated with the idea of an evolutionary significant unit (Table 3.1) does not improve on that of the subspecies category (Mayden & Wood 1995; Kizirian & Donnelly 2004). Some might dismiss this distinction as merely one of semantics. Nonetheless, we cannot ignore the critical ontological issues at stake where biologists are challenged to characterize recently individuated lineages. The youthful properties of the latter may also fall outside the epistemic scope (i.e. operational zone) of Phylogenetic Species concepts. Fortunately, the existence of such lineages falls within the scope of the ESC, under whose ontological auspices recently evolved species can be characterized.

3.9 PRECISION, ACCURACY AND ERRORS IN MICROTAXONOMY

Different treatments of the species category makes for many different errors. One category, whereby species are misconstrued, really does challenge the mind, when pursued to their logical consequences. Then it becomes very clear how they conflict with principles of logic and metaphysics: “like a round square or the colour of the distance between Paris and London (Ghiselin 2002b: 154). A critical subset of errors follow from operational errors in which flawed species concepts are employed to characterize biodiversity, and/or are applied outside their zones of relevance. Taxonomic precision pertains to how closely the real species richness of one or more clades is characterized. Taxonomic accuracy relates to how correctly species’ relationships are classified. This apparently pedantic distinction is critical. Systematists either classify individuated lineages into species, or artificially define populations (or their subsets) into sets they consider to represent historically derived entities. Type I and II errors mainly manifest at the tips of phylogenetic trees. These reduce precision because species richness is overestimated or underestimated, respectively. Type II errors often manifest together with Type III errors. The latter misconstrue evolutionary history. Here, classifications can go very wrong where topology is misrepresented deeper within the framework of a taxonomy (Adams 1998; Cotterill 2003a,b, 2005).

3.9.1 Taxonomic Errors - Types I, II and III

Type I errors can result from unfettered application of certain PSCs, especially PSC1. Thus Vrba’s (1995a) concern (that PSCs are flawed) falls away when it operates within the sanctions of the ESC. The ESC does not foster discovery operations where a species criterion is erroneously employed to treat tiny demes as individuated lineages that might be called separate species. Here, Darwin’s Law delimits

which individuals are, and are not, species; only species lineages qualify to occupy the species category.

An extreme case is classifying all topi, korrigum and tsessebe antelopes into a polytypic “*Damaliscus lunatus*”; although it actually consists of the *korrigum* and *lunatus* clades, and the latter comprises two species. Uncritical lumping of populations into polytypic species - Type II errors - and/or failing to recognize evolutionary distinct lineages and clades - Type III errors - can have far reaching impacts of conservation concern (Cotterill 2003a,b). The ESC’s broad ontological scope, which underpins a Consilient Solution to the species problem, enables accurate and precise characterization of biodiversity. The operational framework (epistemic activities) of the Consilient Solution entails comparing hypodigms of two or more populations to test whether or not they represent distinct lineages. This treatment is diametrically opposed to delimiting organisms into non-historical, phenetic sets. The latter may or may not correspond to distinct lineages, although they might be construed as reproductively isolated species or subspecies in terms of the BSC (Cotterill, 2002b, 2003a,b). The objectivity of the ESC improves on a tradition entrenched in vertebrate taxonomy, which employed trinomials in a polytypic taxonomy (using the BSC and/or a morpho-species concept) to classify mammalian diversity on reproductive isolation and/or phenetic criteria (e.g. Barclay 1933; Ellerman, *et al.* 1953; Ansell 1972).

Another kind of Type II error is highlighted by Willmann & Meier (2000: 106). This is the weakness of some PSCs, which overlook the speciose composition of a monophyletic clade where only apomorphic characters are employed. Such Type II errors are avoided if we compare populations thoroughly to discern precisely what lineages they represent. Type II errors not only mislead wildlife management and conservation policies, but they can seriously confuse interpretations of earth history (as with the example of how speciation rates in mammals related to changing Quaternary environments, Barnosky 2005, see above).

An analogous, simple, treatment is to classify two or more of such entities into a species complex (Kizirian *et al.* 2004). Some taxonomists are tempted to apply the concept of a superspecies (Sylvester-Bradley 1954; Amadon 1968; White 1981). This concept continues to dominate many contemporary taxonomies of vertebrates, including African bovids (Ansell 1972; Grubb 1978). This approach can embed pernicious Type III errors into classifications (Cotterill 2003b). An extreme example is classifying three complexes of alcelaphine antelopes - *Damaliscus pygarthus*, *D. lunatus* and *D. korrigum* - into one superspecies without representing their real evolutionary history (Cotterill 2003a-c).

To conclude, Mayden (1999, 2002) argued that taxonomists who ignore the critical issues in conceptualizing and classifying species place a glass ceiling on the exploration of biodiversity. Type II errors are especially serious because they pack evolutionarily distinct lineages into counterfeit classifications, which history has revealed come to be believed as scientifically credible constructs.

3.10 OUTSTANDING CHALLENGES

The discernment of recent individuation events often severely test the discovery skills of students of speciation. Invariably, neutral genetic markers struggle to detect such instances of individuation. The rich flocks of recently evolved species of fishes exemplify this problem. Here AFLPs (Amplified Fragment Length Polymorphisms) have proved useful to diagnose the genetic individuality of such lineages. Examples include: Albertson *et al.* (1999) and Barluenga *et al.* (2006) for fishes, and Buntjer *et al.* (2002) for bovids. Fisher (1930: 124) presciently noted: “The genetical identity in the majority of loci, which underlies the genetic variability presented by most species, seems to supply the systematist with the true basis of his concepts of species identity or diversity.” Nevertheless, considerable efforts may be required to distinguish the genetic mechanisms that underlie the individuality of two or more lineages: be they homozygous twins or recently individuated species.

It appears likely that this challenge of distinguishing the fuzzier attributes of species will become better refined as novel genetic markers become available. In this regard, the exponential growth in genomic data allied with new techniques in evolutionary developmental biology are developing rapidly. Where practicable to sequence from sufficiently representative hypodigms, these new genetic markers should provide novel insights into the genetic and phenotypic variation of populations (Venter *et al.* 2004; Rogers & Venter 2005; Barluenga *et al.* 2006). Equally, new coalescent-based tools to analyse gene trees can reveal hitherto hidden signals preserved about speciation events (Hey *et al.* 2004; Hey *et al.* 2004; Knowles 2004; Dolman & Moritz 2006). In addition to detecting species lineages, these techniques constitute a novel toolkit amongst the epistemic criteria previously unavailable to estimate aspects of the divergences between species lineages.

3.11 SYNOPSIS OF APHORISMS

Demands for scientific rigour, and far reaching ramifications of the species problem on scientific knowledge makes it very difficult for practicing biologists to avoid taking a firm stance on what concepts and criteria they employ to classify organisms. This decree leans on the following interrelated, inseparable tenets:

- Based on a philosophy of absolute realism, metaphysics is the most fundamental science (Ghiselin 1997); such that the objectivity of any aspect of knowledge a scientist deciphers about the natural world stands or falls on the ontological rigour of the concepts employed to classify structured information. Concepts are the building blocks of any ontology we employ to classify what would otherwise be an impenetrable morass of natural complexity.
- It is critical to distinguish the complementary importance, and especially the reciprocal roles of ontology and epistemology in the life sciences. An ontological framework guides how we carry out practicable studies and create knowledge (Frost & Kluge 1994; Ghiselin 1997; Adams 1998, 2001). These conceptual frameworks structure our epistemological processes of discovery of biodiversity and the ecological complexes in which organisms evolve and persist. In practice, scientists classify interrelated information, for which universal concepts are critical to its communication.
- There is convincing evidence that the Individuality Thesis (Ghiselin 1974, 1997, 2002a,b, 2005a,b; Kluge 1990; Minelli 1999; Ridley 1998; J. Wilson 1999; Coleman & Wiley 2001; Mayden 2002, Wiley 2002) is the most philosophically sound ontology on which to base our conceptualization and characterization of species, and this applies to all biodiversity, extant and extinct. Dissenters, notably Ruse (1998) and Szalay (1999), who argue that species are not individuals, have yet to provide any convincing alternative, and in so doing, identify what ontological entities have been generated by evolution.
- Species are historical individuals bounded in space and time (cf Kluge 1990); such that a lineage exhibits a cohesiveness manifested from recent descent among their parts. Practical delimitation of these entities can be difficult. Only the ESC comes anywhere close to meeting these demands for objective classification of biodiversity across such a spectrum of individuated lineages. The ESC constitutes the best available guide to focus our activities aimed at discovering individuals of the different natural kinds which share the common category of species.
- When biologists speak of species they mean species as composite wholes, not sets comprised of kinds of organisms (Coleman & Wiley 2001). Names of individuals are defined ostensibly, as pointers to a thing (the individual species), or one or more of its parts (organisms). This state of affairs is the solution to the vociferous debate on how we name lineages and clades. These radical changes in taxonomic philosophy and practice follow on a slow revolution in concepts of definition (Ghiselin 2002b).

- The different mechanisms of speciation have created different kinds of species; whose existence can be distinguished with the appropriate epistemic criteria. All these kinds of individuals occupy the species category.
- A species can exhibit heterogeneous properties amenable to complementary discovery methods. A common mistake is to confuse these discovery operations as targeting classes, or sets, and not individuals. Discovery methods provide a robust framework to discover species when combined into Mayden's Nets. These minimize risks of missing real diversity, and so reduce taxonomic errors; where real species richness is overestimated (Type I), underrepresented (Type II), or misclassified (Type III). Hypodigms of populational variation are very useful guides that enable these operations.
- The universal ubiquity of uniqueness comprising biodiversity is summarized in Darwin's Law. This restricts the domain of the species category to include only some individuals. These can only be those lineages formed as historical products of tokogenic descent among organisms. All other individuals are organisms and their parts (organs). These form the parts of species. The latter are encompassed by individual clades.
- The processes of discovery test data about lineages of organisms against a conceptual framework, which is the species category. The best conceptual guide to the boundaries and heterogeneity of the species category is the ESC.
- Efforts to characterize species can flounder if the underlying metaphysics is flawed. Severe ontological limits of PSCs illustrates this problem; as equally as they exemplify inadequacies where operationalism ignores metaphysical realities of the species category. The continued adherence to the BSC reflects the painful process whereby an historical philosophy of biology is rectifying the Eclipse of History that hamstrung the NeoDarwinian Synthesis through the mid-twentieth century.

3.12 CONCLUSIONS

3.12.1 Ontology, Epistemology and Biology

The ontology of species - founded on Ghiselin's (1997) metaphysics of Individualism - explicates why the ESC is the best guide available to characterize species (Wiley 1978, 2002; Wiley & Mayden 2000). Those who disagree may coopt a different concept of the species category, and might advocate the BSC. And perhaps they will continue to couple use of the BSC with the concepts of superspecies and subspecies - to try and rectify problems in its application. Should they stand outside of what has degenerated into an arena of rampant operationalism, advocates of Phylogenetic Species Concepts will

then be able to clarify what entities they are challenged to characterize. If objectively framed within the Individuality Thesis, and thus the ESC, deficiencies within each PSC become obvious.

Arguments for alternatives to the ESC place a formidable onus on those advocating alternate concepts as superior. We await with interest their explications of how such concepts can be framed in an ontology that betters Individualism. The BSC has been, and continues to be, applied to classify biodiversity despite its critical deficiencies. The rampant errors in the resulting classifications leaves practitioners, where they do indeed seek true taxonomies built of real species, to clarify exactly what lineages (or portions) are classified. It is insufficient for biologists to dismiss arguments for the Individuality Thesis as yet another that, in the words of Coyne (1994: 22), “leaves the solid ground of biology for the marshlands of philosophy”. Some might condemn the latter criticism as puerile; but in fairness one has to sympathize with biologists who persist in defending what actually constitute philosophical stances (in this case a partisan operationalism) because the encompassing literature of ontology and epistemology is indeed challenging to assimilate critically. It is interesting that Coyne & Orr (2004) latterly adopted a philosophical position to confirm the reality of species, and flag weaknesses perceived within certain species concepts competing against the BSC. Unfortunately, the ontological credentials of their position are very vague, and these authors chose to dodge any consideration of critical metaphysical criteria distinguishing between individuals and classes.

3.12.2 Darwin's Law

There have been attempts to modify, and sink, the individuality thesis. Griffiths (1999) argued that species are historical essences. Yet, "An historical essence is as much a contradiction in terms as an even prime number" (Ghiselin 2002b: 155). Kitcher (1984) tried to treat species as sets. This exercise failed because there is no concept of an historical set (Coleman & Wiley 2001). Nature has created neither an historical set, nor an historical essence! These failures lead one to acknowledge that some classifications of biodiversity differ so fundamentally in their scientific credibility that they conflict with key goals in systematics (articulated by Cracraft 2002). Even more importantly, should such notions of the ontology of biodiversity prove true, then biology would have to reconcile with the situation that the theory of evolution is completely implausible. I conclude that “...one views species as *Individuals* and not *Classes* or *Natural Kinds*” (Mayden 2002: 181, italics his), or rejects the fundamental theory of evolutionary biology, with so many radical consequences for taxonomy and science. Ultimately, the logical distinction between these world views distills down to the universal ramifications of Darwin's Law. It is on the philosophical foundations encapsulated in Darwin's Law that competing concepts of natural complexes (including species) stand or fall.

It is most unfortunate that we too rarely discuss and teach about how erroneous knowledge is created about evolutionary patterns if one divides up species (and equally other individuals) into artificial categories (i.e. delimited classes or sets). This is a severe weakness within biological pedagogy, and most unfortunately impacts on how evolutionary biology is taught. Retrospective reading of the history of the species debate reveals that vigorous support by prominent spokespersons has propagated certain conceptualizations of species and speciation at the cost of objective overview of what biologists are really challenged to classify and study. Positive feedback appears to support such agendas despite the costs of overruling metaphysical realities. Treating natural kinds as real entities disregards fundamental tenets of Darwinism. Proponents of such proposals have yet to explain how their notions of such taxonomic entities (whether termed subspecies or Evolutionary Significant Units) can be accommodated within an ontology of biodiversity founded on the Individuality Thesis. The prospect of any success in such an endeavour appears so remote (at least within the realms of science) that all biologists, especially systematists, have no option but to abandon such notions.

"...the operational point of view depends for what success it does have on the very element of science which it is designed to eliminate. Operationism was intended as a cathartic to purge physics of all non-empirical wastes, but it proved to be so strong that the viscera were eliminated as well." D. L. Hull (1968: 440, italics his)

"Only the ESC is acceptable as a guide to discovering diversity referable to biological species as Individuals; all other concepts require a predetermined type of divergence or process."
R. D. Mayden (2002: 181)

CHAPTER 4



Expedition vehicle of the Vernay-Lang Kalahari Expedition crossing the Makgadikgadi Pans, 1930. No less than eight specimens of *Kobus leche* were collected in the Okavango Delta during this expedition, which are preserved in the AMNH and FMNH
Photograph: Transvaal Museum

The broad Ndanda Dambo - a seasonally flooded wetland - which drains into the Bulozhi floodplain of the Upper Zambezi valley in northwest Zambia. November 1998
Photograph: F. Cotterill



CHAPTER 4. GEOLOGY AND BIOGEOGRAPHY COMBINED : EVOLUTIONARY DYNAMICS OF THE WETLAND ARCHIPELAGO OF SOUTH-CENTRAL AFRICA

"From the preceding account it will be apparent that within an area of one and half million square miles there is found widespread evidence of warpings of quite considerable magnitude, since they have involved vertical movements in the crust of from one to several thousands of feet" A. L. Du Toit (1933: 17)

4.1 INTRODUCTION

4.1.1 Setting the Stage

Instructive interpretations of phylogeographic and phylogenetic patterns depend overwhelmingly on well we understand the geological history of the landscapes where these organisms occur, and have evolved. Abundant circumstantial evidence of the evolution of lechwe antelopes exhibits interesting relationships with the drainage topology across south-central Africa. Here, geomorphological dynamics have had radical effects, such that landforms have endured marked rearrangement with rivers connected and sundered. Equally, drainage basins originated, endured and dwindled into inconsequence. Unfortunately, the literature detailing this geological history is very scattered. Far more seriously, it is obsolescent. As critically, affinities among many of the region's major rivers and internal basins have never been studied.

An example emphasizes why aspects of geomorphology and geology are so critical to incorporate into this study of lechwe antelopes. This is how the explosive speciation of flocks of cichlid fishes in the Great Lakes relates to geology of Africa's rift system (Greenwood 1981; Verheyen *et al.* 2003), and is often proffered as a textbook example of evolution in action (Salzburger *et al.* 2005). Our understanding of the morphological and genetic attributes of diversity of these fishes is contingent on how reliably we understand the region's palaeo-environments. Combined, climatology and geology furnish the primary information to place biotic patterns and processes into revealing spatio-temporal context. Lake Victoria is the pertinent example here. As with all Africa's Great Lakes, what we know about the geological tenure of Lake Victoria is part of a vast literature on the East African Rift System (EARS) and related landforms (Rosendahl 1987; Chorowicz 2005, Fig. 4.1a). In the case of Lake Victoria's cichlids, conflicting interpretations of landscape evolution can radically alter interpretations of biotic history, reflecting strong control by hydrographic conditions (Johnson *et al.* 1996; Stager *et al.* 2002, 2004; Verheyen *et al.* 2004). Analogously to these cichlids, evolution of lechwe antelopes is correlated as intimately with the deeper history of landscapes, and especially how hydrographic patterns have changed across the Katanga-Chambeshi region (Section 2.5).

The example of lake-dwelling cichlids emphasizes how much evolutionary understanding stands to gain when geological and climatic knowledge structures biogeographical narratives. The argument was introduced in Chapter 1: that explanations of the history of the physical landscape are integral to understand how organisms have evolved. Chapter 2 concluded that the evolution of wetlands through the Neogene and Quaternary epochs appears to have influenced lechwe antelopes greatly. It is important to place these landscapes into the context of yet deeper geological time, because the geological conditions that exercise dominant control over contemporary hydrological patterns and processes have existed since the late Mesozoic. Moreover, Africa's larger-scale structure reflects to a very great deal how its oldest, largest geological formations have responded to tectonics. These very old rocks are mostly of Archaean age. Few of these formations have been emplaced since the Proterozoic.

This chapter synthesizes aspects of the geological history of the African continent directly relevant to understanding the origin of the wetland archipelago within the Katanga-Chambeshi region (Chapter 2). I emphasize aspects of structural geology responsible for strong control over patterns and processes of drainage evolution. Where evidence permits, determinants of landscape evolution are invoked with illustrated explanations. This chapter combines published data to describe aspects of the recent Cenozoic evolution of the study area, from the late Neogene (late Miocene through Pliocene) to the Quaternary. I especially focus on Quaternary history. In addition, original data are presented to explicate the origins of particular landforms. My objective is to construct a narrative of evolution of principal landforms forming the wetland archipelago (described in Chapter 2). I begin with a brief overview of salient geomorphological features of Africa that characterize its extant topography and drainage systems. Their fundamental distinctiveness stands out, compared against the majority of the earth's drainage systems. This section is followed by more detailed reviews of how hydrographic systems have evolved within south-central Africa through the late Cenozoic.

The resulting narrative frames explanations of lechwe evolution in following chapters. This synthesis brings together much scattered evidence. These data have been published under separate aegises by archaeologists, botanists, climatologists, geologists, geomorphologists, hydrologists and zoologists. The first section reviews geological and geomorphological data, which reveal the rich history represented in extant patterns of Africa's drainage. The second section synthesizes biogeographical data. Here, the rationale is that congruent distributions of divergent species reflect a common cause. So geomorphological and biogeographical patterns combine to reveal facets of evolutionary history;

where species' life histories have played out within landforms altered by climatic and geological events.

The geomorphology of much of the Katanga-Chambeshi region awaits detailed study. The seminal, broad-brush reviews of the geomorphology of Katanga and Zambia are now more than 50 years old (Dixey 1943a,b, 1955a,b). With respect to lechwe evolution and Quaternary landscapes, the sum total of what has been written about these landforms and key geomorphological events total a few paragraphs at best. This is especially true of the Bangweulu basin and associated rivers. Fortunately, recent studies of drainage evolution have revealed important aspects of how the Zambezi River evolved (Nugent 1990; Thomas & Shaw 1991; Moore & Larkin 2001; Moore 2003), and provided useful knowledge (which is discussed in detail in Chapter 5). So do the detailed studies of the Quaternary geomorphology of northeast Botswana (Thomas & Shaw 1991, 2002). These insights into the evolution of the Zambezi are, in fact, quintessential to this thesis, and receive full attention. By comparison, the geomorphology of Angola and areas of the Congo basin represented within the Katanga-Chambeshi region have barely been studied. At best, only aspects of their structural geology and hydrographic history are understood. Any details of actual landforms are, at best, sketchy (Veatch 1935; Giresse 2005; Stankiewicz & De Wit 2006).

There is a tradition of applying anomalies and congruent signatures in biotic distributions to infer antecedent relationships among landforms (Simpson 1953; Crisci *et al.* 2003). This especially applies to drainage systems (Skelton 1994). A wealth of valuable biogeographical data does in fact exist for south-central Africa, but requires careful scrutiny to update taxonomies and correct synonymies. Moreover, phylogenetic uncertainties hamstring attempts to relate speciation patterns to palaeoenvironments. Nevertheless, informative signals exist, even where national boundaries and watersheds around single drainage systems delimit published datasets. Improved explanatory power and unprecedented insights follow when syntheses of species distributions cover regions and continents. Bell-Cross (1982) and Skelton (1994) revealed informative signals in distributions of fishes in the Zambezi, Upper Congo and neighbouring systems. Allopatric ranges of species complexes point to vicariance of antecedent habitats. When stitched together, these suites of biotic and geological patterns can point to what landforms existed when and where. These data are the building blocks to be synthesized into the model of drainage evolution presented at the end of Chapter 5, where this summary follows the revised archaeological evidence that helps estimate ages of Quaternary sediments more precisely. These circumstances have created interesting challenges for this synthesis, given that it aims to construct the explanatory framework to underpin understanding of lechwe evolution. Where

resources allowed, the sheer lack of data from so much of the study area dictated focussed study on key landforms.

4.1.2 The Scope and Relevance of this Chapter

The geological setting for this review of geomorphological evolution builds on Chapter 2, in which the principal landforms are described in the context of extant drainage systems. Detailed descriptions of this mosaic of hydrographical patterns and processes have proved difficult to subdivide strictly into either geological or biological sections. The geological section reveals that flexing and faulting of “High Africa” has modified watersheds and basins, to alter topologies of drainage systems repeatedly. And these associated hydrographic changes have altered the biodiversity in these landscapes. The history of these changing landforms and biota is easier to understand when presented in combination. So, this synthesis entwines biogeographical data with aspects of geomorphological history to contextualize geobiotic patterns in new detail. Important findings emerge from this synthesis, which refine understanding of the evolution of the Katanga-Chambeshi region. Aspects of this improved understanding bear directly on consequent chapters that directly address the taxonomy and evolution of lechwe antelopes. These new contributions entail:

1. The employment of high resolution topographic data, in a GIS context, to elucidate local details in how drainage has evolved in two sites. One is in western Angola (Cuanza-Cubango headwaters). The second straddles the Katanga Pedicle (southeast DRC and north Zambia). Here, I reconstruct Plio-Pleistocene drainage evolution in the detail available data permit.
2. The third detailed study area centres on the Upper Zambezi. Aided by high resolution topographic data, a revised stratigraphy of the Victoria Falls Formation (VFF), allied with a more precise erosion history of the Batoka Gorge, is brought to bear on long-standing problems that have obscured understanding of neighbouring landforms, especially the Kafue Flats and northeast Botswana. This synthesis of revised and new datasets reveals previously unavailable insights - as to when palaeo-lakes existed in northeast Botswana and Zambia. The existence of one of these palaeo-lakes does not appear to have been proposed previously.
3. An important finding, revealed in this synthesis, presents new evidence that much of central Angola and Katanga (in both their geomorphical and biotic aspects) shared persistent links with the Zambezian region through the Plio-Pleistocene.

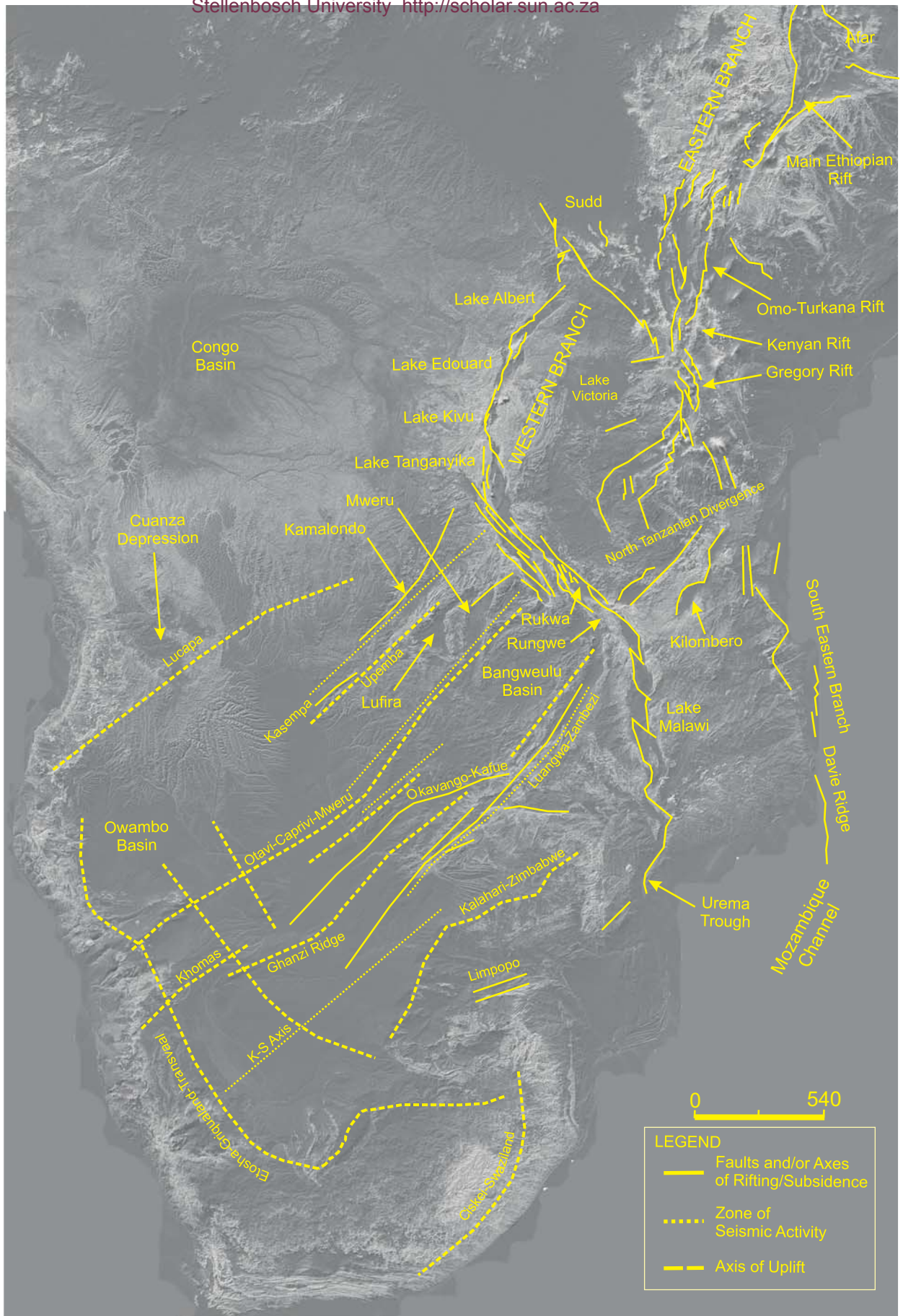


Figure 4.1a. Overview of southern, central and northeast Africa to show the two principal (Western and Eastern) branches (also termed the Albertine and Gregory, respectively) of the East African Rift System (EARS). The principal structural zones are labelled in more detail for the South West Extension of the EARS, which extends across Zambia and Katanga into the Kalahari Basin. Adapted from Rosendahl (1987), Frostick (1997), Tack et al. (2003), Chorowicz (2005) and Haddon & McCarthy (2005).

It is first necessary to place pertinent studies of south-central African drainage evolution into context, which first drew attention to the importance of the Palaeo-Chambeshi drainage system. It also important to frame these papers into the much larger arena in which the evolution of the Bovidae has been studied in great detail. Knowledge of the evolution of African mammals is represented by a large, growing literature, which features strongly in palaeoanthropology, palaeoecology and macroevolutionary theory.

4.1.3 The Palaeo-Chambeshi Drainage System and Evolution of Landscapes and Biota

Du Toit (1933, 1939) first identified important structural controls whereby ancient geological formations controlled drainage across High Africa in fundamental ways. His ideas greatly influenced geomorphological studies of the time, notably Wellington (1955) and King (1953, 1962, 1978). Considered in retrospect, it is interesting that Du Toit's remarkable insights remain important, especially in his explications of how epeirogeny has acted repeatedly to rearrange, and equally to preserve, landforms across High Africa. Du Toit's ideas about crustal flexing and uplift appear repeatedly in the prescient essays by Dixey (1943a,b, 1944, 1950, 1955a,b), which remain unmatched in their overview of the geomorphology of Zambia. These identified several landforms directly pertinent to this study: the Bangweulu basin, Kafue Flats, Mweru graben and Machili Flats. Most importantly, Dixey (1943a) first recognized that the antecedent drainage, predating the the modern Kafue and Zambian Congo systems must have flowed southwest into the Kalahari basin. With reference to south-central Africa, the drainage of Africa that De Heinzelin (1963) postulated to have existed prior to noticeable rifting of Africa (also see Summerfield 1991) appears to have leant on Dixey's insights (Figs 4.1b & 4.1c).

A preliminary review of diversification of reductine antelopes within the Zambezi basin (Cotterill 2000) motivated research into how key events in geomorphological history have controlled diversification of particular vertebrates. These examples included the *K. leche* complex, as then naively understood. A drainage model was developed in this paper to explain anomalous distributions and congruent patterns of speciation. This proposed that the Palaeo-Chambeshi drainage system, bisecting the south-central African plateau, holds significant biogeographical importance. Evidence suggests this vast wetland facilitated dispersals of aquatic biota, but also divided terrestrial species. Thereafter, scission of this long river created new wetlands enriched with vicariant species. This break up of the Palaeo-Chambeshi was invoked to explain the dichopatric speciation of lechwe antelopes (Cotterill 2003c), and tsessebes, notably the speciation of *Damaliscus superstes* isolated in northeast Zambia

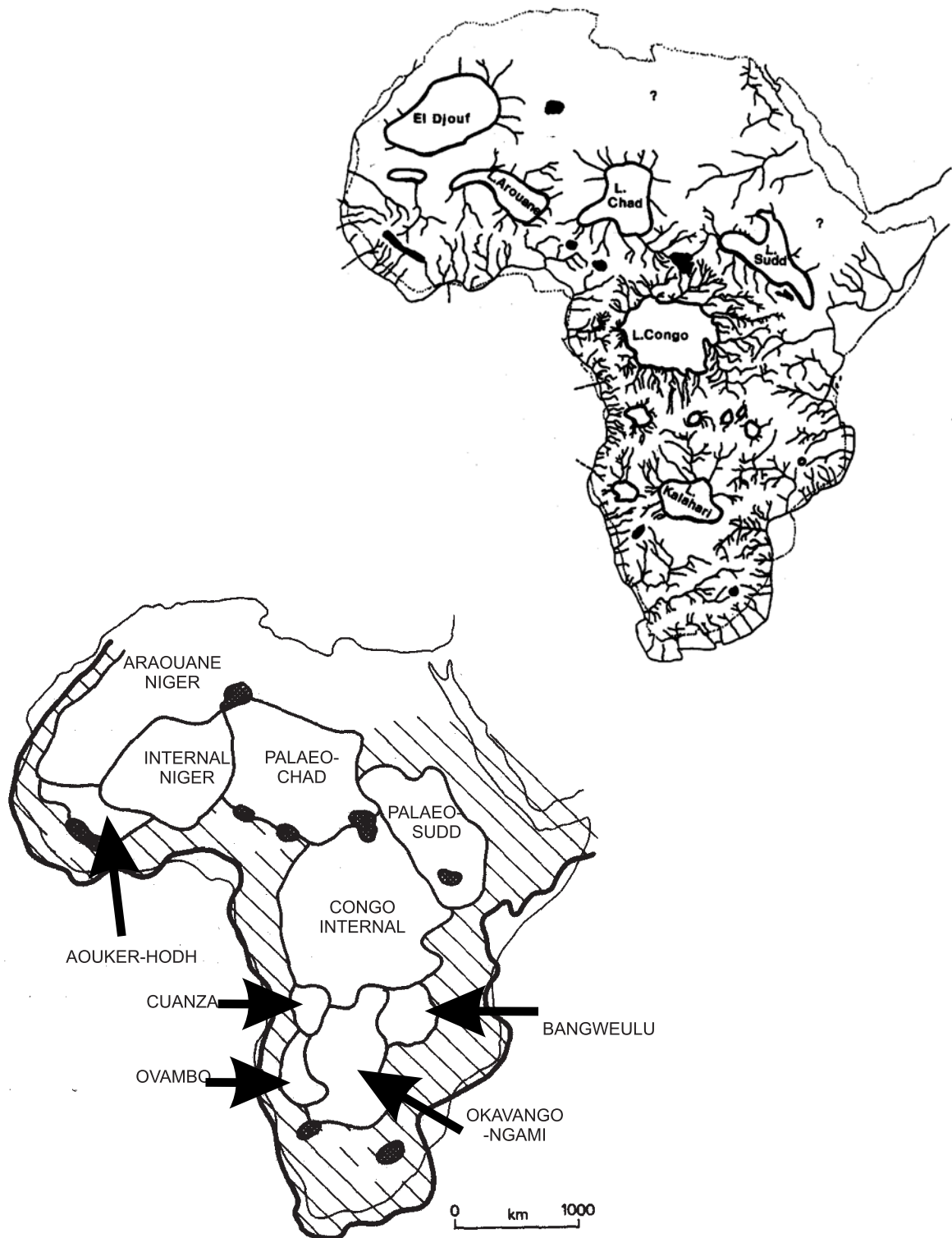


Figure 4.1b (Top). The proposed drainage across late Miocene Africa identified by consensus amongst experts at the Third Congress on African Prehistory, and presented by De Heinzelin (1963). Subsequent research has vindicated the existence of some of these landforms, and refined their tenures and extents (Peters & O'Brien 2001). For example, Lake Kalahari is now recognized as Palaeo-Lake Makgadikgadi (Thomas & Shaw 1991; see Section 4.9, below).

Figure 4.1c (Bottom) presents an equally speculative framework for pre-rift Africa. Here, the principal drainage basins, derived from De Heinzelin's map, were delimited by Summerfield (1991: 426).

(Cotterill 2003a,c). Principal events and stages in the evolution of the Palaeo-Chambeshi system as then known are summarized in Cotterill (2004, 2005).

Research findings since mid-2003 are published in four publications (Cotterill 2004, 2005, 2006; Broadley & Cotterill 2004). These expanded the scope of this drainage model to include additional wetlands. Nonetheless, their explication still centred around hypothesized dynamics of the Palaeo-Chambeshi drainage system. One of these papers invoked drainage rearrangements, through the late Cenozoic, to explain speciation in two complexes of birds restricted to wetland habitats (weaver birds, *Ploceus* spp. and Swamp flycatchers, *Muscicapa aquaticus* complex). I argued that drainage evolution explains vicariant speciation in these and other avian taxa (Cotterill 2004). In a second revision, Plio-Pleistocene changes in drainage and landscapes across Katanga were invoked to explain the region's high species richness of reptiles, and account for endemism and speciation of the endemic Upemba terrapin, *Pelusious upembae* (Broadley & Cotterill 2004). Both biogeographical reconstructions relied on an expanded model of drainage evolution (Cotterill 2003c) to include important wetlands in Katanga. Research to resolve the status and origins of the Upemba lechwe, *K. anselli* Cotterill 2005 motivated this broadened view. It has led on to unanticipated attention to important aspects of the evolution of the biota and landscapes of Katanga. Most of this data (besides Cotterill 2004, 2005) await publication and are formerly presented in this chapter. These detailed data support the theory that a Trans-Katanga drainage system was originally connected with the Palaeo-Chambeshi system. A large, shallow wetland, Palaeo-Lake Lufira was of central importance in this Trans-Katanga system. Cotterill (2003c, 2004, 2005) and Broadley & Cotterill (2004) invoked key aspects of the drainage model proposed by Moore & Larkin (2001), to apply its scope beyond southern Africa to cover northeast Zambia and Katanga.

4.1.4 Evolution of the Bovidae and African Environments

Before developing this chapter further, it is important to establish how a narrative of Plio-Pleistocene history, focused on south-central Africa, relates to the detailed knowledge of the Bovidae across Africa overall. It is equally pertinent to establish how this relatively fine-scaled review (about evolutionary dynamics of lechwe antelopes) relates to more encompassing knowledge of the radiation of the other African Bovidae, and indeed the evolution of other African mammals since the late Neogene. The bovid fossil record, discussed below, relates to interpretations of the phylogeographic history (Chapter 6), and evolution and taxonomy of lechwes (Chapter 7). So before presenting details about the evolution of the Katanga-Chambeshi region, I briefly review the literature pertaining to extinct antelopes. The relevance from this remarkably rich fossil record of the Bovidae (and other

Afrotropical mammals) ramify far beyond mammalian palaeontology; as they have been applied to help understand a broad spectrum of palaeo-environmental and evolutionary phenomena. One reason why the fossil record of African antelopes is so remarkably rich is because understanding of bovid diversity and evolution has benefitted greatly from, and equally informed, palaeoanthropology. Antelopes and hominids occur together in fossil beds in strata extending from the early Neogene through the Quaternary (Fig. 4.1a). The sheer abundance of bovid fossils exceeds that of hominids by orders of magnitude (Gentry 1990, 1992, 2000; Vrba 1995a; deMenocal 2004; Fig. 4.1a).

Syntheses of knowledge about fossil specimens have underpinned reclassifications of the antelopes. These combined fossil morphology with behavioural and molecular studies of extant taxa (e.g. Vrba 1979; Greenacre & Vrba 1984; Vrba *et al.* 1994; Hernández Fernández & Vrba 2005). Detailed reconstructions of evolutionary patterns and processes, constituting the bovid radiation, provide an exceptional model system to reconstruct how biodiversity has evolved through the late Cenozoic. Here, these fossil data have provided the primary means to construct far reaching theories of biotic diversification. Major signals in turnover of bovids are summarized in Table 4.1 (Vrba 1995a; Fernández & Vrba 2005). Syntheses of fossil data about extinct and extant antelopes, in the context of climatic and geological reconstructions, reveal important macroevolutionary patterns (e.g. Grubb *et al.* 1999; Vrba 1995a, 1999; McKee 2001).

Table 4.1. Turnovers of genera of the Bovidae through the Neogene and Quaternary (data collated from Vrba (1995a), Grubb *et al.* (1999), and Hernández Fernández & Vrba (2005)).

Geological Period	Extinctions	Evolution (First Appearance)
Late Pleistocene	11	11
Middle Pleistocene	13	24
Early Pleistocene	33	53
Pliocene	17	
Miocene	57	

Vicissitudes of climate have been invoked as the dominant determinant to explain macroevolutionary patterns of speciation and extinction, notably in Vrba's Turnover Pulse Hypothesis formalized into the "Habitat Theory" (Vrba 1992; Bromage *et al.* 1995). These emphasize how rates of speciation and extinction peak around the Miocene-Pliocene and Plio-Pleistocene boundaries. Both respective events

correlate closely with shifts to colder and arid palaeo-environments (Vrba 1983, 1985, 1992, 1993, 1995a-c, 1999). The Habitat Theory is usefully explicated by Bromage *et al.* (1995). It invokes comparatively abrupt changes in palaeo-environments to explain marked turnovers in biotic assemblages at continental and regional scales. A recent refinement of this hypothesis analysed patterns of speciation and extinction of large mammals within the context of their respective geographical ranges in geological time. Here, too, signals from the bovid fossil record dominate this database, which reveals that most young morpho-species first existed as small populations (in comparatively localized geographical ranges) for hundreds of thousands of years before their distributions expanded significantly (Vrba & DeGusta 2004).

The Turnover-Pulse Hypothesis is by no means universally accepted; as reanalysis of Omo-Turkana fossils revealed more gradual turnovers of bovid taxa through the Neogene (Potts 1996; Behrensmeyer *et al.* 1997; Feibel 1999; Bobe *et al.* 2002). This alternative explanation, the Variability Selection Hypothesis, argues that finer-scaled climatic variability *per se* caused mammals to evolve. Long-term instability was expressed in high amplitude climatic changes, that characterized much of the Pleistocene, and it is invoked to have generated the diverse assemblages of African mammals (Bobe & Behrensmeyer 2004; DeMenocal 2004). An important message we can derive from these contrasting interpretations is that no singular determinant alone explains all complex facets of evolutionary histories. As argued in Chapter 1, multiple causations of historical phenomena prevail, and, in fact, are to be expected. Inductive forces also tend to exhibit lags in their effects, which contributes to the complex dynamics exhibiting in these systems. To conclude, the unprecedented detail and scope of what we think we understand about the evolving biota across Africa through the late Cenozoic owes a great deal to bovid fossils. Geographical coverage of past environments and biota will obviously remain patchy; but these databases continue to improve - closing gaps and uncertainties about extinct fauna and palaeo-environments.

A pertinent signal from the bovid fossil record, with interesting implications for palaeo-environments, reveals that lechwe antelopes occurred more widely than today (Chapter 2, Fig. 2.2). Nevertheless, their fossil record is sparse, which undoubtedly reflects the lack of excavations in sediments of fossil wetlands in south-central Africa. One exception is the site of Twin Rivers, on the edge of the Kafue Flats (Chapters 2 & 5). Nonetheless, an important signal in the database reveals a pulse of speciation events centred around 700 Kya, associated with first appearances of many extant forms. Based on the BSC, these total no less than 27 speciation events (Vrba 1995a). They include the first records of fossils morphologically similar to extant *K. leche* (Chapter 2).

4.2 METHODS OF DATA ANALYSIS AND SYNTHESIS

4.2.1 Synthesis of Published Literature

This chapter is a synthesis of published knowledge about the geology, geomorphology and past climates of the region historically occupied by lechwe antelopes of the *K. leche* complex. Consideration of biogeographical data forms an equally significant part of this reviewed knowledge. The latter focuses on species restricted to wetlands, whose extant distributions reveal influences of landscape evolution. I term these informative patterns “biotic signatures of landscape evolution”. The temporal scope of this review extends from the late Miocene to the present. It has proved most challenging to place a firm geographical framework around this review. The core region corresponds to all landscapes in south-central Africa where lechwe antelopes are known to occur. Nevertheless, examples and features are included from elsewhere in Africa.

It is far beyond the scope of this study to compile a fine-grained study of the entire archipelago, to compare the biodiversity and biophysical properties of each wetland in detail. So only focal landforms have been singled out for more detailed descriptions. These regions include the Cuanza-Cubango headwaters (western Angola); the Katanga Pedicle (southeast DRC and north Zambia; the Kafue Flats and northeast Botswana. Chapter 5 pays detailed attention to the Quaternary history of the Batoka Gorge; because updated understanding of their evolution refines understanding of coeval events in allied drainage basins. A timeline of principal geochronological units is depicted in Chapter 5, in association with principal events and periods in the palaeoclimatic and archaeological record, as deciphered for important landforms within the Katanga-Chambeshi region.

4.2.2 Geomorphological Datasets

Topographical and topological details of landforms were analysed, and are illustrated and presented in a geospatial context using GIS (Geographical Information System) technology. I obtained geospatial datasets available in the public domain to create an integrated database of map layers. ArcInfo 3.3, ArcView 3.3, and ArcGIS 9.1 (ESRI) were employed to compile and analyse this integrated database. Coverage of drainage and pertinent cadastral data was obtained from United States Defense Mapping 1: 1 000 000 datasets. The vegetation map of Africa was digitized from White (1983). I also interpreted relevant hardcopies of maps for Katanga directly. These included the series of orthophoto sheets for Katanga held in the geospatial archives of the Department of Geology, Royal Museum of Central Africa, Tervuren, Belgium. These 1:100 000 sheets are part of the database employed by Lepersonne (1976) to map the geology of the Democratic Republic of Congo at a scale of 1: 2 000

000. Notes and data translated manually from this dataset are applied here; although these geospatial data were not obtained in digital format.

Published areas of drainage catchments were obtained from published literature and the electronic database compiled by Shahin (2002). High resolution topographic data are especially valuable to analyse variations in landscape patterns in the context of a Digital Elevation Models (DEMs). Their fine-scaled resolution reveal essential subtle variations in topography across vast expanses of south-central Africa, not least the immense wetlands populated by lechwe antelopes. The exceptionally shallow gradients across these landforms are lost in the coarse grain of older DEM datasets (e.g. the ~ 1 km² GTOPO30 dataset applied for example by Karner *et al.* 2000). An excellent, high resolution and publicly available topographic dataset is derived from the Shuttle Radar Topography Mission (SRTM3). This was compiled by NASA from data covering 80% of the earth's surface collected over 11 days during February 2000. The publically available dataset has a reduced resolution of 3 arc seconds, such that each data pixel corresponds to 90 m² of landscape (Lebrun *et al.* 2006; Ustun *et al.* 2006).

The initial data conversion and migration of the encoded SRTM3 data (of the relevant coverage) into an ESRI compatible format was carried out at the South African National Biodiversity Institute (SANBI). The resultant Digital Elevation Model (DEM) - hereafter termed the 90m DEM - comprises an interpolated raster layer compiled from the unit 90m (8100m²) data pixels. This 90m DEM and integrated geospatial data were employed to create all the maps in this study (e.g. Figs 2.1 & 2.2). Some of the high resolution “cut-outs” from the geospatial database also incorporate structural geological features on published geological maps. These data sources are cited accordingly. The unprecedented resolution of topographic detail in this combined database illustrates important and revealing properties of landforms. This 90m DEM is central to synthesize all biogeographical and archaeological evidence available to this review.

The 90m DEM can suffer from errors across large expanses of very flat terrain. For example, the SRTM3 data overestimated elevation across the Etosha basin by 0.16% on average, as gauged by a control DEM generated from 10m contours of 1:50 000 maps of the same region (Hipondoka 2005). Where possible, I checked elevations obtained from analyses of focal areas within the study region, with the SRTM elevation data compared against the most detailed topographic maps available (for Katanga, DRC and Zambia). Where I employed this 90m DEM within northern Botswana, the underlying precision of the SRTM data was checked against previously published maps, notably those

detailing precise elevations of landforms formed by fossil lakes mapped by Cooke (1979), Cooke & Verstappen (1984) and Thomas & Shaw (1991). Gani & Abdelsalam (2006) and Ustun *et al.* (2006) have detailed the remarkably high precision and accuracy of this dataset, as applied to the mountainous terrain of Ethiopia and Turkey, respectively.

4.2.3 Biogeographical Datasets

The biogeographical patterns represented among different taxa of fishes are applied in this chapter to identify past connections between drainage systems, and so infer how the topologies of these systems have changed. Much of this data was compiled originally by Bell-Cross (1972, 1982), Bell-Cross & Minshull (1988), Skelton (1994), Malaisse (1997), and Marshall (2000). I have followed the taxonomy in *Check-list of the Freshwater Fishes of Africa* (hereafter CLOFFA) compiled by Daget *et al.* (1984, 1986, 1991). CLOFFA also structures Fishbase (www.fishbase.com), but with some recent amendments. More recent revisions have been published about certain taxonomic groups of fishes, and some taxonomic problems solved. These sources were employed and are cited where appropriate. Preserved specimens vouch for these distributions have been cited in these works and the taxonomic and distributional reports they reference. Principal collections housing these specimens include the ichthyological departments of the Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe, the Royal Institute, Brussels, Musée Royale d'Afrique Centrale, Tervuren, Belgium, and the South African Institute for Aquatic Biodiversity Research, Grahamstown, South Africa (Bell-Cross & Minshull 1988; Skelton 1994, 2001).

4.4 DYNAMICS OF AFRICAN CLIMATES

Reconstructions of palaeo-environments integrate details of past climate and geomorphology. It most important to acknowledge our refined understanding of biotic evolution owes a big debt to reconstructions of past climates. The causes of these dynamics of palaeo-climates are still only partly understood. The remarkable detail has been synthesized from numerous databases. Reconstructed profiles of changing sea temperatures especially illuminate how climates changed across continents, including Africa (Zachos *et al.* 2001; Schefuß *et al.* 2003; DeMenocal 2004; EPICA *et al.* 2004; McManus 2004; Ravelo *et al.* 2004). The revolution in radioisotope dating in geology has been equally important (DeMenocal 2004). It is this combination of climatic reconstruction with geochronology that has proved so powerful to place extinct taxa into precise palaeo-environmental context.

The inherent variability of past climates at global and regional scales (and especially across Africa), forms the subject of a vast, and expanding, literature, and is catalysed by concerns over unprecedented climatic changes caused by anthropogenic agencies (deMenocal 2004). Nevertheless, evidence for

climatic and palaeo-environmental variation obtained from within south-central Africa is sparse (Runge 2001; Sturmhuber *et al.* 2001). Deacon & Lancaster (1988) emphasized that reconstructions of palaeo-climates are only as robust as the data available, which reflect local palaeo-environments. Such datasets are the marked exception for the Katanga-Chambeshi region, especially for conditions pre-dating the Late Pleistocene (Gasse 2000). Very few profiles extend further back into the Late Pleistocene than 200 Ka BP (Partridge 1997; Barham 2001). This obviously limits direct reconstructions of antecedent environments on the African plateau before the late Quaternary. Nevertheless, reconstructions of the Marine Isotope Stages (MIS), based on fluctuating $^{18}\text{O}/^{16}\text{O}$ signals derived from preserved sediments, provide far reaching spatial resolution (Brain 1981, 1985). The glacial periods represented in lower amplitude periods (lower ^{18}O levels) are inferred to reflect relatively arid, drier climates. These manifested in substantially reduced precipitation across much of Africa, and they are invoked to explain the peaks of dust deposited in polar ice cores during glacials (EPICA *et al.* 2004). Drastic declines in levels of Africa's Great Lakes also coincide with arid climates across equatorial Africa in the Late Pleistocene (Delvaux 1995; Cohen *et al.* 1997; Sturmhuber *et al.* 2001).

Avery (2003) concluded that her reconstruction of climatic variability through the Middle Pleistocene at Twin Rivers (central Zambia) agreed closely with reconstructions of global climate derived from marine isotope stages. Barham (2000, 2001, 2002) also applied profiles of marine and cryospheric palaeo-climates to reconstruct dynamics of xeric and mesic environments across central Africa through the Middle Pleistocene. Recent reviews (notably Zachos *et al.* 2001; Ravelo *et al.* 2004; DeMenocal 2004) reveal strong consistent support in their reconstruction of climatic change through the Cenozoic, and especially since the Oligocene. Their analysis included pertinent data for the African hinterland derived from marine sediments and reconstructions of the African monsoon rainfall (Trauth *et al.* 2005). A cave stalagmite from southern Botswana recorded changes in local climates over the past 51 Kya, which closely reflect mesic conditions through the interglacial MIS 3 to the xeric conditions of MIS 2 in the Last Glacial Maximum (Holmgren *et al.* 1995), while the 90 m core from the Pretoria Saltpan archives a detailed record of 200 Kyr (Partridge *et al.* 1997), and the other is the Congo delta. The latter is especially pertinent as profiles of clay minerals in sedimentary record over 200 Kyr, in the Congo Fan, reflects peaks in freshwater discharge during interglacials 1, 5 and 7 (Gingele *et al.* 1998). Partridge *et al.* (1997) demonstrated a 23 Kyr cycle in rainfall, which correlates with prevailing SeaSurface Temperatures, as preserved in Marine Isotope Stages. To conclude, these climate records (also sited closest to the Katanga-Chambeshi region) reveal predominant control by orbital forcing.

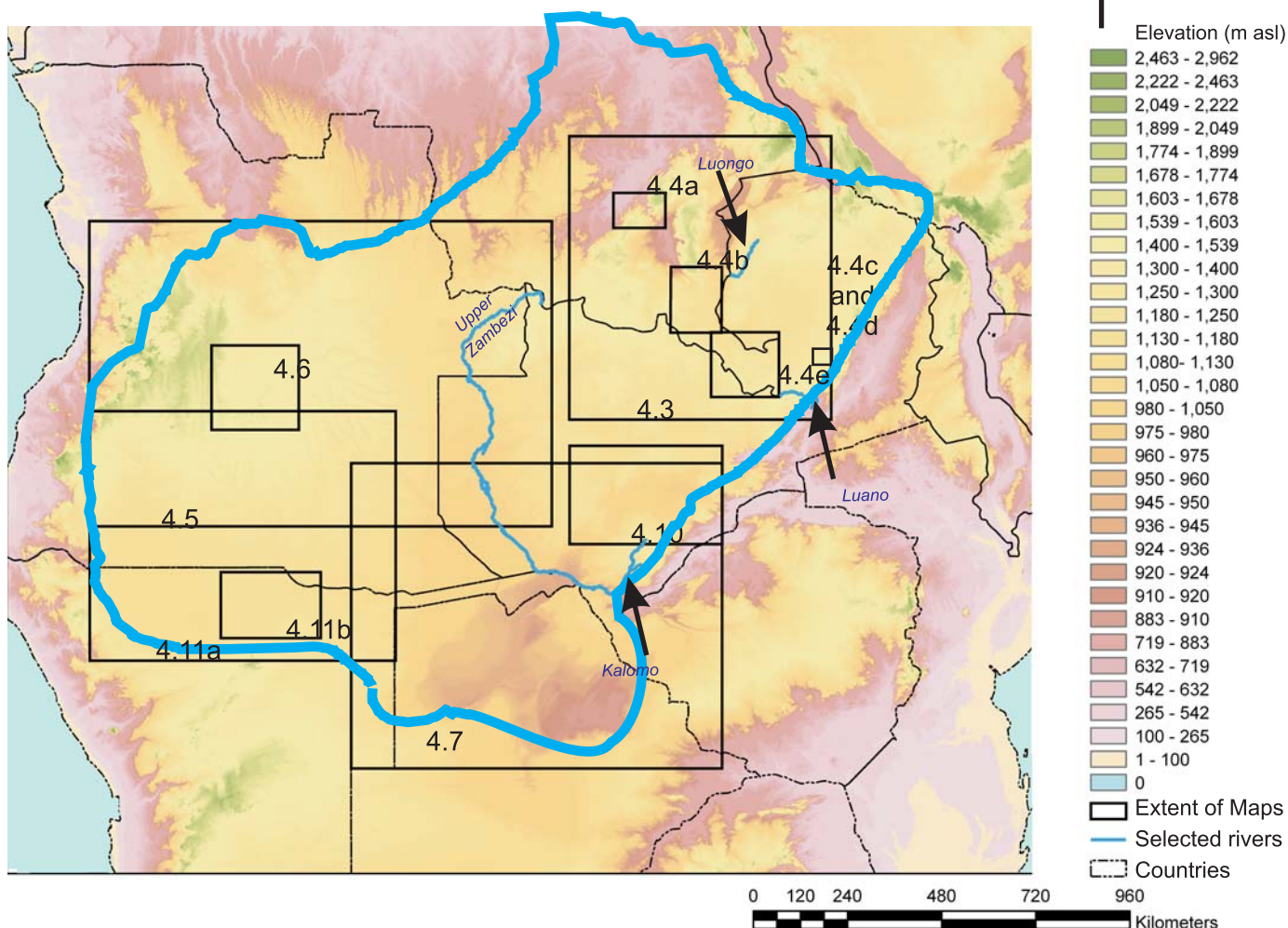
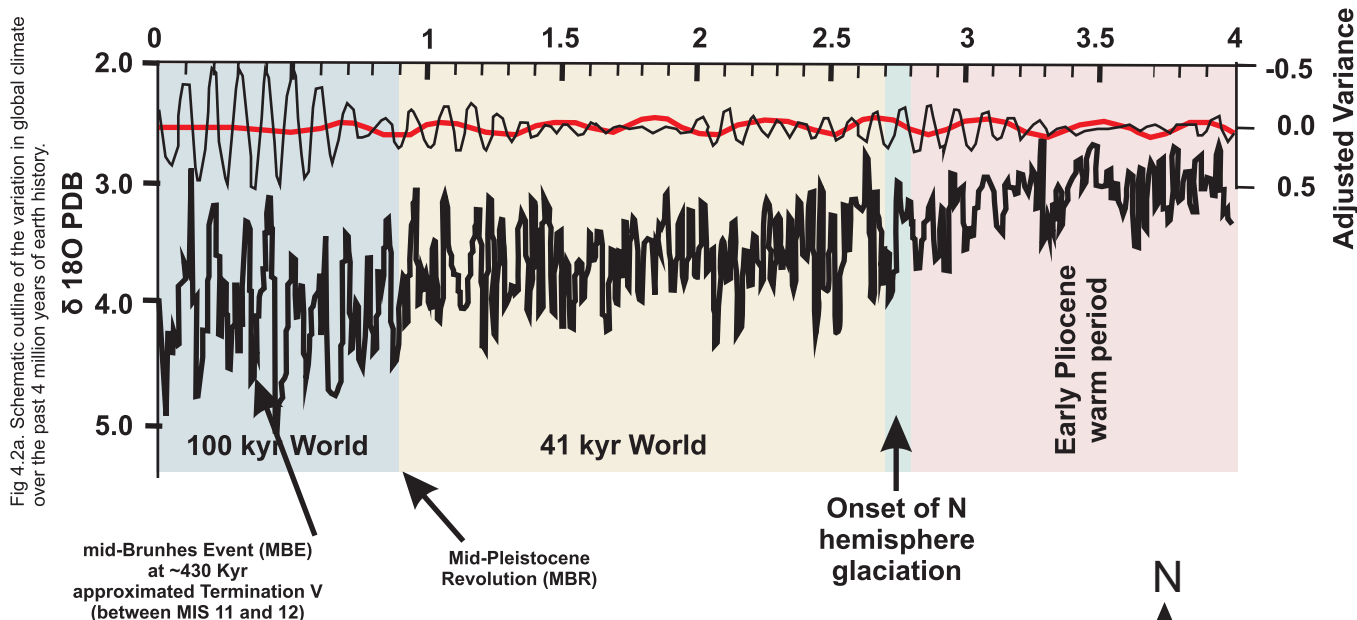


Figure 4.2a. (Top) Schematic outline of the variation in global climate over the past 4 million years of earth history. Note increases in variability over the Pleistocene. Modified from Zachos et al. (2001) with amendments from Schulz & Zeebe (2006).

Figure 4.2b (Bottom) Topographic map illustrating the scope, links and detail of attention paid to each of the principal landforms comprising the wetland archipelago across the south-central African plateau. Extent of the Katanga-Chambeshi region depicted by solid blue line. The labelled boxes denote respective extents of detailed maps, presented in this chapter, which depict landforms in more detail.

Recently published databases, notably the new EPICA ice-core from central Antarctica, have extended fine scaled resolution of palaeo-climates into the Early Pleistocene (EPICA 2004; McManus 2004). These findings extend, strengthen, and confirm reconstructions for palaeo-climates from the Neogene to Recent previously derived from the Vostok core and marine sediment records (EPICA 2004). The overall scenario reconstructed from all available data is complex. The three principal thresholds through the Neogene and Quaternary can be summarized (derived from Potts 2001, Zachos *et al.* 2001, Ravelo *et al.* 2004 and DeMenocal 2004; Fig. 4.2a):

1. A shift in the periodicity of regular cycling in which cold, drier periods alternated with warmer, mesic periods. A major transition occurred in the early Pleistocene (~1.0 Ma BP) when the 41 Ka yr periodicity was superseded by the ~110 Ka periodicity of Milankovitch cycles. The latter persisted through the Pleistocene to manifest in 32 glacial cycles over 1.65 Myr, represented in significant expansions and contractions of the Earth's cryospheres.
2. The mid-Pleistocene Revolution that involved a shift from a "41ka World" to the "100 Ka World" occurred about 0.9 – 1.0 Ma (Ravelo *et al.* 2004; Lisiecki & Raymo 2005). This was accompanied by increased amplitude in the magnitude of the oscillations in global temperature represented by the four glaciations through the more recent Pleistocene (Schulz & Zeebe 2006).
3. Compared to climatic variation through the late Neogene, the overall trend has entailed an increased cooling of climates through the Quaternary.

Firmer details of climatic change over the past 1 million years have recently become better resolved. The important threshold of the mid-Pleistocene Revolution (MPR) was followed by the mid-Brunhes Event (MBE) at ~430 Kyr. The latter corresponds to Termination V, between MIS stages 12 and 11. Both events were associated with global cooling that manifested in sequential increases in global ice volume. The earlier MPR is significant, for it marks the transition from 41 to 100 Kya cycles that delimited the frequency whereby glacial and interglacials intervened (Zachos *et al.* 2001; EPICA 2004). I invoke the significance of these events in Chapter 5.

Aridity increased markedly during certain of the cooler, drier periods across the African hinterland. Evidence suggests this was when wind erosion redistributed aeolian sediments across the Kalahari Basin in the coldest Pleistocene glacial periods (Barham 2000, 2001; Shaw & Goudie 2002; Thomas

& Shaw 2002; Haddon & McCarthy 2005; McFarlane *et al.* 2005). An important consequence of these arid Pleistocene periods was the expansion of desert and xeric habitats in southwest and northeast Africa. This was when an intermittent arid zone linked the Namib-Karoo and Somali arid biomes. Existence of this postulated “Arid Corridor” was first proposed early in the 20th century to explain anomalous biogeographic links between Africa’s northeast and southwest arid biomes. Numerous examples of vicariant speciation are attributed to strong control through effects of Pleistocene palaeoclimates (Van Zinderen Bakker 1969). Roberts (1937) and Wells (1967) presented mammalian examples; and representative pairs of vicariants include hyaenas (*Hyaena brunnea* and *H. hyaena*), Bat-eared foxes, *Otocyon megalotis*, and antelopes include *Madoqua damarensis* (Gunther 1880) isolated from the dikdik radiation in northeast Africa (with *M. kirkii* its sister vicariant) and the hippotragine antelopes, *Oryx gazella* and *O. beisa* (Grubb *et al.* 1999).

It is important to emphasize that controversies and uncertainties weaken what is understood about the mechanisms and finer details of climatic history briefly summarized above. Uncertainties remain over the fundamental pacing of African climatic variation (deMenocal 2004). The interactions between the different mechanisms of astronomic forcing of Earth’s climate (cf Zachos *et al.* 2001) might well have been coupled in non-linear ways; so the search for such patterns may be miscast should inherent stochasticity underlie the evolution of complex changes in climates.

4.5 A BRIEF, DEEP, HISTORY OF “HIGH AFRICA”

4.5.1 Emplacement of Cratons and Consolidation of the African Continent

Africa’s principal rivers, floodplains and lakes drain very ancient geological platforms. The main components of this geological structure are the cratons and especially High Africa. These ancient cores are of Archaean and Proterozoic age. This stability of these ancient cratons truly is of legendary antiquity, as testified by how they have survived protracted structural upheavals since Archaean times, since at least 2.5 billion years ago where continental lithosphere has been recycled into the mantle. This antiquity is exemplified by the granitic-greenstone structure of the Kalahari-Zimbabwe craton that was consolidated by the late Archaean. Nomenclature of Africa’s major structural cratonic units varies among authors. The principal structural components of the Zambian plateau were consolidated ~560-550 millions years ago when the Angola-Kalahari plate collided from the south with the Congo-Tanzania plate. This event forged the underlying lithosphere of what is now south-central Africa, and in so doing, consolidated the mineral rich Lufilian Arc of Katanga and northern Zambia, which includes the Copperbelt. These rifting events in Proterozoic times were preceded, and followed, by intrusions of granitic magmas, which helped consolidate older, and also younger rocks (Porada &

Berhorst 2000; Rainaud *et al.* 2005). Here I follow Griffin *et al.* (2003) who emphasize the prominence of the Kalahari craton which underlies a large portion of southern and south-central Africa, including a large area of the Katanga-Chambeshi region.

The response of cratons to plate tectonics (and thus lithospheric dynamics) has had important consequences for how long landforms have existed on surfaces of these continents. The characteristic response of cratons to uplift, tension and compression is warping and quite minor faulting. This is especially apparent across the elevated interior of Africa, which has been uplifted repeatedly. These more subtle epeirogenic dynamics, across cratons, contrast with more obvious effects of the diastrophic orogeny, which has faulted and folded the mobile belts and younger formations abutting and dividing cratons. Thus, the uplift and rifting of Africa has manifested especially in spectacular diastrophy between and around cratons. This relative quiescence of the craton-rich African plateau has had important consequences for landscape evolution, by buffering landscapes from effects of perturbations (Summerfield 2001; Twidale 2003). A well documented biotic significance of these ancient landforms is signified by localized persistence of primitive plants on Africa's oldest land surfaces. These may be of Gondwana age (Craw *et al.* 1999; Heads 2004).

4.5.2 Principal Structural Controls: the uplift, faulting and warping of Africa

At a continental scale, the African hinterland is a vast elevated plateau across which a pattern of broad, gentle basins and swells are impressed (Burke 1996). Africa is being sliced from north to south by the narrow incisions of the East African Rift System (EARS), which may possibly reflect active individuation of the Somali plate as it slowly breaks away from the African plate (Chorowizc 2005). Repeatedly, cratons have controlled profoundly how magmatic upwelling has manifested under, and within, the African plate. This has important ramifications for much of the continent's geology, especially the overall geometry of the EARS (James *et al.* 2001; O'Reilly 2001). The roots of cratons extend 250 - 300 km deep into the lithosphere. Geophysical evidence suggests they have exercised an ancilliary function by focussing magmatic pulses from hotspots under the African plate. This mechanism explains how diastrophism and volcanism has become concentrated within the narrow zone of the EARS. In contrast, Africa craton-rich regions have instead been uplifted and warped (Ebinger & Sleep 1998). To borrow Wilson's (1990) model (describing the ancient cratonization of Zimbabwe's granite-greenstone terrain) these cratons have behaved like billiard balls as the entire African plate has shifted across the Earth. Furthermore, whilst stationary during the Cenozoic, it has been uplifted and distorted. Remarkably, each craton has maintained its individuality since Archaean and Proterozoic times.

Persistent uplift, driven by mantle hotspots under the African plate, has bowed the continental lithosphere (Nyblade & Robinson 1994; Summerfield 2001; Gurnis 2001). The anomalously low mantle temperatures under Africa's cratons contrast against hotter portions of thinned lithosphere underlying the African rift system (Ritsema & Van Heijst 1999). The projected depths of these cratons' "roots", extending over 250km below the extant continental surface, are much deeper than the zone where Africa is being rifted. Here lithospheric depths average 40 ± 5 km (Chorowicz 2005). This zone of thinned lithosphere extends south from the Arabian Gulf under the EARS, and southwest under Katanga through to the Kalahari Basin (Fig. 4.1a). Along with volcanism, these rocks have responded to uplift by cracking. This contrasts against cratons that have tended to warping, and at most only faulted slightly (Bonavier *et al.* 1995; Karner *et al.* 2000). It is difficult to overemphasize that this overall composition and structure of Africa's crustal rocks has controlled the evolution of landforms, especially rivers and hydrological basins in the most profound ways (Summerfield 1991).

These very deep spatial and temporal aspects of Africa's history have controlled drainage evolution profoundly. Localized areas of Africa's surface have been downwarped as the continent was uplifted, creating the larger scale pattern of swells and basins (Burke 1996; Summerfield 2001). As recognized originally by Du Toit (1933, 1939) recurrent uplift explains how sagging basins have come to be encircled by raised watersheds along lines of crustal flexure (epeirogenic axes). These localized zones of high relief have persistently controlled hydrological processes, such that epeirogenic axes correspond to ancient watersheds initiated across Mesozoic Africa, and earlier on Gondwanaland (Moore 1999; Moore & Larkin 2001; Haddon & McCarthy 2005).

Africa has remained relatively static over the past ~30 million years. This anomalous behaviour of the African plate is attributed to several factors, but is not conclusively understood (Coblentz & Sandiford 1994). The possible mechanisms invoked are: (1) Africa has escaped influences of slab pull at its margins, whilst the surrounding oceans have expanded since the Mesozoic. (2) Uplift over mantle plumes (especially the Karoo and Afar plumes) would explain how Africa has remained comparatively stable since the Mesozoic (Moore & Blenkinsop 2002). The continent has, nonetheless, been slowly rotated. The same agencies appear to have driven the warping and rifting of the continent's interior (Burke 1996; Bumby & Guiraud 2005). Prior to the Pliocene, dates proposed for earlier uplifts of Africa are very controversial. Despite inadequate evidence, Burke (1996) suggested a date of ~30 Myr, while Moore (1999) suggested that three concentric epeirogenic axes reflect sequential uplift events over many millions of years that await precise delimitation. An equally telling consequence (of this protracted stability of the African plate) is represented by the deep biomantle of

the African surface, which reflects crores (tens of millions) of years of subaerial weathering. This began in Mesozoic times - as represented by deep regoliths (Twidale 1988, 2003, 2005; Section 4.5.6).

The persistence, through a remarkably long duration, of “High Africa” driven by recurring tectonic activity - with integral continental warping and rifting - has manifested in repeated elevation of southern and eastern Africa. This pattern has persisted since before Gondwanaland split up in the late Mesozoic. It appears that this uplift has persisted because Africa originally occupied the central core of Gondwanaland, and has thus been isolated from zones of subduction long after the supercontinent broke up (Gurnis, 2001; Moore & Blenkinsop 2002). The number of plumes, and their location, probably accounts for ultimate control of drainage basins across the Katanga-Chambeshi region (Section 5.8). This determinant also explicates evidence for how coeval landforms have become widely distributed across Africa.

4.5.3 Geomorphological Controls on Biotic Evolution

The unique bimodal topography of Africa has a complex history, the product of recurrent uplift and episodes of plate tectonics, that can be traced back into the Palaeozoic. It has since been augmented by recurrent episodes of uplift since at least Triassic times (Doucouré & De Wit 2003). Sustained and repeated uplift of the entire African continent has been attributed to the African Superswell, associated with anomalies in mantle convection under southern and eastern Africa (Nyblade & Robinson 1994; Partridge & Maud 2000). In consequence, landforms of southern and eastern Africa have been altered in repeated events through the Neogene and Quaternary. Of potentially profound significance to evolution of biodiversity across the Katanga-Chambeshi region, is the widespread evidence for significant uplift that occurred in the late Pliocene (Cox, 1989; Partridge *et al.* 1995; Lithgow-Bertelloni & Silver, 1998; Ebinger *et al.* 2000).

This Pliocene event enacted two far reaching consequences. Firstly, climatic consequences were extreme. Adiabatic consequences of Pliocene uplift are hypothesized to have lowered average temperatures across the African hinterland by up to ~10°C. Widespread aridity followed on this cooling, and grasslands and savannas expanded as moist forests contracted. These changes correlate with the appearance of several new genera of mammals, pertinently *Damaliscus*, *Kobus*, and *Homo* (Pickford 1990; Partridge *et al.* 1995). Secondly, associated crustal flexing and faulting altered drainage patterns across the continent through widespread diastrophism and epeirogeny. Striking signatures are the deep canyons left by down-cutting rivers along the continental margins, after southern and eastern Africa were raised hundreds of metres comparatively rapidly. Inland, these

tectonics manifested in a multitude of different local effects, especially where faulting and warping expressed its more gentle effects across vast regions of the hinterland (Burke 1996; Partridge 1998). Pertinently, it appears the Zambezi River established its extant topology, for the first time, in the late Pliocene (Moore & Larkin 2001).

Actually, this late Pliocene uplift of Africa needs to be recognized as one event, albeit major, in a long history of tectonic activity, because the East African Rift System (EARS) has radically altered east and south-central Africa since the early Cenozoic. Rifting began in the Oligocene, with further deepening of valleys in the Albertine and Gregory rifts proceeding sporadically into the Pleistocene. Several hundreds of kilometres wide, the entire EARS extends for over 8 000 km from the Red Sea south to Botswana, Mozambique and the Limpopo valley (Chorowicz 2005). Details of the evolution and geology of the EARS fill a large literature, of which Rosenthal *et al.* (1987), Ebinger (1989) and Chorowicz (2005) provide syntheses. Of considerable relevance to this study is the South West Extension of the EARS. Its three principal arms branch off from the southern end of the Tanganyika graben. The northern system extends through Lakes Mweru and Mweru-Wantipa across Katanga to northern Barotseland (Kasempa Gorge, Zambia), and probably further west. The second underlies the Muchinga escarpment, skirting around the Chambeshi and Bangweulu depressions. The third is represented by the Luangwa valley, and splits into three further arms: the Luano graben; the Kafue-Okavango graben; and the Gwembe trough in which Lake Kariba is impounded (Fig. 4.1a).

Control by the EARS on the evolution of biodiversity is widely acknowledged, and the subject of active research. Its importance as a principal template of hominid evolution - termed the East Side Story - is well known (e.g. Coppens 1999). Besides its ultimate control in driving adaptive radiations and the explosive speciation of flocks of cichlid fishes in the Great Lakes (Verheyen *et al.* 2001; Salzburger *et al.* 2005), rifting has controlled mammal speciation. For example, Denys *et al.* (1986) and Denys (1999) emphasized the importance of tectonic controls on evolution of murid rodents across and along the EARS. The distinct differences between assemblages of extant mammals in eastern and southern Africa invokes control by a geographical barrier within the EARS (Grubb *et al.* 1999). The volcanically active Rukwe-Rungwe region, between the Malawi and Tanganyika rifts, has been singled out as the node that likely constrained mammals' dispersals (Cotterill 2003c). Faulkes *et al.* (2004) suggested the EARS controlled primary cladogenesis in bathyergid moles; where the break in extant distributions of the two main clades of fossorial rodents corresponds to the Rukwa-Rungwe region. Another example of its influence is the divergence between two clades of alcelaphine

antelopes, with the *Damaliscus korrigum* and *D. lunatus* clades divided to the northeast and southwest of the EARS, respectively (Cotterill 2003a,c).

4.5.4 Evolution of Hydrographic Patterns

For well over a century, a vast research effort to understand how rivers evolve has accumulated into a large literature in geomorphology. There are three principal mechanisms whereby the topology of a river can evolve (Bishop 1995):

- channel diversion more commonly occurs in senile rivers, and entails the capture of neighbouring channels through the process of avulsion;
- river capture, where erosion of a river's headwaters pirates the course of an established river. This is exemplified by the Middle Zambezi's piracy of the Upper Zambezi, Upper Kafue, and Cuando (Chobe) rivers;
- beheading is a category of river capture involving headwaters of two abutting catchments, where the streams of one capture the neighbouring channels. Often, little, if any, obvious evidence is preserved in the landscape to reflect such events, which are invariably related to tilting of the landscape.

Following the revolution in the earth sciences, with the theory of plate tectonics embraced as its universal paradigm, geomorphological research has emphasized how continental flexing and faulting is a dominant mechanism of drainage evolution. A large literature has since grown to reveal how tectonic activity, manifested within and across continents, has altered, and equally preserved, hydrographic patterns (Bishop 1995; Allen 2005; Goudie 2005). Details of the documented examples are published in many studies of drainage evolution in southern Africa (e.g. Dollar 1992; Moore & Larkin 2001). It is important to acknowledge that tectonic controls were invoked by Dixey (1943a,b, 1944, 1955a,b) and Wellington (1955), following Du Toit (1933, 1939) who emphasized how uplift, manifesting through epeirogeny, has radically controlled Africa's drainage.

4.5.5 Ancient, Big Rivers

Potter (1979) concluded that the significance of big rivers in Earth history is an overlooked and underworked theatre of geological enquiry. A spectacular example is the Mississippi, whose principal channel formed over 250 million years ago. Catchments, principal channels, and depocentres of those ancient, big rivers, which have been studied, reveals how some have persisted over hundreds of millions of years. The endurance of such landforms raises fascinating questions pertaining to what

factors, notably tectonics, have aided their escape from erosion. More synthetic questions pertain to where big rivers have occurred on which continents, and their abundance overall. Above all, a singular challenge is to single out factors that explain why certain big, ancient rivers have been so long lasting (Potter 1979).

Although the contemporary Zambezi and Congo are striking examples of big rivers, their current topologies formed recently in the late Cenozoic, when each gained major portions of river channel very recently in Quaternary times (Chapter 5). Protracted persistence of the most ancient of rivers invariably reveals an intimate association with ancient cratons. As with streams (Hynes 1975), every river is ruled by its valley. After initial incision, rivers tend to persist in their courses especially if buffered from tectonism by the comparative structural stability of cratons. Available evidence reveals that several of the larger rivers on “High Africa” are indeed ancient. The channels of the Cuando, Luangwa, Okavango and Upper Zambezi have not changed perceptively since the early Mesozoic (Moore & Larkin 2001). Antecedents of their modern topologies were likely represented in the endoreic tributaries that debouched their catchments into the Kalahari basin (Haddon & McCarthy 2005). This more ancient history of what today constitute the big rivers in the Katanga-Chambeshi region awaits detailed research. The current evidence points to a relative antiquity of these endoreic basins established on Gondwana (Summerfield 1991). Certainly, their importance to African biogeography deserves closer attention from students of the continent’s biodiversity. In this respect, the relative antiquity of the Palaeo-Chambeshi river raises interesting, important questions. Stankiewicz & De Wit (2006) recently argued that the Upper Chambeshi was originally part of a Palaeo-Congo River, which then flowed east into the Indian Ocean. This configuration was disrupted by rifting along the EARS in the late Oligocene, which means the Palaeo-Chambeshi only attained its topology thereafter, perhaps early in the Miocene. Overall, besides the invaluable works of Veatch (1935) and Cahen (1954), the history of the Congo basin has barely been studied. For example, very little is known about Palaeo-Lake Congo, beyond its sketched outline (Peters & O’Brien 2001; Fig. 4.1b). This state of knowledge of the Cenozoic hydrography of the Congo basin exemplifies the immense opportunities facing students of African hydrography.

4.5.6 Erosion Surfaces, Hydrography and Drainage Systems

The extent, age and properties of erosion surfaces greatly influences antecedent, and extant, hydrography and hydrological processes. The immense plateaux of the African hinterland forms a mosaic of discrete erosion surfaces, each of which reflects its geomorphological origins; such that these portions of plateau can be loosely grouped into categories reminiscent of their common genesis.

Classification of all Africa's land surfaces into a complementary system of erosion surfaces had been accomplished by the mid 20th century (King 1953; Cahen 1954; Dixey 1955a,b; Lister 1979, 1987). Uncertainty and controversies prevail over their absolute ages. This applies especially to landforms that have formed since the Oligocene, whereafter intense erosion modified large regions of Africa (Taylor & Howard 2000). Legendary difficulties are associated with attempts to date large areas of tropical Africa covered by younger Kalahari sediments (presumed to postdate the Miocene). No universal nomenclatural system can be applied to either surfaces or sediments of the Kalahari basin (Haddon & McCarthy 2005; Hipondoka 2005), despite earlier attempts (e.g. Mabbutt 1957). Fortunately, certain more recent aeolian and weathered sediments are intimately associated with hominid artefacts, an association that conveniently constrains their date of formation (Du Toit 1933; Clark 1950, 1963, 1964; Bond 1964; Chapter 5). And their relationships to underlying strata has direct relevance to delimit when significant events rearranged entire drainage systems across the Katanga-Chambeshi region.

Controversies over their actual age aside, the concept of an African erosion surface remains a valuable heuristic concept to frame explanations about the origin and extant structure of a large portion of the Katanga-Chambeshi region. These surfaces dominate river catchments across the Palaeo-Chambeshi archipelago. King (1953, 1962) invoked peneplanation as the dominant mechanism that formed erosion surfaces - driven by coastal uplift rejuvenating erosion by headwaters of drainage systems. And the African surface was a favourite example cited to support this explanation. Nearly universal acceptance of peneplanation declined after the theory of plate tectonics came to revolutionize important aspects of geomorphology through the late 20th century. Instead, it now seems far more plausible that persistent uplift, effected through epeirogeny, can explain the antiquity of the African surface for many crores of years (Summerfield 1991; Burke 1996; Twidale 1992, 2003).

Their distinct gentle topography is underlain by deep regoliths - landforms testifying to many millions of years of weathering. Their properties exercise peculiar controls over hydrological patterns and processes (McFarlane 1991). In fact, the gentle topography and deeply weathered biomantle, characterizing the African surface, are consequences of deep weathering of the landscape since Cretaceous times. In escaping rifting, prolonged quiescence of the underlying cratons has facilitated their subaerial etching of underlying bedrock by chemical weathering. This rotted subsurface extends to depths averaging tens of metres, and locally reaches hundreds of metres under the surface. Africa's deep regoliths are an important legacy of persistent erosion surfaces caused by several determinants: repeated uplift and warping of high Africa; seasonal and longer term changes in climates; and bioturbation of biomantles. At more local spatial scales, chemical weathering has lowered local highs

in the land surface, as it created the colluvial mantle (Twidale 1988, 2005; Burke 1996; Taylor & Howard 2000; Johnson 2002; Clarke 2003).

4.5.7 The African Surface, Dambos and Geological Controls on Vegetation

That the African surface invariably overlies deeply weathered mantle, which began to form in the late Cretaceous, has interesting had ramifications on ecological and biogeographical patterns and processes. These ancient land surfaces manifest in interesting edaphic and geomorphological controls, which control patterns and processes overwhelmingly. This especially applies to the Zambezian wetlands of south-central Africa (Williams 1978; White 1983; Timberlake *et al.* 2000). Moreover, Africa's ancient topology determines structuring of savanna vegetation at a continental scale. The miombo woodlands on plateaux contrast against the valleys, pertinently the Luangwa - with its thickets and woodlands, dominated by large expanses of deciduous mopane savanna, *Colophospermum mopane*. Each of these plant assemblages occupy very different erosion surfaces that contrast markedly in geological age (Cole 1963, 1982, 1986). Significantly, Africa's arid corridor most likely expanded and contracted across the Luangwa valley (Chapters 6 & 8). The extensive swathes of Zambezian grasslands are closely associated with dambos and wide, shallow valleys emplaced over deep regoliths. Besides their control over hydrological processes, dambos support significant components of the region's biodiversity (Williamson 1977; White 1976, 1983; Timberlake *et al.* 2000; Moore *et al in press*; Chapter 2).

This local redistribution of weathered sediments has further buffered the landscape from erosion. This has proved critical to the origins and persistence of dambos across the Katanga-Chambeshi region (whose importance was emphasized in Chapter 2). As with the broader aspect of the African surface, these dambos appear to have been planed flat. These porous regoliths exercise important controls over hydrological processes in river catchments. Subsurface waterflow is especially focussed in dambos. In the flatter parts of Angola and Zambia, dambos often straddle interfluves, and are often not connected, or only partially linked, at the surface into fluvial systems. Their partial association with extant drainage topologies is further evidence that dambos are older, residual landforms (McFarlane 1989; Goudie 1999a; Von der Heyden 2004).

The remainder of this section, reviewing geomorphological evolution across south-central Africa, examines the principal events whereby wetlands have originated, or their precursors have been rearranged. I begin with the northerly situated regions neighbouring Lake Tanganyika, and then shift the lens of enquiry west and south in scrutinizing complementary zones of activity. As will become

clear, nearly all these events appear closely correlated, which makes it difficult to treat or understand any one of them as an entirely isolated entity (Fig. 4.1a).

4.6. RIFTING ACROSS KATANGA

4.6.1 Tectonics, Formation and Erosion of the Upemba (Kamalondo) rift and the Katanga Plateaux

Seismicity characterizes the margins of the Congo basin; and this is particularly obvious in the formation of the Upemba (Kamalondo) Trough (Deffontaines & Chorowicz 1991). The Upemba wetlands lie in a Karroo trough, the Kamalondo depression, which Dixey (1946: 365) recognized had been “rejuvenated by additional faulting and warping in post-Pliocene time”. Precise details of the lacustrine history of the Kamalondo depression do not exist, although Bailey (1986) suggested the contemporary shallow lakes and floodplains are vestiges of a formerly contiguous lake.

Dixey (1946) interpreted the Kundelungu Plateau as a residual landform that survived peneplanation. Yet, it is difficult to explain how hanging valleys (characterized by high waterfalls off vertical scarps) have persisted on the Kundelungu (Fig. 4.3). Otherwise, peneplanation of these highlands would have culminated in more completely incised valleys. It appears the pronounced relief of the Kundelungu and Lufira depressions formed contemporaneously with the Kamalondo and Mweru graben, during widespread tectonic activity in the Plio-Pleistocene. Neotectonic diastrophism around the Kamalondo and Lufira depressions means that rifting has been renewed across inherited landforms (Tack *et al.* 2003); and it does not conflict with theories of how the Kundulungu-Lufira complex first formed under tectonic controls in the late Proterozoic, discussed by Porada & Berhorst (2000). New geophysical data not only reveal the importance of neotectonic activity across Katanga, but also underwrite the need to reappraise Katanga’s structural geology. As with the Mweru Rift system, the Lufira and Upemba systems have been profoundly influenced by neotectonic activity since the late Neogene. This has propagated through the southwest extension of the African Rift system across Katanga (Mondeguer *et al.* 1989; Sebagenzi & Kaputo 2002; Tack *et al.* 2003). The significance of this tectonism to the isolation of the Kamalondo graben is discussed below (Section 4.6.4), and again later in this chapter, where indicator taxa point to a prolonged period of isolation of the drainage basin. This constitutes the strongest evidence for the existence of Palaeo-Lake Upemba (Section 4.11.9).

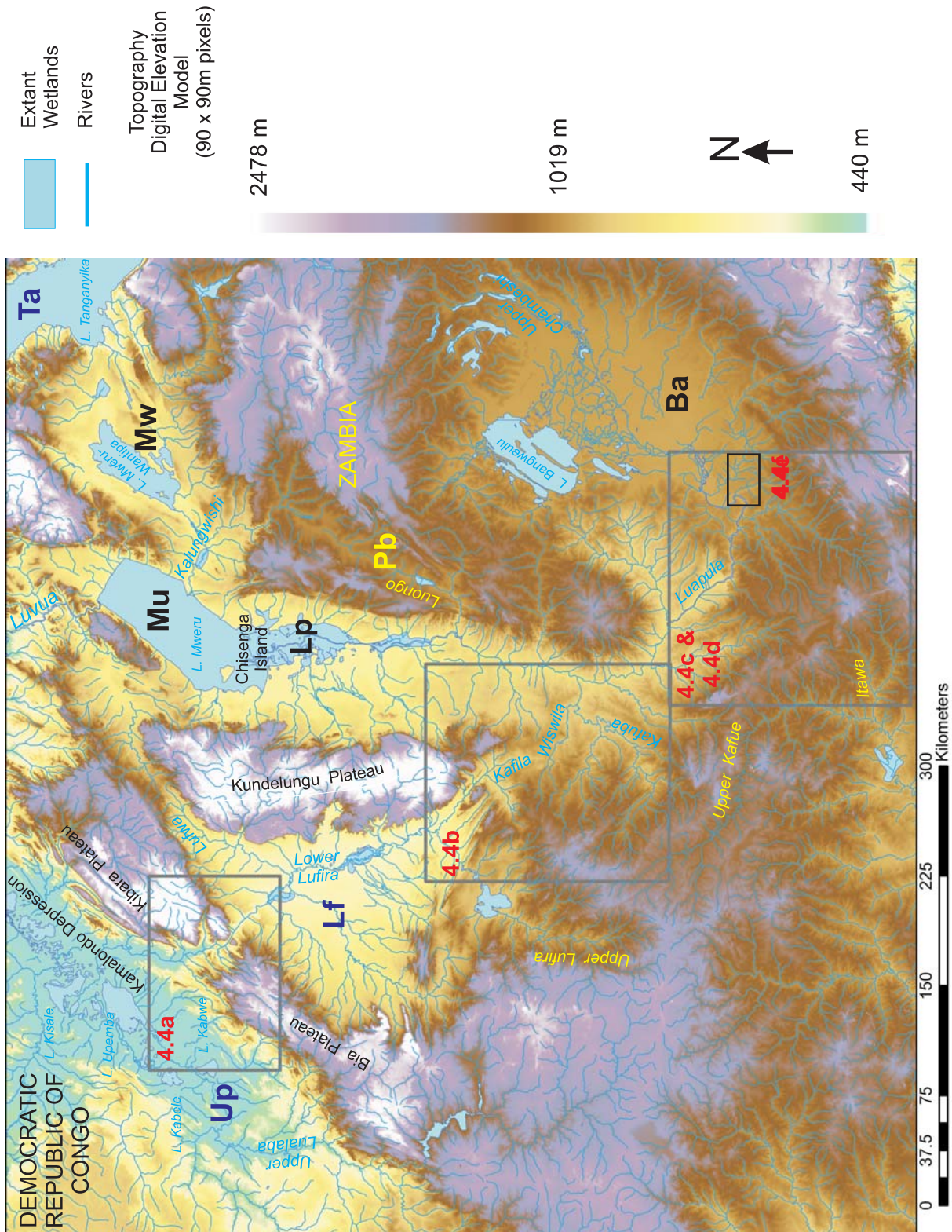


Figure 4.3. Topography (NASA 90m DEM) of eastern Katanga, DRC. The region is bounded by the Congo-Zambezi watershed to the south, the Kundelungu plateau and Lake Mweru to the north, and the Bangweulu basin river to the east. Principal rivers and landforms are labelled. The hypothesized channel of the Palaeo-Kafila is highlighted. It is proposed that a headwater of the Lower Luapula, the Wiswila, pirated the Palaeo-Kafila. Abbreviations follow Fig. 2.2.

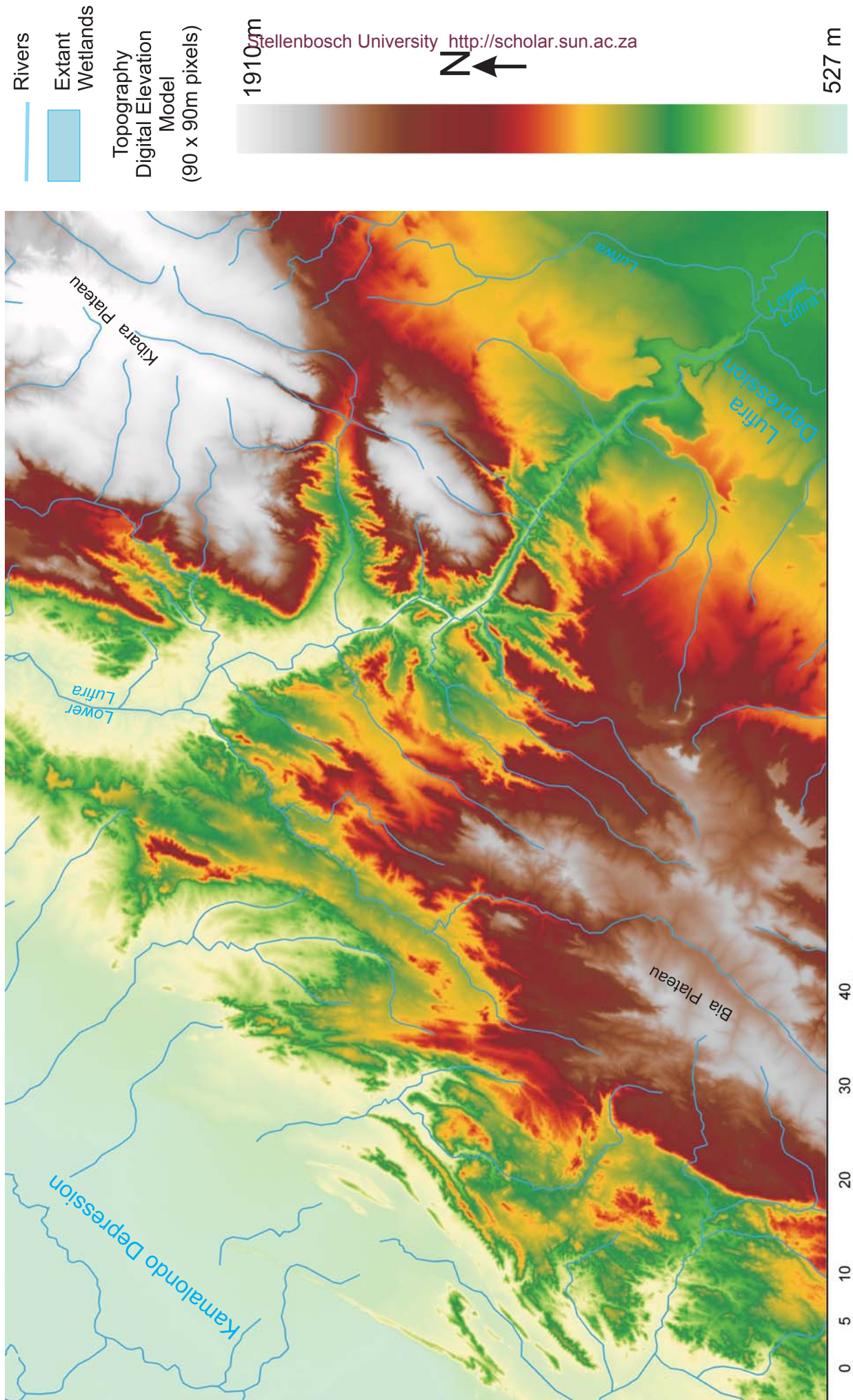


Figure 4.4a. Detail of the steep gorge incised by the Lufira river across the Upemba horst, which is divided into the Bia and Kibara plateaus to the south and north, respectively.

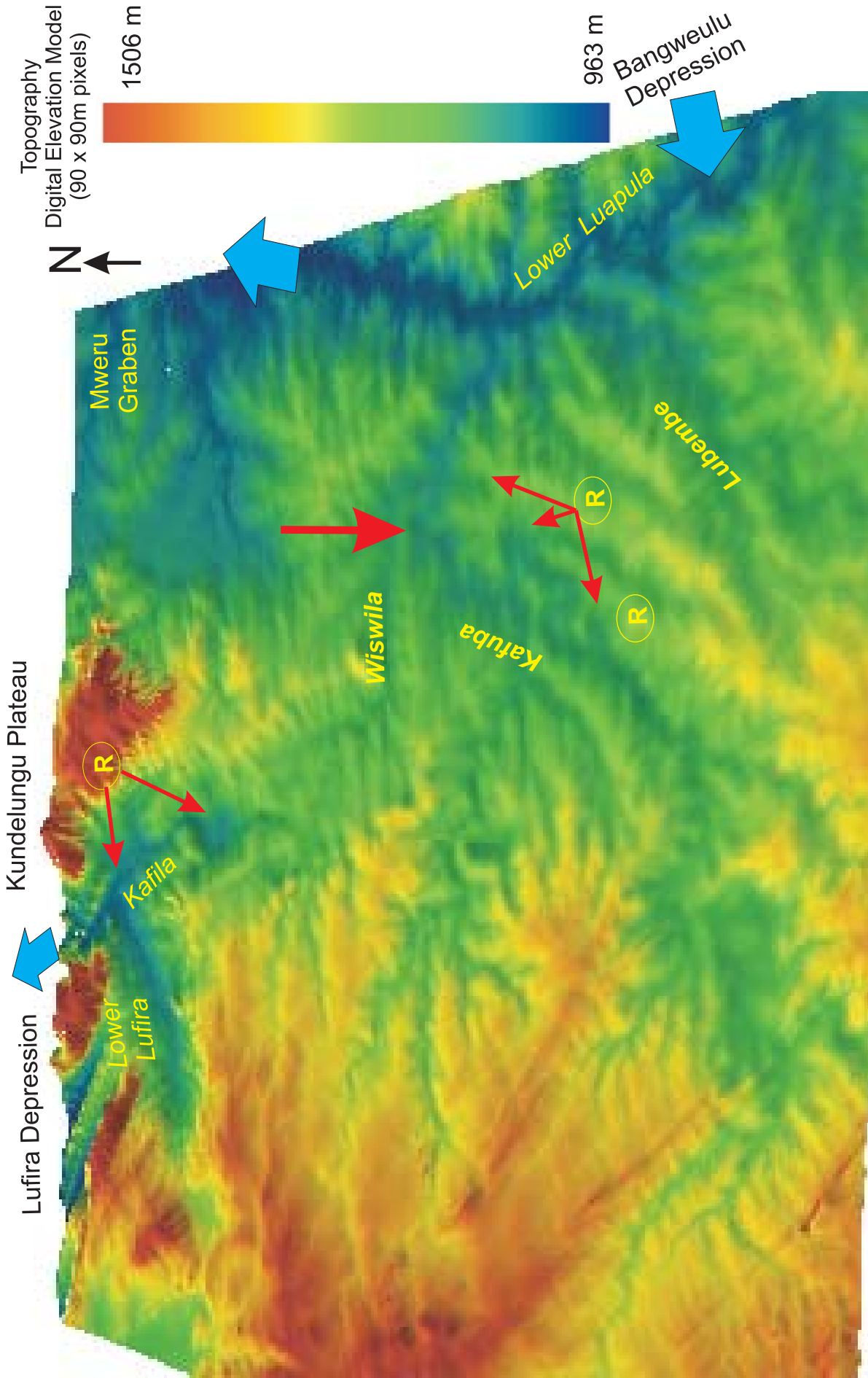


Figure 4.4b. The vertical component is emphasized slightly (z value = 0.001) in this three-dimensional depiction of the Katanga Pedicle, compiled in ArcScene 9.1. The arrow depicts the hypothesized location where scission of the trans-Katanga drainage system occurred. This likely involved headwater erosion by a Luapula tributary, the Wiswila, that pirated the Palaeo-Kafila. The extant Kafila and Wiswila headwaters are distinctly underfit in the Palaeo-Kafila channel (Fig. 4.3). Ria lakes (R with arrows) indicate the senile drainage along this channel. The broad, blue arrows denote directions of extant drainage into and from depressions around the Katanga Pedicle

4.6.2 Plio-Pleistocene Rifting of Lake Mweru and Associated Events

Dixey (1944, 1946, 1955a) concluded that Lake Mweru occupies a shallow rift valley, whose escarpments trend south, then curve southeast where they meet the Bangweulu basin. This hypothesis was confirmed and expanded by Mondeguer *et al.* (1989). Moreover, available geophysical data constitutes convincing evidence that neotectonics has exercised dominant control across this region (as with Katanga to the west). Temperature gradients, and patterns of earthquake activity, point to a zone of crustal instability extending southwest from the rifting associated with the Tangangika-Rukwa-Rungwe-Malawi graben (Sebagenzi *et al.* 1992, 1993). These events have also formed the shallow lakes and floodplains across the Mweru Wantipa region of northern Zambia (Mongeur *et al.* 1989), supporting vast floodplain grasslands described by Vesey Fitzgerald (1970).

Based on the upper limits of perched lacustrine sediments, Dixey (1944) concluded that Lake Mweru was over 103 m deeper than present. It began to drain after the Luvua River captured the lake as its source. Since then, incision by the Luvua has partially drained Lake Mweru. Grading of sediments across the lower reaches of the Luapula created the Kashiobwe Flats. Post-rifting, erosion upstream by the Lower Luapula River and its catchment widened the Mweru graben. Several hanging valleys, notably the Luongo River, testify to the considerable modification of this region through rifting. Balon & Stewart (1983) contrasted the youthful Lower Luongo against the senile upper Luongo River. The Mansa River exhibits a similar topology (Fig. 4.3). Dixey (1944, 1946) suggested that the Mweru rift was warped in the Pleistocene. Significant erosion in the Upper Chambeshi valley was possibly also initiated by uplift that began in the Pliocene, with repetitions through the Pleistocene. Increased erosive capacity of the lower Luapula not only lengthened the Mweru graben, but culminated in important piracy events. The most pertinent to lechwe evolution entailed the capture of the Upper Luapula with its Chambeshi headwaters. This last event appears to have been relatively recent in the chronology of events whereby tectonism has modified landforms around the Mweru graben.

4.6.3 Northeast Zambia, the Bangweulu Flats, and the Upper Chambeshi

Before reevaluating the evidence, it is obviously necessary to consider previous explanations of drainage evolution around the Bangweulu basin. Dixey (1944, 1955a) argued it is remarkably similar to the Lake Victoria basin in east Africa, and proposed that both were formed by crustal warping. Formation of the Bangweulu basin created an endoreic drainage system, sustained in part by the Upper Chambeshi. Upstream of Bangweulu, the Upper Chambeshi valley also contains a significant depression in the shallow, albeit extensive, Bwela Flats. Furthermore, several, smaller, circular depressions (averaging 10 - 20 km diameter) are scattered along the axis of the Upper Chambeshi

valley, northeast of Bangweulu (Dixey 1944). And more significantly, a zone of thinned crustal lithosphere skirts the southern margin of the Bangweulu craton, and underlies the entirety of the Upper Chambeshi valley, including the Bangweulu and extends across lower Katanga (Bonavier *et al.* 1995; Chorowicz 2005, Fig. 4.1a).

The plateau north of the Bangweulu depression is riven with faults, which trend southwest - northeast (Mondeguer *et al.* 1989). These manifest in numerous waterfalls across the Kalungwishi and other north flowing tributaries of Lakes Mweru and Tanganyika (Anonymous 1965). It is tempting to relate this history of rifting around the Mweru graben to better understood events along the Tanganyika and northern Malawi rifts. This began with deepening of the Mpulungu basin around 4 Myr BP (Cohen *et al.* 1993). An early Pliocene age of the Mweru graben would correspond to inaugural rifting of the Rukwa and Songwe graben. It is noteworthy that major rifting activity formed the principal landforms of southern Tanganyika, and those to the south in the Rukwa-Rungwe region. A more recent, significant episode is the widespread diastrophism that is constrained by Rungwe volcanics to 420 - 550 Kyr (Delvaux *et al.* 1992). Its timing and ramifying effects is confirmed by more widespread evidence, in the form of uplifted sediments, extending north along the Albertine rift (Ebinger 1989).

4.6.4 Palaeo-Lake Lufira and a Trans-Katanga Drainage System

Significant deposits of alluvium in the Lufira depression suggest that it was formerly the depocentre of a more extensive catchment. Today, inflow into this large alluvial basin is comparatively restricted. Possibly, a larger catchment debouched through the existing Lufwa river into the Lufira depression. The broad, deep Lufwa valley hosts a minor river today. Yet, down-cutting of the deep (>1600m) Lufira Gorge to divide the Bia and Kibara plateaux, suggests intense and recent erosion followed uplift events since the Miocene. I suggest that a precursor of the Lower Lufira river (here termed the Proto-Lufira) flowed southeast across the Upemba horst, with the Lovoi, and also included likely precursors of what would become the southern tributaries of the modern Upper Lualaba river. One would expect that the Proto-Lufira would have been intimately associated with the Palaeo-Chambeshi river. This means that the Proto-Lufira river likely initiated erosion into the Upemba horst, accompanying Pliocene uplift.

More recent tectonic activity, possibly the Middle Pleistocene Rukwa-Rungwe event (but perhaps earlier) lowered the Kamalondo and Lufira depressions. This event is invoked to have created an endoreic drainage system contained within the Kamalondo depression (which would have formed the ancient lake proposed by Banister 1986). This is termed Palaeo-Lake Upemba. I hypothesize this

tectonism not only fragmented the Proto-Lufira river, but reversed directions of flow in the resulting rivers. This event was of biogeographical significance, because endoreic drainage systems prevailed after this uplift, each centred within its respective graben. This stage persisted until the Lufira reestablished its flow across the Upemba horst, now flowing northwest into the Kamalondo depression, and deepening the Lufira Gorge (Fig. 4.4a). The crescent-shaped delta debouching into the eastern edge of the Upemba Swamps points to recent and significant erosion upstream (see frontispiece to Chapter 6). It is further possible that the link between the Upper and Lower sections of the Lufira river have been broken and reconnected more than once, in concert with tectonic activity along the Upemba horst.

I suggest the significant deepening of the Lufira Gorge possibly occurred at the stage when the Upper Chambeshi was linked with the Lufira. Thus, a river of considerable size (even under arid climates) incised the Lufira Gorge. Persuasive evidence for the former geomorphological unity of this trans-Katanga drainage system is a large fossil channel, today occupied by the underfitted Kafila River. I propose that its precursor - the Palaeo-Kafila - linked the modern Lower Lufira contiguously through to the Palaeo-Chambeshi system (Fig. 4.4b).

This configuration of the Palaeo-Kafila was disrupted by a headwater stream of the Luapula, backcutting from the catchment into the deepening trench of the Mweru graben. Piracy of the Palaeo-Kafila probably occurred near Kibaya. This was an important event toward creating the modern topology of the Lower Luapula. There is a distinct capture elbow where the Kafubu (its tributary the easterly flowing Wiswila that drains the fossil channel of the Kafila-Lufira) joins the Lower Luapula (Figs 4.3 & 4.4b). It is interesting to note that evidence (presented below) suggests this proposed trans-Katanga drainage system was linked with the Palaeo-Chambeshi. Thus it not only reached the Kalahari basin, but extended far to the west – to the Etosha and Cuanza near the Atlantic coast (Figs 2.1 & 4.1a). Its existence, followed by scission, is invoked below to explain dispersal and vicariance of a suite of indicator species. I suggest this break up of the trans-Katanga system occurred before deepening of the Lower Luapula valley had extended southeast to ultimately capture the Palaeo-Chambeshi.

4.7 THE CONGO-ZAMBEZI WATERSHED, AND SCISSION OF THE PALAEO-CHAMBESHI SYSTEM

4.7.1 Previous Studies and New Evidence

Dixey (1943a) concluded the Southern Equatorial Divide to be an ancient landform. This interpretation needs to be reconciled with evidence for major tectonic activity propagating southwest across the region from the Albertine rift. Pertinently, widespread rifting activity began in the late Neogene, and has persisted through the Quaternary. Reevaluation of this geological history, in deserving detail, will entail many ambitious studies. So I focus on events and patterns, along parts of the Southern Equatorial Divide, most pertinent to biogeographical aspects of this review. One objective here is to identify the former channel(s) where the Palaeo-Chambeshi traversed the Congo-Zambezi divide. The overarching catalyst for this exercise is to appraise and clarify a keystone hypothesis pertaining to drainage evolution in the region, which was first proposed by Dixey (1943a, 1944) and reaffirmed by Jackson (1962, 1986). Jackson (1986, 2001) identified the “Mukuku Hook” as representing the location where the Lower Luapula pirated the former southwest course of the Palaeo-Chambeshi River. The 90m DEM reveals hitherto hidden details of landscape evolution across this southeast edge of the Mweru Rift System. The landforms revealed by these new datasets confirm that Quaternary landscape evolution, as represented by drainage features, has been more complex than originally envisaged by Dixey and Jackson.

The chances appear remote that similar evidence of wind-gaps and other relict signatures of antecedent drainage systems have survived active erosion within the Upper Kafue to the south. Fortunately, landforms within the relief straddling the Congo-Zambezi watershed (corresponding to the international border between the DRC and Zambia) represent vestiges of the African surface of much greater age. These appear to have been only locally modified as the Upper Kafue and Chambeshi-Luapula drainages established their current configurations.

One's first impression from studying the available spatial data (especially topologies of drainage in the 1: 1 000 000 US Defense dataset, and 1: 100 000 orthophotos) is of remarkably senile drainage systems traversing very gently-sloping terrain. It suggests the meandering river channels across the Katanga Pedicle were established after slight crustal flexure accenuated the South Equatorial Divide. It is revealing to analyse extant drainage patterns, and related landforms, to try and discern where geomorphological activities have structured the landscape. This approach can reveal cryptic evidence for tectonic activity (Schumm *et al.* 2000). For example, Jackson *et al.* (1996) used drainage patterns across a tectonically active area to identify cryptic patterns of faults and folding. Similarly, Vétel *et al.*

(2004) used anomalies in drainage patterns to detect subtle patterns of neotectonic activity, and deeper tectonic controls on drainage, in the Turkana rift valley.

So, it is not surprising that the combination of the high resolution DEM and orthophotos reveal striking signatures of neotectonic activity around the margins of the Bangweulu basin. These include many anomalous flares in the drainage, which manifest in localized widening of river channels. Moreover, overall, a marked orientation in geometry of regional drainage manifests in rectilinear topologies of streams, and also contorted catchments. According to overall drainage geometry (Summerfield 1991; Schumm *et al.* 2000) dense concentrations of anomalous flares allied with stream morphologies, in this local study area, all point to pronounced geological control over drainage. And I invoke control by relatively recent tectonics. Overall, the geometry of the drainage reveals lineaments that point to a network of faults, trending SW-NE across the Katanga pedicle and the southern margin of the Bangweulu basin (see frontispiece to Chapter 8). This inference conforms with the detailed mapping of the structural geology of the Ndola area of Zambia by Moore (1967), bordering the southwest edge of the Katanga pedicle. It is instructive to compare the drainage morphology across the Katanga pedicle (Fig.4) with the dendritic drainage topology of the Cuanza headwaters (Figs 4.5 & 4.6), whose streams have recently eroded their catchment.

Dixey (1943a) drew attention to a wind-gap northeast of Ndola, which he suggested represents the abandoned channel of the former course of the Chambeshi, when it formed the headwaters of the Proto-Kafue River. This windgap is superimposed on the Mufilira anticline, and may represent the former passage of the Palaeo-Chambeshi River across the Congo-Zambezi watershed. One presumes that the Palaeo-Chambeshi then flowed through the channel of the Kafulafuta River, today a major southwesterly tributary of the Upper Kafue. Today, this river, the Muniengashi, has reversed its flow (northeast), as a south bank tributary of the Luapula River. The oblique axis of its northbound channel contrasts against the southwesterly flow of the Upper Luapula. Prior to reversal in its flow, I suggest this river flowed southeast through the Kafulafuta valley to incise this windgap. Very recent erosion has deepened both fossil channels after their uplift. This explains the raised lip at the watershed over the Mufilira syncline (Fig 4.4c). My reconstruction is contingent on what direct dating techniques (using cosmogenic isotopes) of these fossil and new landforms will reveal, in tandem with fieldwork. This is vital to test what are presently hypotheses about where palaeo-channels existed, and to further delimit the sequence of events. So this model of what happened to the Palaeo-Chambeshi drainage system is one that future geomorphic studies can falsify and improve on.

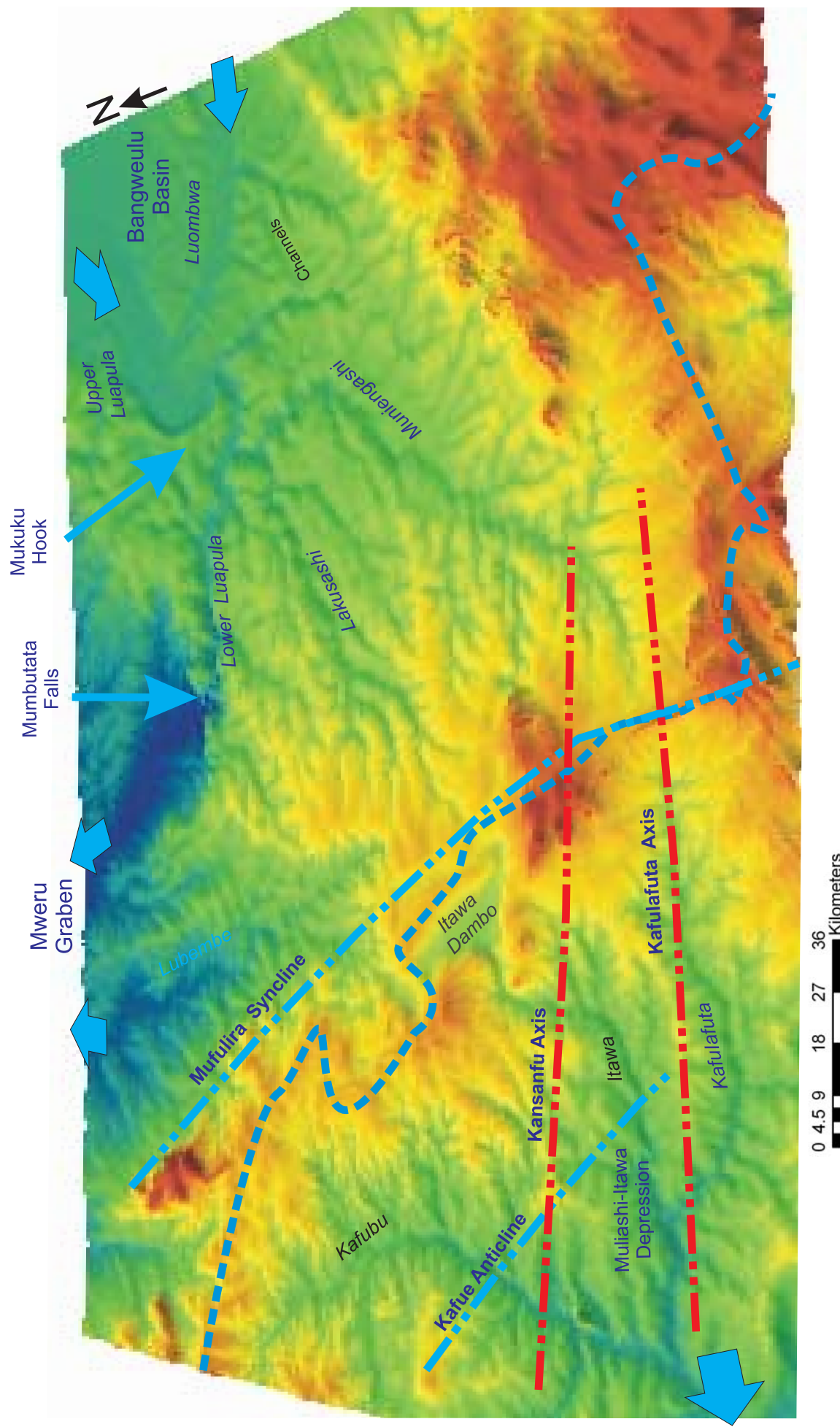


Figure 4.4c. High resolution detail of the Congo-Zambezi watershed in relation to principal structural controls of the landscape north of Ndola in Zambia. Note the Itawa dambo straddling the extant axis of the Congo-Zambezi watershed (blue, dashed line) along the southern edge of the Katanga Pedicle, DRC. Orientation of structural features denoted by bold, dashed lines. Geological data summarized from Mendelson (1961), Moore (1967) and Lepersonne (1972). The Itawa dambo straddling the Congo-Zambezi watershed is inferred to represent a fossil drainage channel of a southerly flowing river. The vertical component is emphasized slightly (z value = 0.001) in this three-dimensional depiction compiled in ArcScene 9.1.

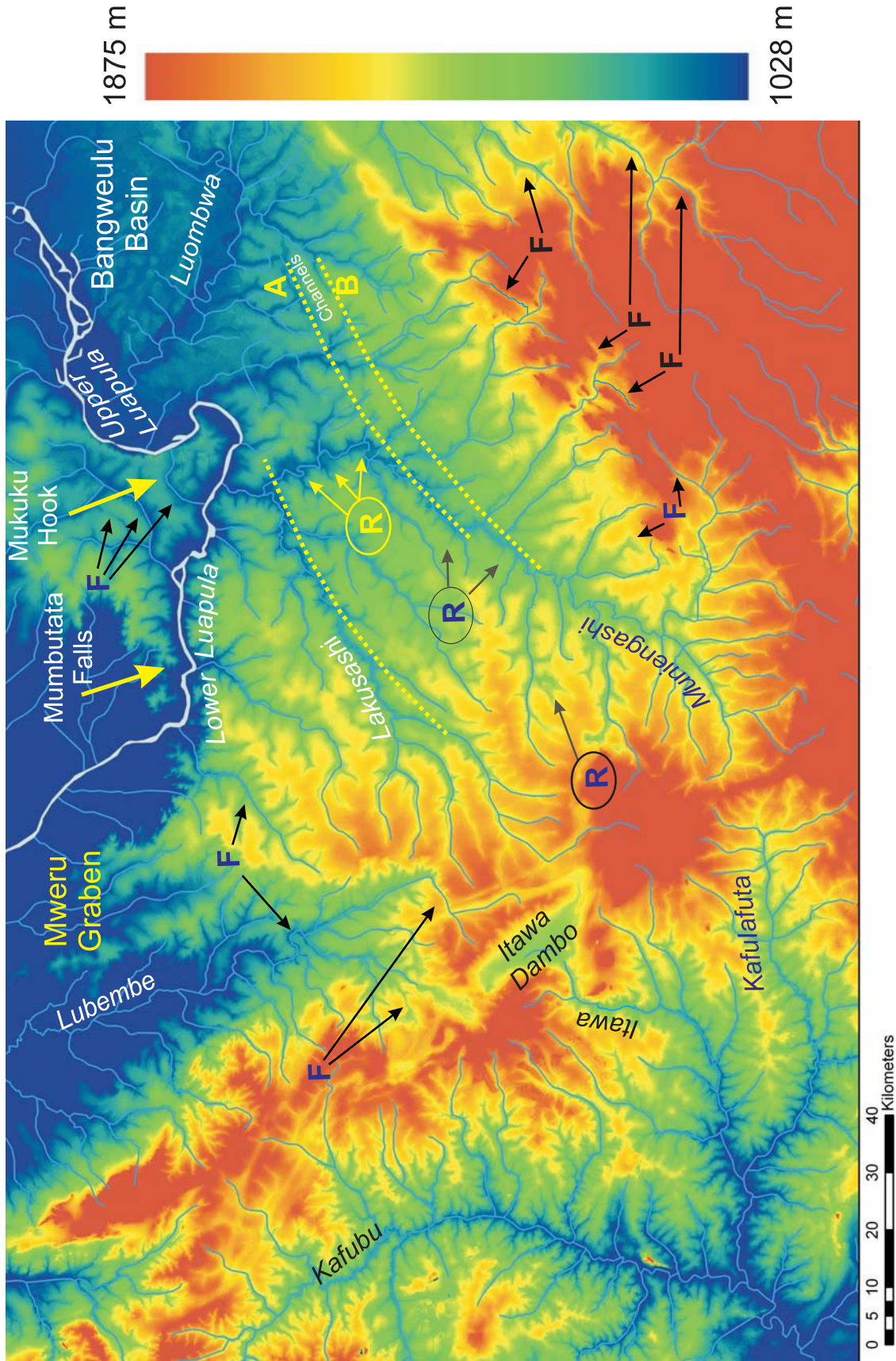


Figure 4.4d. The same region, detailed in Fig. 4.4c, depicted here at high resolution to illustrate finer detail of drainage. Southwest-northeast trending fault lines have been exploited by drainage lines. Representative examples (F) are arrowed. The existence of a pronounced fault is also invoked to account for the Mumbutata Falls across the Luapula river. Dotted yellow lines depict alignment of principal river channels, invoked to reflect the topology of former courses of the Palaeo-Chambeshi drainage system. Anomalous Flares (labelled “R” and arrowed) have formed in zones of comparatively senile drainage, that likely reflect local pooling along rivers in zones of local subsidence. This effect is especially pronounced in zones of Anomalous Flares along the Muniengashi, south of the Luapula. Here, the meanders of the Muniengashi are more pronounced, compared to the river’s topology upstream and downstream of this zone. The pronounced bend on the extant Luapula, termed the “Mukuku Hook”, appears to represent an artefact of piracy of the Palaeo-Chambeshi river by the Lower Luapula River.

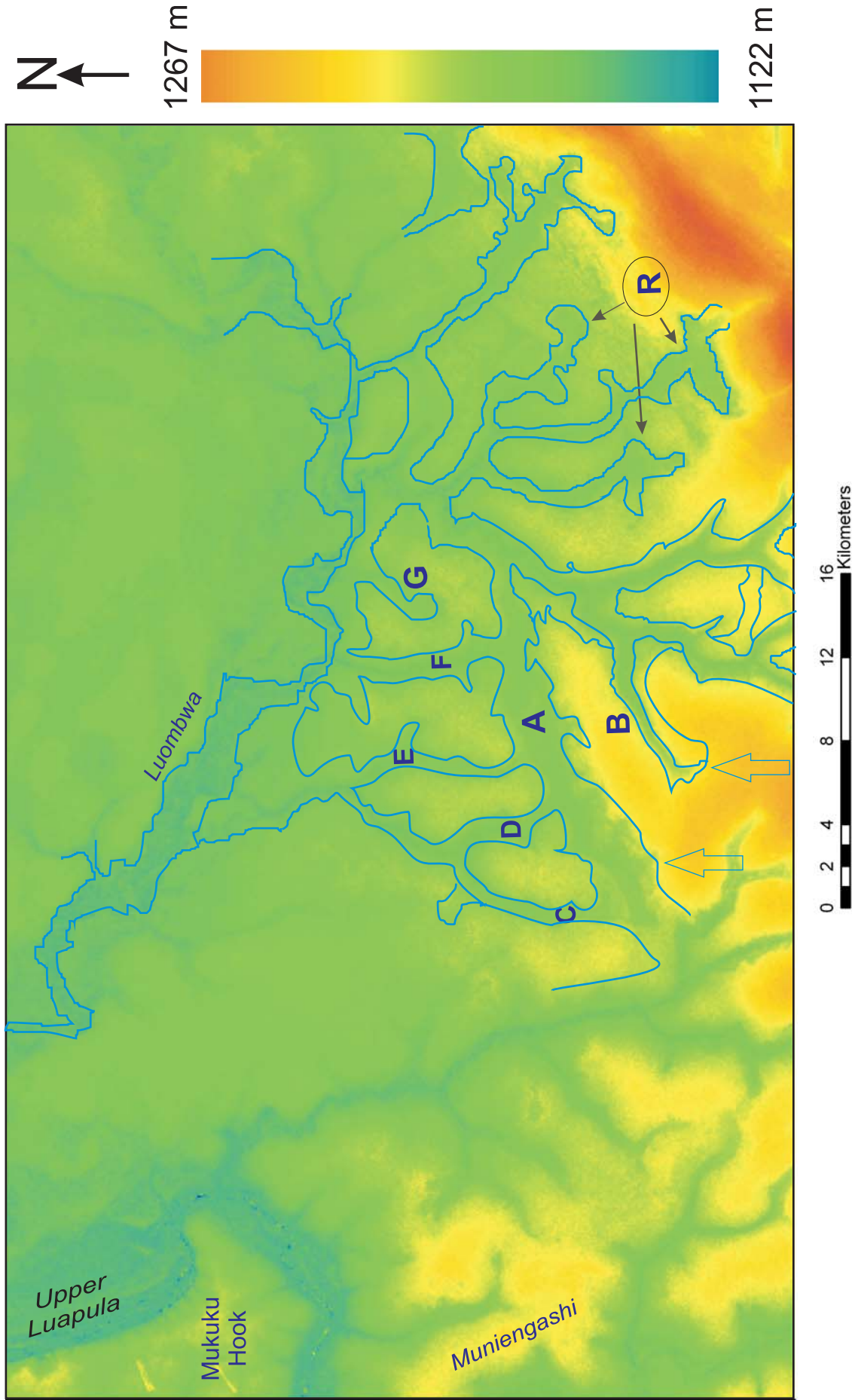


Figure 4.4e. High resolution detail of part of the scene in Fig. 4.4d, along the southwest edge of the Bangweulu basin, south of Mukuku Hook. Two abandoned channels (labelled A and B) lie southwest of the Luombwa river, and due southwest of Mukuku Hook. The larger (A) is over 3 km wide and at least 18 km long. These are inferred to represent former courses of the Palaeo-Chambeshi river, prior to its piracy by the Luapula. Their relative positions also suggest sequential migration of the principal drainage axis to the northwest. These channels and Anomalous Flares (R, arrowed) are invoked to reflect artefacts of strong tectonic control over drainage evolution in this portion of the Bangweulu basin. Outlines of abandoned channels and Anomalous Flares were traced from 1: 100 000 orthophoto labelled Kabunda (Department of Geology, Royal Museum of Central Africa, Tervuren, Belgium).

Additional evidence for antecedent drainage patterns in this region do not appear to have been reported. This especially applies to a “donut-shaped” perched dambo straddling the Congo-Zambezi watershed to the northeast of the town of Ndola, north Zambia. Today, this dambo forms the source of the Itawa stream, which contained in the Muliashi-Itawa Depression, flows SSE toward the Upper Kafue River, (Moore 1967, Figs 4.4c,d).

This dambo is unusual in two respects. One is its topology, over 5 km wide. Secondly, it straddles an ancient watershed, but has escaped erosion. Morphology of the Itawa dambo could merely reflect local weathering in a karstic landscape. Yet its location in relation to regional drainage suggests the landform might represent at least one fossil river channel. Its alignment to the Lubembe stream suggests the Itawa dambo corresponds to former passage of a major drainage system. Its channel widened in the dolomite, compared to surrounding harder rocks, to erode the channels over 5 km wide. Either way, it clearly constitutes a drainage channel under strong geological control. I suggest the Itawa dambo represents where a significant river flowed southwest across the Mufilira Syncline. Since then the Lubembe has reversed its course to the north as a tributary of the Lower Luapula (Figs 4.4c,d). Detailed fieldwork is required to elucidate the geological history of the Itawa dambo, with respect to structural geology, and antecedent drainage systems.

The very flat landscape southeast of the Mukuku Hook contains a preserved drainage channel, at least 4 km wide and 20 km long (labelled A), with the smaller vestige of a parallel channel (B) to its south (Fig. 4.4e). It exhibits an interesting association with channels (C-F) trending north-south. I suggest channels A and B represent abandoned courses of a river that flowed southwest, associated with north bank tributaries (C-G, Fig. 4.4e), which drained a northern catchment. Their juxta-positioning can be explained by the migration of principal drainage channels (then trending NE - SW) to the northwest. Here, existing stream channels may have been adopted and modified, progressively, by the southwesterly flowing river. Its northward migration was tracked by northern tributaries, but erosion and sedimentation of the principal river, when flowing in channel A, quite obviously obliterated their antecedent connections with channel B. I invoke a tilting of the landscape to the northwest, which accompanied progressive deepening of the Mweru trough to explain sequential abandonment of drainage channels, as evident southeast of Mukuku Hook (Figs 4.4d,e). (These fossil channels are easily seen on the frontispiece to Chapter 8.)

Today, the penultimate stage in this evolution is represented by the position of the Luapula River north of these fossil river channels. Rifting of the Mweru graben has been associated with its subsidence

extending southeast to affect the raised western and southern lips of the Bangweulu basin. Radical alterations of drainage culminated in river piracy by the Lower Luapula. The evidence for channel abandonment suggests this only occurred after the channel of the Palaeo-Chambeshi had reached the position where the Upper Luapula is today, leaving antecedent channels to the southeast (Fig. 4). These events along the western edge of the Bangweulu basin likely represent local effects of regional tectonics that affected the entire subcontinent (Sections 4.5 & 4.6). It is instructive to look west from the Katanga-Zambian border to the Southern Equatorial Divide in Angola, where evidence of river captures have been relatively well preserved (Section 4.9).

4.8. DRAINAGE EVOLUTION ACROSS THE SOUTHERN EQUATORIAL DIVIDE

4.8.1 Kasai-Upper Zambezi River Captures

Veatch (1935) first suggested that the Kasai had pirated headwaters of the Upper Zambezi. The geomorphology of the region was studied in detail by Bell-Cross (1982). Here, the topology of the Kasai drainage exhibits a parallel geometry. Its west-east trending drainage parallels the northern lip of the Cameia depression. Bell-Cross (1982) emphasized that the Kasai is a steeper, faster flowing river compared to the senile nature of the Upper Zambezi. Figure 4.5 reveals the marked contrast between the drainage density in the Cameia depression, compared to the Kasai in the north. The senile drainage around the Cameia depression contrasts against the distinctly rectangular drainage pattern of the Kasai's headwaters north of the extant watershed (Fig. 4.6).

4.8.2 Evolution across of the Cuanza-Cubango Watershed

A second zone of significant rearrangements of the drainage is contained in the cup-shaped catchment of the Cuanza's headwaters. Here one sees textbook examples of both river piracy and beheading; where Cubango headwaters; whereby captured by the Upper Cuanza River (Fig. 4.5). Further note how the range of lechwe antelopes extends north across this zone into the Cuanza drainage system (Fig. 4.6).

4.9 THE KALAHARI BASIN AND ITS PALAEO-LAKES

"In southern Africa the name Kalahari refers to a structural basin, a group of sediments and an ill-defined desert region; all of which are intimately linked yet also possess distinct characteristics. There is little doubt that environmental changes have played an important part in the evolution of the Kalahari in all three of these contexts, but over differing time-scales and spatial extents. A major issue in unravelling the key factors in the evolution of the Kalahari has been to distinguish the consequences of climatic changes from those due to exogenic factors, particularly those resulting from geomorphic developments that have ensued from the

establishment of the present tectonic setting, which can be traced to the break-up of Gondwanaland." D. S. G. Thomas & P. A. Shaw (1993: 97)

4.9.1 The Kalahari Basin, Okavango Graben and Palaeo-Lakes in northeast Botswana

It is important to distinguish the Kalahari desert and basin (Fig. 4.1a) from the Mega-Kalahari which extends further north across the Congo basin (Thomas & Shaw 1991). Evidence for geomorphological evolution in the Kalahari basin can be traced far back into the Cenozoic. This history has involved complex rearrangements of rivers, lacustrine sediments, and aeolian sands. Its original formation was probably initiated in the Late Cretaceous and perhaps earlier in the Mesozoic by downwarping of a major portion of the continental interior. Kalahari group sediments infilled this basin through the Cenozoic as a shifting mosaic of inland deltas deposited sediments up to 450m thick (Haddon & McCarthy 2005). These changes have been strongly controlled by the underlying older country rocks, and especially regional landforms expressed as repeated continental uplift and warping, all focused along epeirogenic axes (du Toit 1933; Moore 1999). Tectonic activity has exercised recurring control over the timing and localization of these river systems terminating in the Kalahari basin. It is important to note that the Okavango and Chobe swamps occupy a shallow rift valley extending northeast, where it is contiguous with the Kafue Basin (Figs 4.1a & 4.7a). Thus, today, the Barotse, Okavango and Chobe-Linyanti wetlands represent extant representatives of this history of landscape evolution that entailed complex events. Through the Quaternary, the northeastern part of the Kalahari basin has formed a theatre of radical changes in drainage systems, involving large lakes and long rivers. This history has entailed an intricate interplay of lake tenancy in concert with rearrangements of endoreic rivers, driven by climate and tectonics (Thomas & Shaw 1991; Moore & Larkin 2001; Haddon & McCarthy 2005). This involved not only the Upper Zambezi, but also connections with wetlands today isolated in Katanga and Zambia (Bell-Cross 1982; Cotterill 2004, 2005, Section 4.6).

Seismic activity across the Okavango delta has been invoked as an important control over its Quaternary evolution, and recent earthquakes confirm current activity. The structure of these underlying fault systems are inferred from seismic focii and surface geology. The latter exhibits especially striking evidence of the principal faults in remote sensed geospatial data (Gumbrecht & McCarthy 2001; Fig. 4.7a-b). Through the past four decades, intensive research confirms that the Okavango, although the largest extant wetland in the Kalahari basin, represents a young, transient landform - the culmination of a long history of inundations and desiccations of the graben, in which many large endoreic rivers have supported major wetlands (Wayland 1950, 1954; Grove 1969; Cooke 1976, 1979). Their fossil deltas testify to their tenures, as represented in how the Palaeo-Chambeshi system formed the Machili Flats (Section 4.1, Figs 2.1 & 4.7a-b). These studies further revealed that

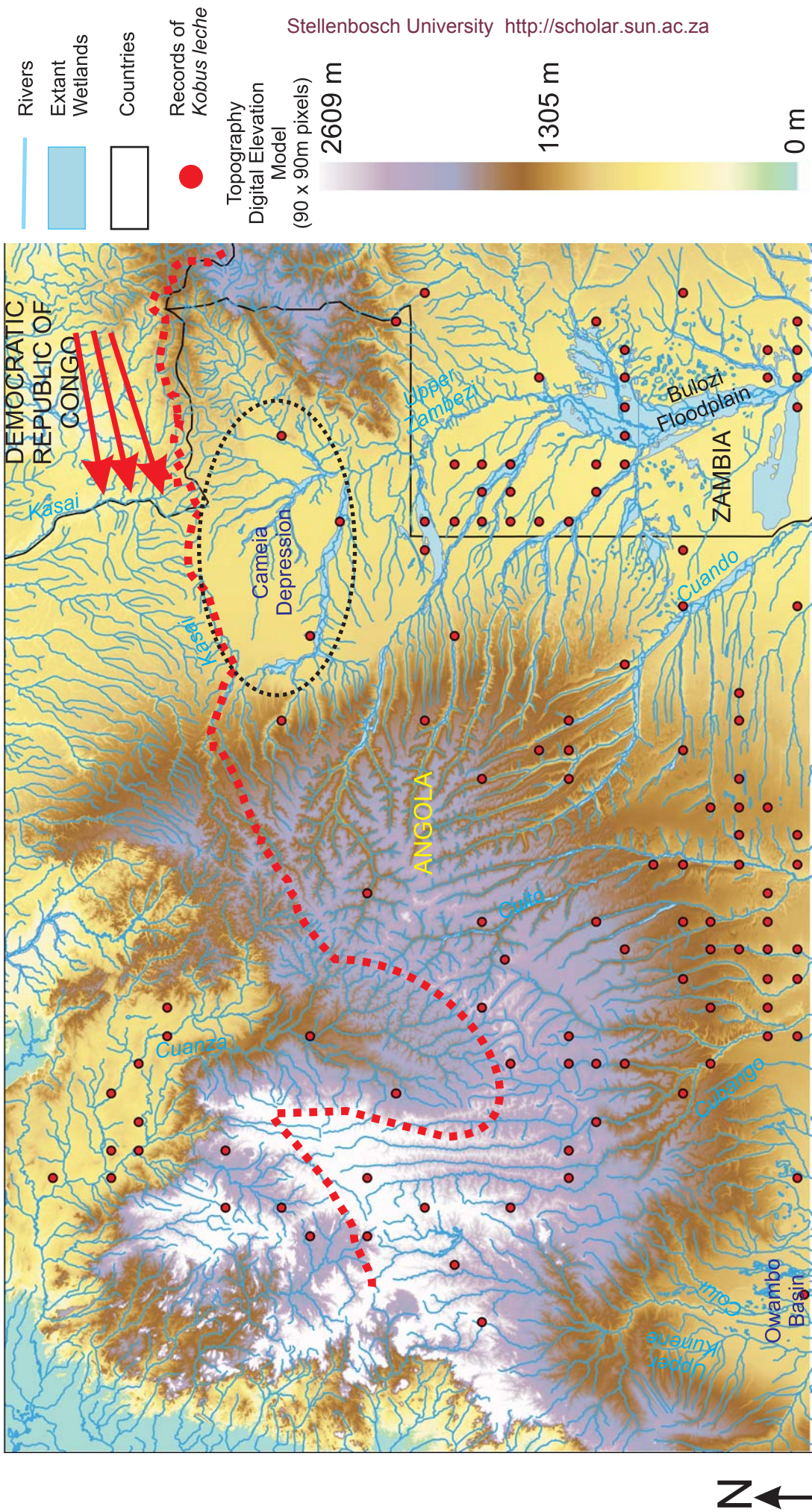


Figure 4.5. The watersheds of the Angolan plateau dividing the headwaters of the Cubango, Kunene, and Upper Zambezi from the north flowing drainage of the Congo and Cuanza basins. Lechwe antelopes, *Kobus lechwe s.s.*, formerly occurred widely across the shallow valleys south of the Great Equatorial Divide (red dotted line), and also along the valleys of the Upper Cuanza and Upper Kunene rivers (Chapter 2, Fig. 2.2.). Red arrow denotes related capture elbows, suggested by Veitch (1935) and Bell-Cross (1982) to represent sequential piracies of Upper Zambezi headwaters by the Kasai river. This event has been invoked to explain dispersals of several species of fishes into the drainage systems of south-central Africa (Section 4.11). Aspects of drainage evolution around the headwaters of the Upper Cuanza river is detailed in Fig. 4.6. The Cameia depression (denoted by the dotted line) may previously have contained a more extensive lake, when impounded by tectonic activity.

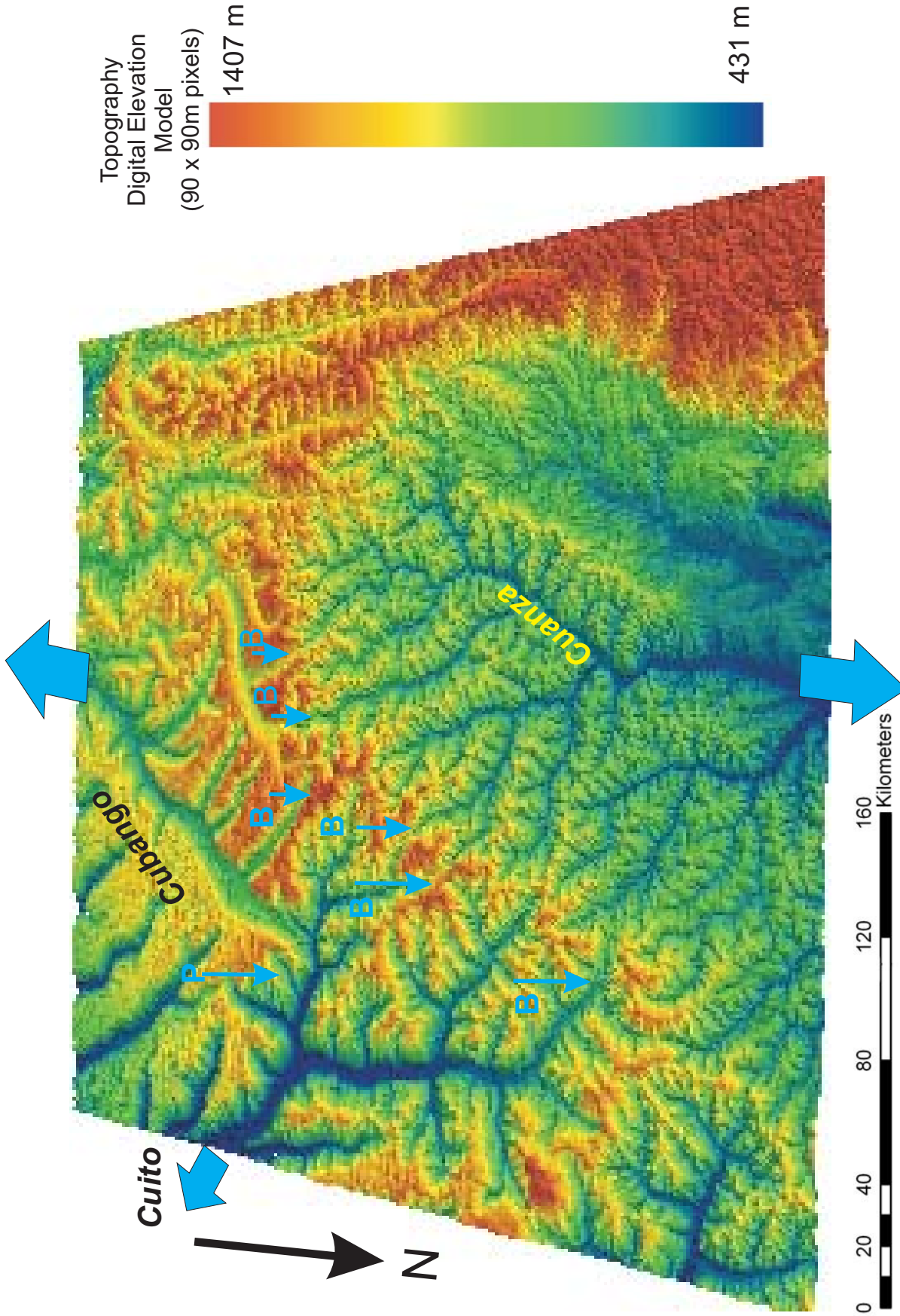


Figure 4.6. Detailed topography of the headwaters abutting the Cuanza-Cubango watershed in western Angola. The vertical component is emphasized slightly (z value = 0.001) in this three-dimensional depiction of ArcScene 9.1. The arrows (B) depict channels of the southerly flowing headwaters of the Cubango, which have been beheaded by the northerly flowing Upper Cuanza. Note the channels of both systems are still contiguous. A distinct signature of river piracy is depicted by the arrow (P); where a southeasterly headwater of the Cuito river (incising at a slightly lower elevation) has captured a source of the Cubango.

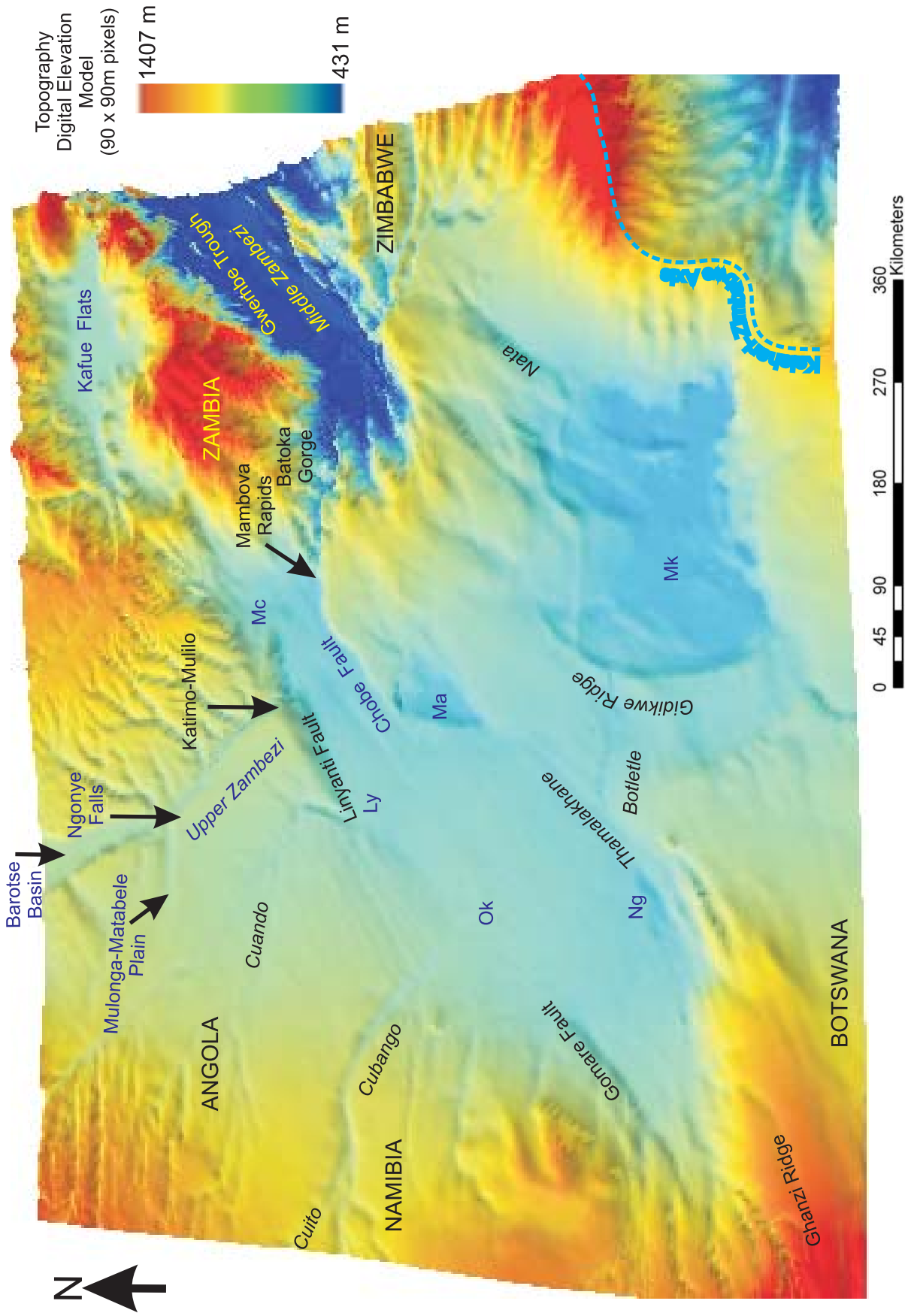


Figure 4.7a Detailed topography of the Okavango-Kafue graben in northeast Botswana which extends northeast into central Zambia. The principal fossil-lacustrine formations in northeast Botswana are indicated by fluctuating shorelines formed by fluctuating palaeo-lakes: Palaeo-lake Makgadikgadi (PLM), 945m maximum (a); Palaeo-lake Thamalakthane, 936m (b); and smaller lakes at 924m (c); 920m (d); and 910m (e) in the Chobe (C), Linyanti (L), Mababe (Ma), Makgadikgadi (Mk) and Ngami (N) sub-basins (modified after Thomas & Shaw 1991). Concentrations of stone tools, representing hominid living sites, are preserved within these shorelines. As discussed in detail in Chapter 5, these artefacts were knapped from silcretes that had already formed fossil lake floors during the Early Stone Age (ESA) and Middle Stone Age (MSA), and reflect PLM and PLT, respectively.

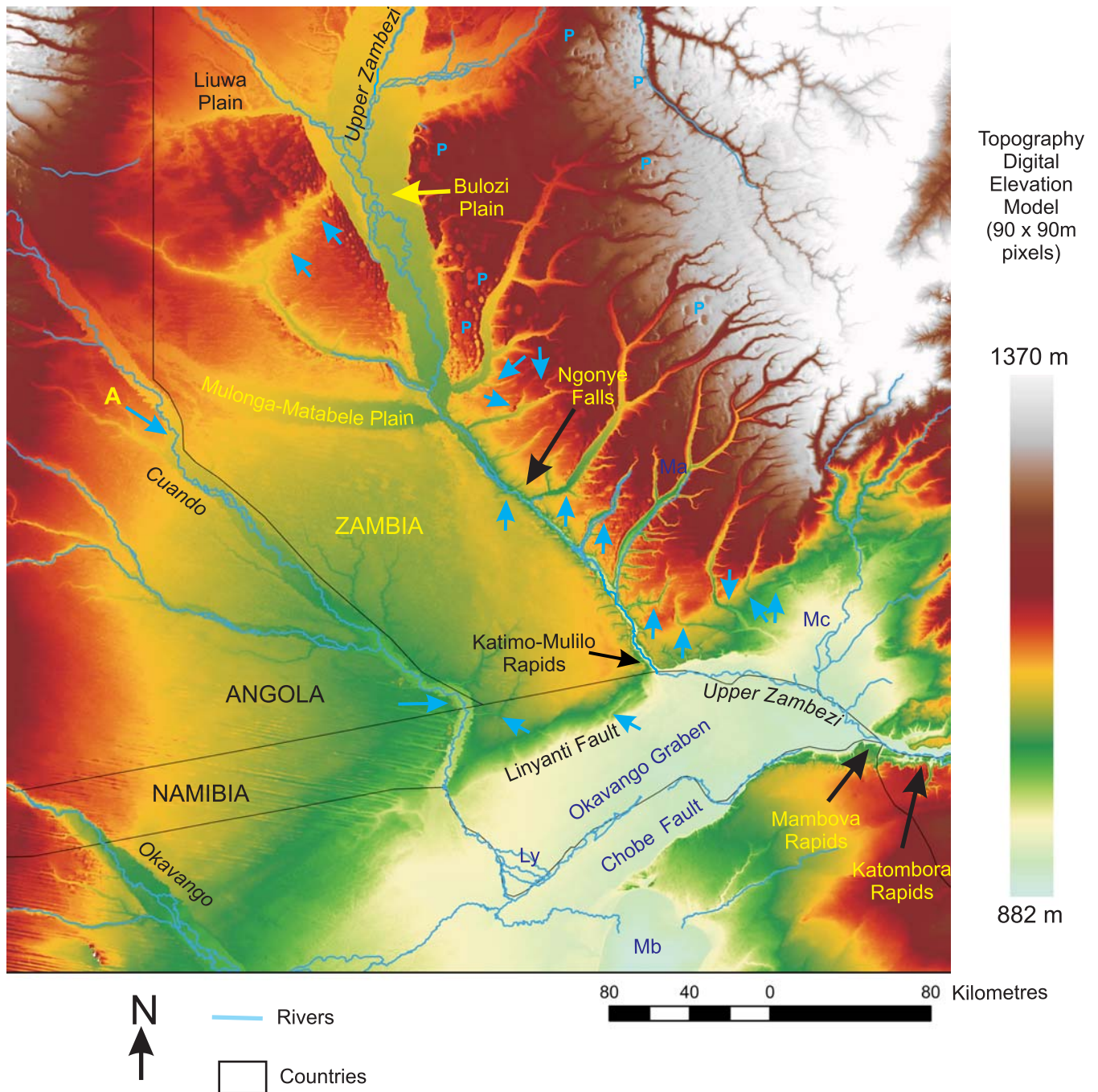


Figure 4.7b. Details of landforms that link the Buluzi depression and Okavango graben. The Mulonga-Matabele plain is interpreted as an abandoned course of the Cuando river, from its tenure as an Upper Zambezi tributary. The Cuando then abandoned this course to flow into the Okavango graben. The sharp elbow in the course of the Cuando (arrowed at A) is inferred to represent distinct fault control at this point, immediately west of the Matabele-Mulonga plain. The blue arrows point to sharp changes in the topologies of rivers, which are invoked to represent strong structural control by lineaments and faults. Note the clusters of pans (labelled P) formed across the vast deposits of Kalahari Sands east of the Upper Zambezi valley.

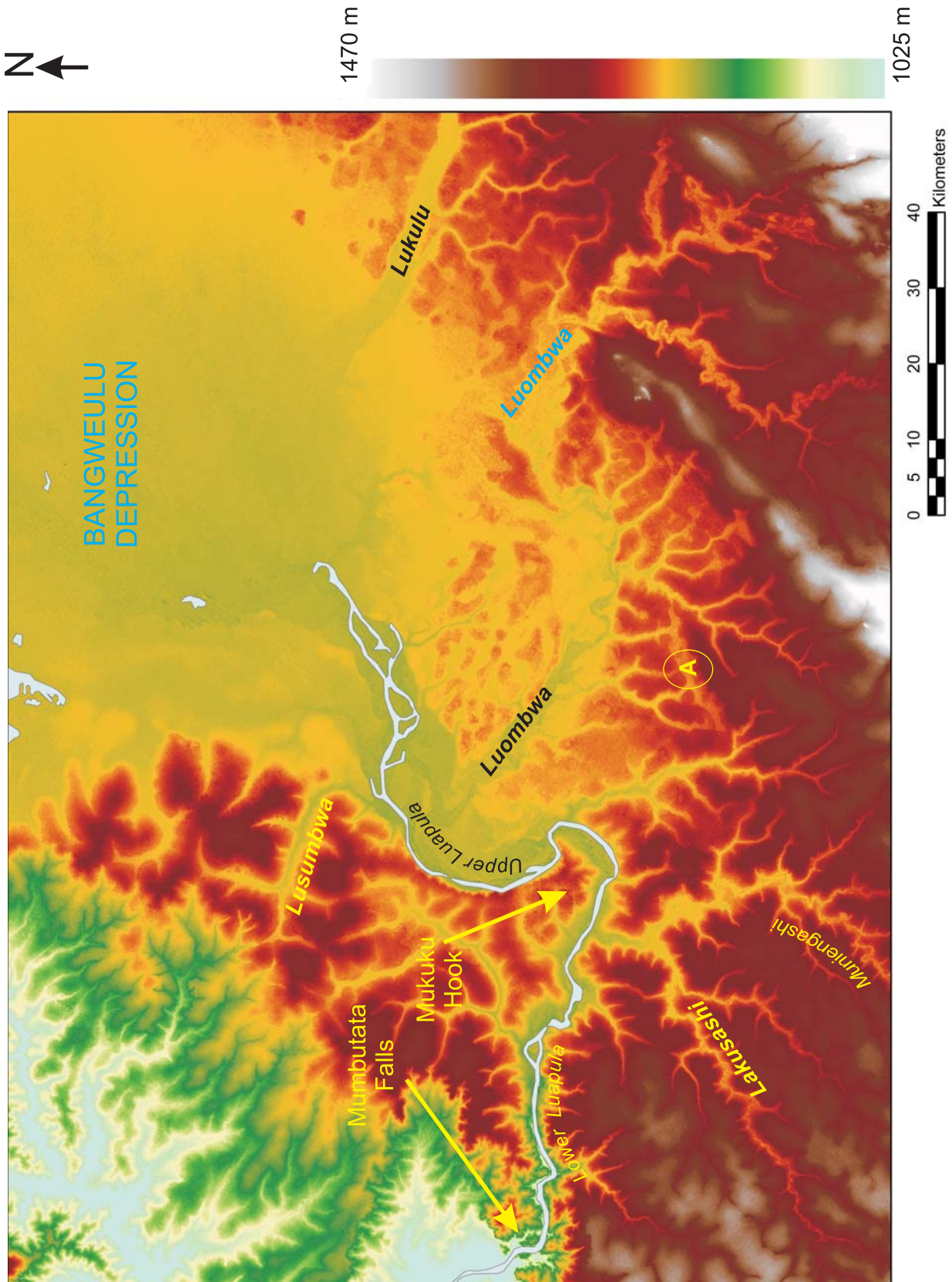


Figure 4.7c. Topographic detail of the southwest portion of the Bangweulu depression, depicting many of the landforms illustrated in Fig. 4.4. The swollen channels of the Luombwa and Lukulu rivers, debouching on to the Bangweulu floodplain, exhibit similarities to that of the Matabele-Mulonga plain adjoining the Buluzi floodplain (Fig. 4.7b).

the three principal basins in northeast Botswana supported different large shallow lakes at various stages through the late Cenozoic. Evidence for their persistent inundation is in the form of concentric strandlines and fossil shorelines (Cooke & Verstappen 1984; Thomas & Shaw 1991, Fig. 4.7a-b). Mapping of co-temporaneous sediments reveals no less than four episodes of inundation (Fig. 4.7a-b, Chapter 5), which are inferred to have formed distinct lake stages (Thomas & Shaw 1991). Their existence reflects that drainage had been impounded, repeatedly, within these depressions. This entailed control over the channels of the Upper Zambezi and Cuando rivers by uplift by the active Chobe Fault, which is evident at Mambova rapids, where the over-capping Karoo basalt has been fractured. The Katombora rapids also represent an fault line associated with the boundary of the Okavango rift system. Structural control in this region is subtle, but is readily discerned by remote sensing techniques (Fig. 4.7). Uplift along these axes, with associated depression of the Okavango graben, accounts for drainage impoundment (Modisi 2000; Moore & Larkin 2001). It is interesting that limestones (12 - 15m deep) flank the Zambezi upstream of Katombora rapids. These sediments today lie up to 42.5 m above the present bed of the river. This deposit exhibits evidence of uplift, such that streams incised the calcareous sediments to below water level, and these gullies were subsequently infilled with sandy sediments (Clark 1950). These limestones are interpreted to represent a protracted lacustrine phase that reached (at least) this northeast margin of the Kalahari Basin. It further follows that eastward flow in the Zambezi was reduced, if not non-existent, downstream of Mambova at this time (Chapter 5).

Lacustrine and alluvial sediments, believed to be of late Pleistocene and Holocene age, lie between the Chobe and Linyanti faults, and in turn overlie a larger expanse of older sediments. These formations extend northeast into Zambia, where their stratigraphy awaits detailed description (Section 5.7). Overall, this older alluvium extends over at least 120 000 km² of northeast Botswana and southwest Zambia, where the Machili Flats extend northeast to the Kafue Flats (Dixey 1944, 1950; Thomas & Shaw 1991). It is assumed that this considerable extent of late Cenozoic sediments reflects the former existence of a large shallow lake that covered a large part of northeast Botswana. This hypothesis for a Palaeo-Lake Makgadikgadi (PLM) was first suggested by Grove (1969). Subsequent mapping of fossil sediments, including preserved shorelines has revealed four principal lake levels. The preservation of off-shore sandbars, whose persistence was sufficiently prolonged to preserve signatures of their existence as geological strata. These lie at the 945, 936, 924 and 910 m a.s.l levels: which correlate with past tenures of palaeo-lakes (Cooke & Verstappen 1984; Thomas & Shaw 1991; Fig. 4.7a, Chapter 5). Shaw (1988a,b) also invoked the existence of a Palaeo-Lake Thamalakhan stage, represented by 936 m fossil shorelines across northeast Botswana. Thomas & Shaw (1991) also

pointed to more equivocal evidence that an even larger palaeo-lake covered the region (McFarlane & Segadika 2001). The significance of this largest landform is discussed in the next chapter (Section 5.7).

Major uncertainties still prevail over the ages of these palaeo-lakes, despite considerable research efforts directed at understanding the intricacies of Quaternary history of this polyphasic depocentre. Details of the respective tenures of these palaeo-lakes are important to understanding how antecedent drainage systems, associated with these lakes, may have influenced lechwe antelopes. This study has devoted some attention to the problems and controversies, because these lakes are inferred to have strongly influenced the local biota directly. Evidence available reveals that these palaeo-lakes functioned as hubs of considerable biogeographical importance, because they linked rivers with far flung catchments (Section 4.11).

Grove (1969) argued that Palaeo-Lake Makgadikgadi could only have existed at its highest level - to form the 945m shorelines - if sustained by inflows from the Upper Zambezi. At a minimum, an annual inflow totalling 88 km^3 would have been required to meet the hydrological budget to maintain a lake over $60\,000 \text{ km}^2$ in extent. Based on current hydrological conditions, the Chobe and Okavango could only sustain lakes of 2000 km^2 (Mababe depression) and 5000 km^2 (Ngami), respectively. Nugent (1990) and Thomas & Shaw (1991) reaffirmed Grove's conclusion that the Upper Zambezi would have provided a crucial contribution to the hydrological budget of PLM, as calculated under Holocene climatic conditions (Table 4.2). On the assumption that PLM persisted through far more erratic climatic conditions during the Pleistocene, then this endoreic drainage budget might have been too small, especially under arid climates when annual precipitation was reduced to 60% of modern levels (as estimated by Partridge *et al.* 1999). The inflow budget under conditions of pluvial conditions (> 30% higher rainfall) introduces the interesting possibility that PLM would have formed an intermittent source of the mid-Zambezi, and may even have strongly governed this river's flow. Evidence for this hypothesis is, however, sparse.

It is interesting that total catchments of PLM are estimated to have approximated 1 million km^2 (Table 4.2). The tenure of PLM was possibly coeval with that of the Trans-Katanga drainage, and Palaeo-Luongo, then linked with the Palaeo-Chambeshi. The latter's combined catchment (flowing from the northeast) would have substantially raised total runoff into the Okavango-Kafue graben. The total area of this palaeo-catchment would have been about five fold larger than the $194\,000 \text{ km}^2$ catchment that maintains the contemporary $\sim 68\,000 \text{ km}^2$ of Lake Victoria, whose volume probably exceeds that of PLM! High annual rainfall provides nearly 85% of the total hydrological budget, which not only

Table 4.2. Comparisons of three scenarios of endoreic drainage budgets that would have maintained the postulated Palaeo-Lake Makgadikgadi (PLM), whose existence was first suggested by Grove (1969). Input for precipitation follows Nugent (1990), who assumed a rainfall regime of 450 mm of annual rainfall over a lake 60 000 km² lake: here, upwardly adjusted for the larger area of 80 000 km². This is a more conservative estimate within the upper domain of 120 000km² proposed by Goudie (1999b). Annual drainage budgets follow Nugent (1990), augmented with new data from Shahin (2002) - also the source for catchment areas. From left to right, the total inputs summarized in the bottom row represent the entire Palaeo-Chambeshi^A, the Palaeo-Kafue^B (after scission of Upper Chambeshi and Bangweulu basin), and the extant drainage system. Total catchments of drainages into the Okavango-Kafue graben are highlighted in square brackets.

Input (Source)	Annual Inflow (km ³)			Comments
	Palaeo-Chambeshi ^A	Palaeo-Kafue ^B	Extant ^C	
Okavango River	10.5	10.5	10.5	Both catchments have changed through the Quaternary, due to headwater captures upstream
Chobe (Cuando)	3.3	3.3	3.3	
Upper Zambezi (UZ)	35	35	35	Based on extant topology. Run off was larger before the Kasai pirated UZ headwaters
Precipitation over Okavango Delta	5	5	5	This statistic for extant wetland provided for comparison
Precipitation over Palaeo-Lake of ~80 000 km ²	36	36	36	Region includes that covered by Okavango Delta
Palaeo-Chambeshi (P-C)	27	-	-	Includes Upper Chambeshi and Bangweulu basin, and extant Upper Kafue
Palaeo-Kafue (P-K)	-	12.6	-	Entire Upper Kafue system
Total Accumulation	^A 117 km ³ [1 015 204 km ²]	^B 102 km ³ [913 710 km ²]	^C 90 km ³ [760 650 km ²]	

maintains Lake Victoria, despite high evaporation, but also spills over into the Nile River (Shahin 2002).

4.9.2 Geochronology and Bioturbation of Palaeo-Lake Sediments and Kalahari Dunes

Establishing the absolute ages and tenures of these late Cenozoic palaeolakes in the Kalahari basin presents severe challenges, which geochronologists have yet to overcome. Thermo-Luminescent (TL) and radiocarbon are the two methods applied, amongst the geochemical techniques available (Thomas & Shaw 2002; Duller 2004). Radiocarbon (C^{14}) dates of Kalahari carbonates (mostly preserved as calcretes) have proved unreliable (Thomas & Shaw 1991; Thomas *et al.* 2000). Not least because they represent a basket of dates representing repeated accretions within the “dated” nodule (McFarlane & Segadika 2001; Moore & Larkin 2001; Moore 2003). Watchman & Twidale (2002) concluded that the tradition of trying to date calcretes using the radiocarbon technique should be abandoned, due to multiple contaminations that plague such attempts.

Ringrose *et al.* (2005) obtained thermoluminescent (TL) dates from siliceous sediments in fossil lake shorelines across the principal depressions of northeast Botswana, especially those located around the margins of the Makgadikgadi depression. These TL dates represent an estimate of how long mineral particles have been buried. Typically, quartz particles have been dated using TL techniques, but are prone to errors that require careful corrections (Duller 2004). The complicated signals in their dataset led Ringrose *et al.* (2005) to invoke Pleistocene climatic cycles to explain the spectrum of ages estimated for fossil shorelines. Respective luminescent dates were purported to represent when fossil shorelines were formed through alternating periods of arid and mesic climate through the Quaternary. Their comparison (Fig. 4.8) reveals that these dates are geologically inconsistent, not least because older sediments overlie younger formations with respect to these dates (Cotterill *et al. unpublished*).

It appears that bioturbation is a problem that awaits deserving recognition. It detracts from the authenticity of geochemical and geochronological dates published for Kalahari basin sediments (McFarlane & Segadika 2001; McFarlane & Eckardt 2004; McFarlane *et al.* 2005, see below). Quantifying more precise dates around the tenures of these palaeo-lakes in the Kalahari basin has major ramifications for several arenas of scientific understanding besides geomorphology (Thomas & Shaw 1991). The persistence of such a huge body of water would have exercised important control over not just local, but regional climates (McFarlane & Segadika 2001): analogously to that of Palaeo-Lake Congo when it existed further north (Peters & O'Brien 2001). Increased evaporation over such immense wetlands would have interacted with global determinants invoked by deMenocal (2004) at

larger scales. Thus, PLM likely increased local and regional precipitation. This would have mitigated against the regional aridity that prevailed during (Ringrose *et al.* 2005). Pertinently, associated dynamics in floodplains around the flat terrain bordering PLM would have significantly influenced habitats available to aquatic organisms, lechwe antelopes. Furthermore, PLM likely augmented mesic conditions during interglacials.

These challenges and problems entailed in dating lacustrine sediments also afflict dates proposed for aeolian landforms in the Kalahari Basin. Large expanses of the Kalahari basin are characterized by aeolian dunes. Only those in the arid areas of southwest Africa are active (Mean Annual Rainfall < 100 mm). Fossil dunes cover large areas of eastern Angola, northwest Botswana, northwest Zimbabwe, and southwest Zambia (Shaw & Goudie 2002). They relate to neighbouring landforms, especially extinct and extant wetlands, in interesting antecedent and consequent patterns of formation. These Kalahari Sands (KS) were deposited during periods of persistent arid climates in the Quaternary, associated with colder, arid conditions in the southern hemisphere, and more globally in glacial maxima (Thomas & Shaw 1991). Obtaining reliable ages for these Kalahari dunes will provide invaluable insights to delimit fossil landforms with unprecedented precision.

McFarlane & Eckardt (2004) and McFarlane *et al.* (2005) demonstrated that saprolite underlying 60 m high aeolian dunes in the Kalahari of northwest Botswana has been transported to the dune surface. This activity is attributed to activities of termites to considerable depths. Burrowing mammals, especially mole-rats (Mammalia: Bathyergidae) may also have turned over sediments at shallower depths. Indeed, reconnaissance exploration exploits patterns generated by bioturbation, because indicator minerals have been transported to the surface of Kalahari sediments from Kimberlite bodies buried under up to 150m of Kalahari sediments. Such surveys were followed by drilling programs, which confirmed bioturbating agents had transported magnesium and chromium-rich ilmenite placers, from underlying kimberlite pipes, up into the aeolian overburden (Lock 1985).

Despite these confounding problems, the confidence placed in TL dating of Kalahari sediments (Thomas *et al.* 2000; Shaw & Goudie 2002; Thomas & Shaw 2002) has been applied to support far reaching conclusions. Most recently, episodes of aridity derived from TL dates of aeolian dune systems were applied to frame a regional model of climatic change. Its projections, based on inferred past climatic dynamic, have considerable socio-economic importance for the southern African subregion (Thomas *et al.* 2005). Inconsistent signals need to be explained. For example, inferences that young

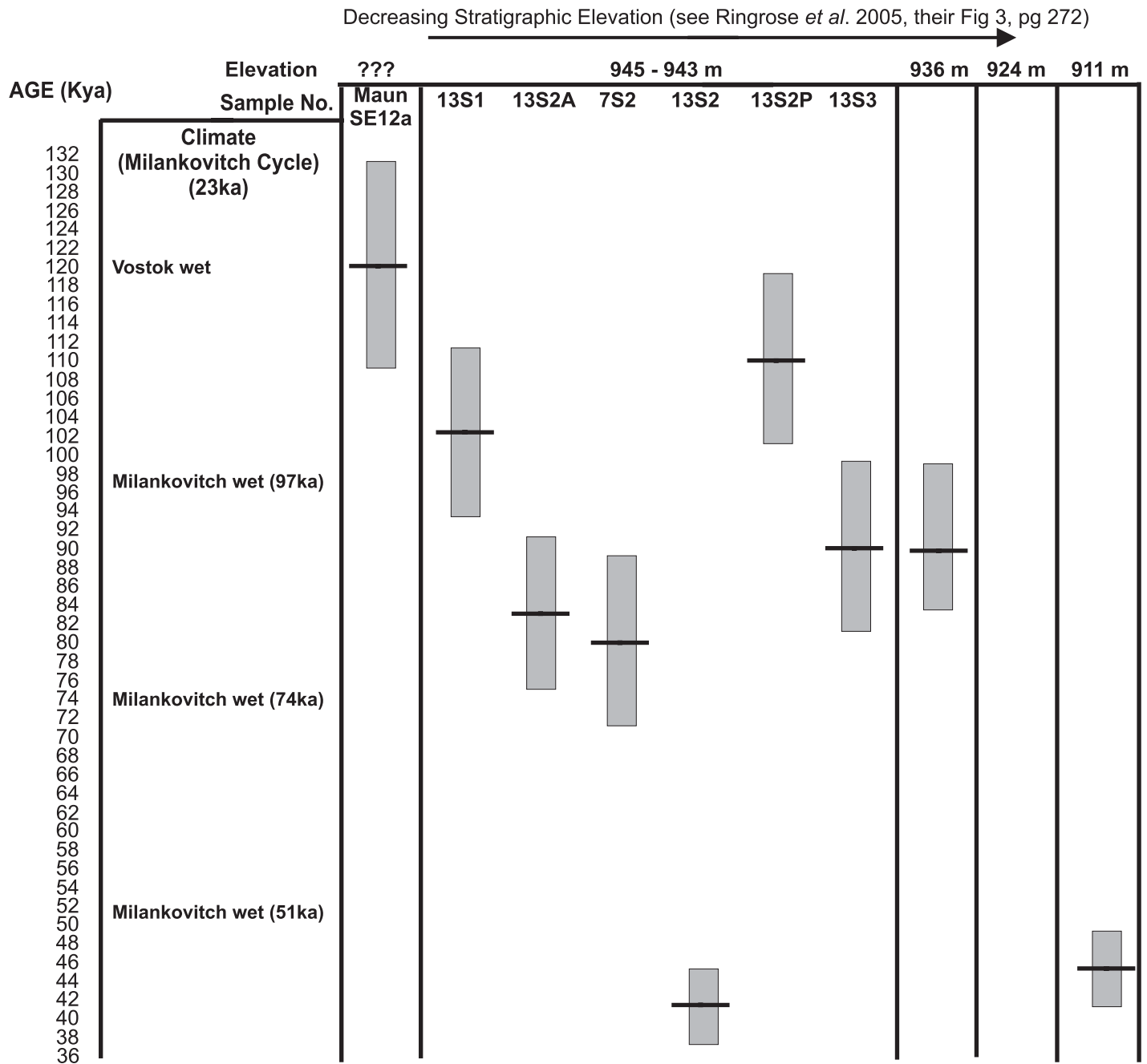


Figure 4.8. Summary of Thermoluminescence (TL) dates determined by Ringrose *et al.* (2005) (their Figure 3, pg 272) for a stratigraphic section associated with the 943-945m shoreline of the proposed Lake palaeo-Makgadikgadi. Horizontal bars show TL ages; grey tone denotes the quoted analytical error associated with each age. Attention is drawn to the lack of any systematic correlation between the TL age and the associated stratigraphic height. (Modified from Cotterill *et al.* *unpublished*).

dunes have been incised by even more recent faults, and/or supplanted by wetlands are all based on unreliable evidence. Equally, the conclusion that Kalahari dunes were active during the Holocene in southwest Zambia (O'Connor & Thomas 1999) was not confirmed by TL dating of Kalahari dunes in northwest Zimbabwe (Munyikwa *et al.* 2000). Above all, reconstructions that propose palaeo-environments based on this information, derived and delimited by dates of deposition (and associated arid cycles) across the Kalahari basin, have yet to be tempered against realities that these sediments have been severely bioturbated.

To conclude, the geomorphological anomalies and inferred ages of landforms (that appear correlated with palaeo-environments) appear to owe more to the activities of termites than the vagaries of past climates. Darwin (1837, 1881) conclusively demonstrated how local activities of burrowing organisms engineer small patches in landscapes. Over long time periods, these effects ramify and scale up to influence regional and continental landscapes. Thus, bioturbation manifests in major effects when it operates over geological time scales. Considerable evidence confirms that soil-dwelling organisms (not only microbes) have modified the earth's surface to unprecedented depths (Johnson 2002). It is difficult to overemphasize that termites have quite literally turned deep layers of the African continent upside down. Tricart (1972: 189) noted how "the African savannas are the domain of giant termitaries and of the most evolved and active termites." White (1983) emphasized that termites have been a dominant, ubiquitous pedogenic agent in many of Africa's soils. This is confirmed by many studies, notably Malaisse (1978) and Crossley (1986). This behaviour of termites is ancient. Evidence of subsurface termite activities are preserved in Pliocene strata in Olduvai Gorge (McBrearty 1990). Termite activity under mesic conditions in tropical Africa can generate 0.5 m soil / 1000 yrs (Runge & Lammers 2001). In the Congo basin, Cahen & Moeyersons (1977) described how termite activities have redistributed Stone Age artefacts through Kalahari sediments. McBrearty (1990) presented conclusive evidence for bioturbation of African sediments by termites, which only foolhardy geochronologists can afford to ignore. Earthworms fare poorly in Kalahari sediments but termites flourish. In summary, all radiocarbon dates for Kalahari calcretes cannot be applied to geomorphological or evolutionary reconstructions. Despite prominent attention paid in recent scientific literature, it is most unfortunate that the purported TL dates advanced for aeolian and lacustrine landforms cannot be applied to geomorphological and biogeographical problems in this study.

4.9.3 The Kafue Flats, the Machili Flats, and Evolution of the Upper Kafue River

The Kafue River exhibits a profound dichotomy in its profile. This is also seen in other rivers in the Katanga-Chambeshi region, whose catchment flows across "High Africa" and then down a steep

escarpment into a rift valley (Bell-Cross 1982; Ellenbroek 1987; Fig. 4.2b). The landform dividing these two very different rivers is the Kafue Flats. Dixey (1944) proposed that the Upper Kafue originally flowed southwest into the Kalahari basin; and suggested a wind gap along its southwest margin reveals the position of this former course (Figs 4.7a & 4.9). Most recently, given it is very difficult to treat these two landforms in isolation, Haddon & McCarthy (2005) treated the Okavango-Kafue graben as a unified geomorphological entity.

The late Cenozoic alluvial and lacustrine facies of the Kafue Flats have formed across a deep rift valley, infilled with Karoo sediments. The fault boundaries to the graben are further revealed by lines of hot springs that trend east to west, in parallel with the axis of the Kafue Flats. Moreover, the Kafue Flats are positioned on an axis that extends northeast from the Okavango, across the Lukanga Swamps, to the Bangweulu basin and the Chosi swamps in northeast Zambia (Dixey 1944). Dixey (1955a) suggested all these “sagging basins” originally formed in the Mesozoic, through epeirogenic flexing. Subsequently, drainage systems were superimposed across these landforms (Fig. 2.1 & 4.1a,b). Where published data exist (notably across the Kafue Flats and Lukanga Swamps), aeromagnetic profiles reveal marked lineation trending NE-SW, which correspond to a congruent trend in extant seismicity (Katongo *et al.* 2002).

4.9.4 Lake Patrick – A Middle Pleistocene Palaeo-Lake

The stratigraphy of the Kafue Flats has been sparsely studied. Profiles of isolated borehole profiles, from the southern edge of the basin, reveal that Karoo sediments underlie the Kafue Flats to at least 450m (Smith 1962). Based on incomplete data available, it is not possible to draw any sharp distinction between the younger sediments on the Kafue Flats, and those forming the Machili Flats. Any such differences can be expected to be subtle and reflect local differences in the deposition histories of the modern Upper Kafue. Dixey (1950: 23) describes the Machili Flats as extending northeast for ~72 km from the Simalaha (Mambova) Flats, along the Upper Zambezi, to Mulanga (16 54'S; 25 20' E, Ansell 1978). Where the Ngwezi River enters the Machili Flats, extensive deposits of coarse gravel are exposed. These contain ESA artefacts contemporaneous with the Old Gravel II (OG II) of the Victoria Falls Formation. Here, an inspection pit revealed that 4.4 m gray, stiff clays overlie 1.8 m coarser facies - sands, grits and gravels (Dixey 1950).

A similar inspection pit to the northeast, on the Kafue Flats, revealed the oldest stratum to comprise 4.5 ft (1.4 m) of weathered pipe sandstone on Karoo sediments; overlain by 1.5 ft (0.5m) pebbly gravel under 36.5 ft (11.1m) clayey sediments. "Pebble deposits overlying the Pipe Sandstone contain stone

implements referable to the Older Gravels (lower Middle Pleistocene) of the Victoria Falls area." (Dixey 1944: 38). Based on this evidence, I infer these pebble deposits formed through aggrading river action, before overlying sediments were deposited during the tenure of Lake Patrick (see below). The facies underlying the Kafue Flats, south and southeast of Namwala, illustrate similarities to the region around Victoria Falls (Dixey 1944; Figs 4.7a & 4.9, Chapter 5). At the youngest, these gravels are Middle Pleistocene and likely older. So it is tempting to infer that the deposition of these artefact bearing deposits was contemporaneous with Older Gravels II around Victoria Falls. Thereafter, a lacustrine phase followed, with deposition under mesic conditions during an interglacial, which corresponded to the timing of the ESA-MSA transition (Chapter 5).

The origin of the soils covering the Kafue Flats has incited controversy. Ellenbroek (1987) argued that the exceptionally high clay content of the soils on the floodplain of the Kafue Flats reflected an alluvial, not a lacustrine origin, as originally suggested by Van den Moor (1956). An alluvial origin is difficult to reconcile with Dixey's (1944) descriptions of strata underlying the Kafue Flats, in which clays dominate the upper facies to a depth of over 11 m. These soils also contain a high proportion of calcareous nodules in upper profiles. These can be interpreted to reflect a history of seasonal exposure under lacustrine conditions: with differential migration of minerals through hydrological action. These may then have abetted by bioturbation, since the lake dried out. Moreover, alluvial facies would exhibit a higher proportion of coarser grained sands and also gravels. Dixey (1944) described the stratigraphy exposed in a well sunk through an abandoned course of the extant Kafue River (~50 km NNE Monze). This comprised over 18 m of gravelly alluvium.

Since Ellenbroek (1987) published his thorough study of floodplain ecology, a geomorphological report described the stratigraphy of sediments exposed at the northern edge of the Kafue Flats. This is near Twin Rivers, the MSA archaeological site (Simms 2000). Here, deep deposits of lacustrine sediments confirm that a large, shallow lake - called Lake Patrick - occupied ~ 17 000 km² of the Kafue Flats during the Middle Pleistocene. Uranium series dating (²³⁰Th/ ²³⁴U) of tufa in the Twin Rivers formation, and also of tufa capping the lacustrine sediments (exposed in an incised stream bed) reveals that Lake Patrick had probably ceased to exist before ~250 Kya. It probably no longer existed even 300 Kya, because the palaeo-lake bed had already been deeply incised by eroding streams before the tufa formed at ~200 Ka BP. Thus, Simms (2000) concluded that these Uranium-series dates actually underestimate the upper age of the palaeo-lake, as it had likely dried out earlier in the Middle Pleistocene.

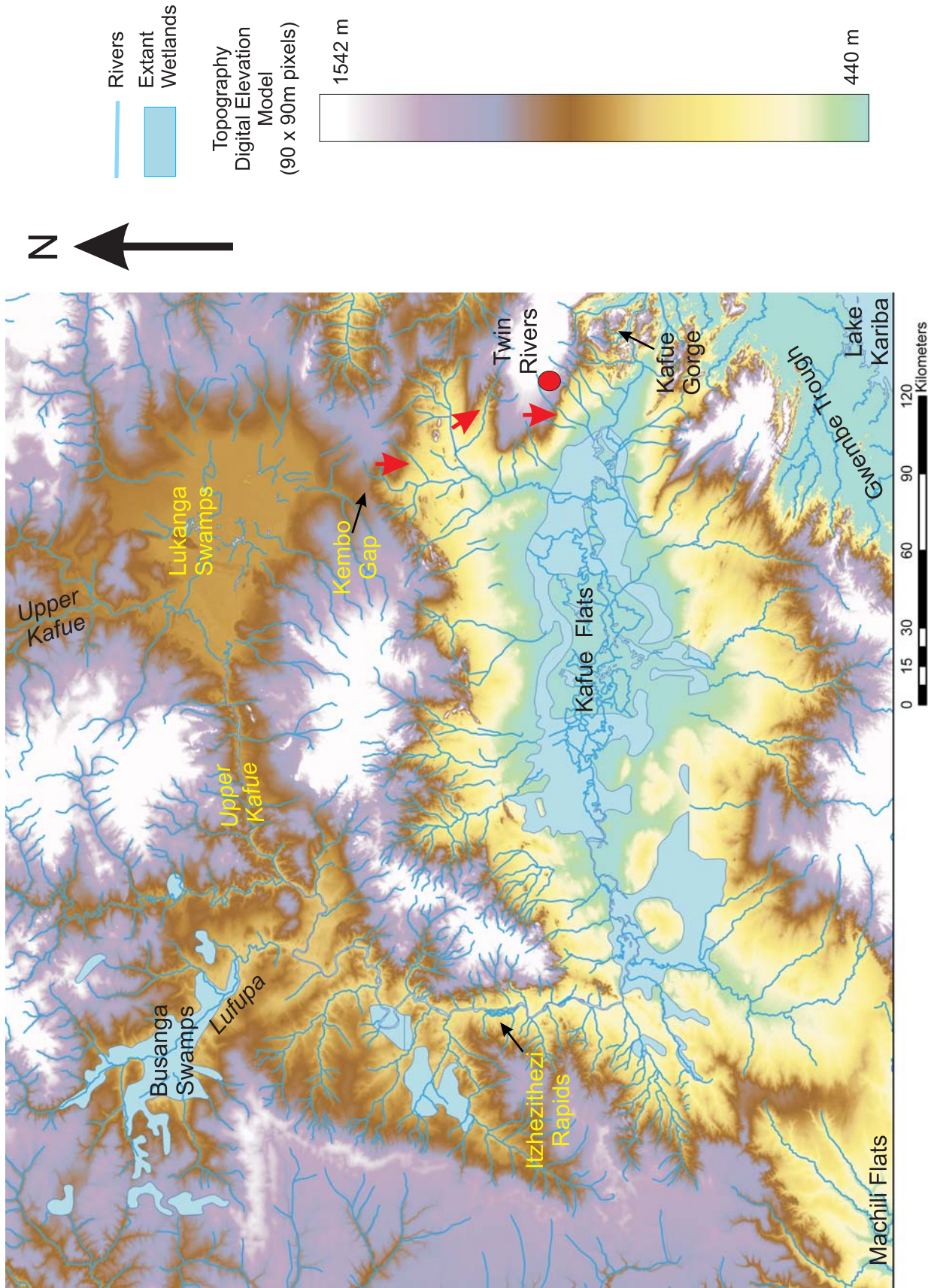


Figure 4.9. Detail of the extent of alluvial and lacustrine sediments of the Kafue Flats and Lukanga Swamps, divided by the Kembo Gap, a region of low relief. Location of the Middle Stone Age archaeological site of Twin Rivers (Chapter 5) is also labelled. Arrows approximate locations of exposed lacustrine sediments along streams, which Simms (2000) inferred, represent the tenure of Middle Pleistocene Lake Patrick, with an estimated extent of $\sim 17\,000\text{ km}^2$. Note the spatial proximity of the Busanga and Lukanga Swamps (supporting populations of Red lechwe, *Kobus leche*) in relation to the Kafue Flats, where the Kafue lechwe, *K. kafuensis*, has diverged. The Kembo Gap (arrowed) forms the nebulous watershed between the Kafue Flats and Lukanga Swamps.

The Kafue Flats lie close to the Lukanga Swamps, and the two basins are separated by a low axis of relief, representing the Nyama Dislocation Zone, trending E - W (30 – 70 km width); where the crustal block, dividing the two depressions, is shearing westwards against adjacent cratonic formations. This Nyama ridge is incised by two valleys, one occupied by the extant Upper Kafue River in the event. The second saddle – hereafter the Kembe Gap - northeast of Chibensi Hill, a very shallow watershed (barely 15 km wide) divides the Kafue and Lukanga floodplains. It is feasible that aquatic organisms, including lechwes, have dispersed across this very broad shallow valley, today occupied by the headwaters of the Kembe River (flowing south on to the Kafue Flats). This would have especially feasible during high rainfall periods in the Pleistocene. Moreover, this facile watershed represents an axis of relief, trending E – W, which appears to represent an axis of uplift that manifests at the abrupt scarp of the Itzehetzi rapids across the Upper Kafue. Two parallel N – S trending faults underlie this saddle, and appear to represent a subtle structural link between the Kafue and Lukanga basins (Katongo *et al.* 2002). This line of relief represents part of the geological controls, involving faulting focused along the Nyama and Kapiri-Mposhi Dislocation Zones, which Katongo *et al.* (2002) invoked to explain an epeirogenic origin of the Lukanga basin. It is also possible that past epeirogenic events uplifted this axis to impound the Upper Kafue periodically: with radical consequences on the hydrology of the Lukanga and Kafue basins to its north and south, respectively (Fig. 4.9).

4.9.5 The Cameia Depression and Palaeo-Lake Bulozhi

The geomorphology of Barotseland has barely been studied (Williams 1986; Moore 2003). From his interpretations of Landsat Satellite imagery, Williams (1986) suggested the central floodplain of the Upper Zambezi – the Bulozhi plain – has formed over a downfaulted block. This would mean the Barotse depression is a shallow graben. Moore (2003) suggested that uplift across the Zambezi downstream of Senanga would have impounded the Upper Zambezi to create a large, shallow lake, here termed Palaeo-Lake Bulozhi (Fig. 4.7b). Its flooded area may have approximated that of Palaeo-Lakes Caprivi and Thamalakhane in the Okavango graben (described by Shaw 1988b, Thomas & Shaw 1991).

Key evidence for the existence of this lake lies in the eroded ferricretes exposed along the banks of the Zambezi at N'gonye Falls, and described by Clark (1950). They formed unconformably on Karroo sandstones (eroded smooth by the Zambezi). These ferricretes are capped by aeolian Kalahari Sands. Since such sediments form only under seasonal semiarid conditions, their formation across the course

of the Zambezi can only be interpreted as taking place when the river flow had ceased entirely (Section 5.6).

The significance, and origin, of the Matabele-Mulonga plain has long been obscure (Williams 1986). Moore & Larkin (2001) suggested it marks incipient capture of the Cuando by the Upper Zambezi. I suggest it actually testifies to the converse. A more logical hypothesis is that the Cuando was formerly an Upper Zambezi tributary, but was diverted (most likely by tectonism) into the Okavango graben to attain its modern course. The influences of past and neotectonic activity are clearly evident across Barotseland. Strong structural control over drainage topology is evident in sharp diversions of river courses, in which contorted topology is not uncommon. Evidence for recent uplift is evident in the clusters of pans formed on the Kalahari Sands east of the Zambezi. These are reminiscent of Ria lakes around courses of river channels (Schumm *et al.* 2000), impounded by tectonic uplift across the Katanga Pedicle (Section 4.6, Fig. 4.7b). They are also very similar to networks of pans, in parts of the Central Kalahari, which have formed under strong structural control, as described by Wormald *et al.* (2003). It is inferred that a large portion of the Barotse region has been recently uplifted, which would account for the senile drainage, with runoff pooling locally on its relatively flat landscapes. The swollen channel of the Matabele-Mulonga plain also points to impoundment of its runoff, which possibly occurred during the Palaeo-Lake Bulozhi stage. It is instructive to compare the geomorphology of the Matabele-Mulonga plain against the channels of the Luombwa and other major rivers, where they debouch across the Bangweulu floodplain (Fig. 4.7c). The congruence in morphology of these swollen channels adds support to the hypothesis that the Matabele-Mulonga channel reflects debouchment on to a seasonal lake. These intricacies of geomorphological history centred on the Bulozhi depression are significant to understand aspects of the phylogeography of lechwe antelopes, especially *K. leche* (Section 6.4, Fig. 4.7b).

North of the Barotse basin, Lake Camiea floods a shallow depression, across which the Upper Zambezi has eroded its channel along the southeast margin (Fig. 4.5). This wetland formerly supported lechwes (Chapter 2, Figs 2.2 & 4.5); and a population of swamp-dwelling weaver birds also appear to be isolated here (Dean 1996; Section 4.11.4). Formation of the Cameia depression is most plausibly explained as representing an inland basin similar to the Bangweulu and Lukanga depression in the east. Study of its sediments should prove most useful. They can be expected to have preserved signals of palaeo-environments. They should also reveal whether tectonic activity impounded drainage (notably that of the Upper Zambezi) within the Cameia basin. This would have created a shallow lake of

substantial area (Fig. 4.5). Bell-Cross (1968, 1982) placed great emphasis on drainage evolution in the Congo basin, just to the north of the Cameia depression, where headwaters of the Kasai River pirated Upper Zambezian tributaries (Section 4.11).

4.10 DRAINAGE EVOLUTION AROUND THE OWAMBO DEPRESSION: PALAEO-LAKE KUNENE, AND PALAEO-LAKE ETOSHA

A recent study by Hipondoka (2005) has revealed new, and important, aspects of drainage evolution centred around Etosha Pan, Namibia. The Etosha depression is centred within the much larger Owambo depression. The extant topology of the Kunene represents the loss of a major south flowing river, which debouched into the Owambo basin. Up until the late Pliocene, this was the principal endoreic tributary of palaeo-lake Kunene, until it was disrupted by the piracy of the Upper Kunene by the Lower Kunene in the vicinity of the Falls. Hipondoka (2005) confirmed earlier suggestions, notably of Wellington (1938), that this deflection of the Upper Kunene to the Atlantic occurred in the vicinity of Calueque (Fig. 4.10a).

Widespread downcutting by rivers into the continental margin was initiated by extreme uplift of Africa in the late Pliocene (Partridge *et al.* 1995; Partridge 1998; Section 4.5.3). Cosmogenic dating of Namib landforms by Van der Wateren & Dunai (2001) placed a minimum age of 2.81 ± 0.11 Mya BP on incision of west-flowing Kuiseb canyon in the Namib desert. It appears that the entire gorge had been eroded to a significant depth by the early Pleistocene (1.28 ± 0.09 Mya BP). Hipondoka (2005) suggested the Lower Kunene also incised its gorge in the same period.

A late Pliocene date for the deflection of the Upper Kunene to the Atlantic Ocean is also supported by signatures in the stratigraphy of the Owambo basin. The Owambo basin did not dessicate entirely after the end of the Pliocene. A Palaeo-Lake Etosha stage followed, now sustained by the smaller Cuvelai drainage system flowing from the north. The swampy conditions in Palaeo-Lake Etosha were sufficient to support sitatunga antelope, *Tragelaphus spekei*, as revealed by Holocene fossils (Hipondoka 2005). This interesting evidence that the Owambo basin supported an immense Pliocene lake, then replaced by a Pleistocene palaeo-lake, has interesting implications for the biogeography of lechwe antelopes. There was likely a persistent connection from the eastern margin of the Owambo basin to the Cubango River - and thus with the Okavango graben. This drainage link would have involved the Omuramba Omuthiya with the Namungundo River, an east flowing tributary of the Cubango River (Hipondoka 2005; Fig.

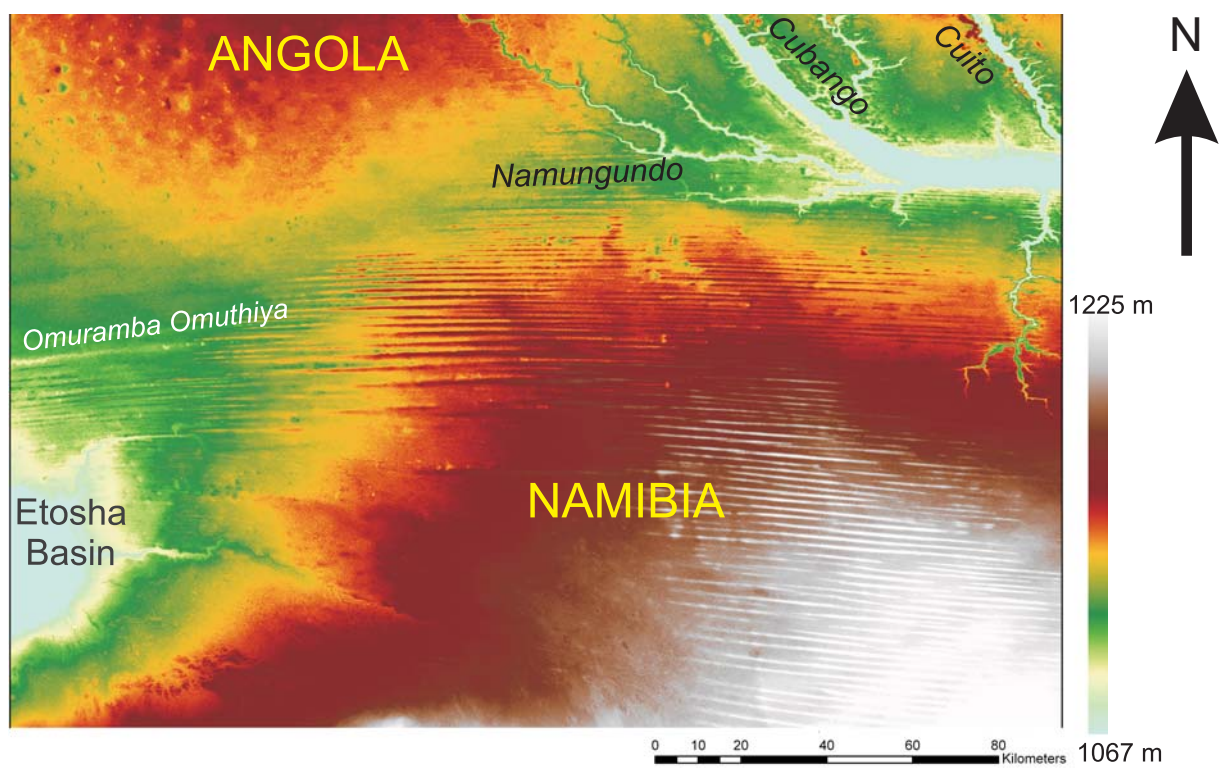
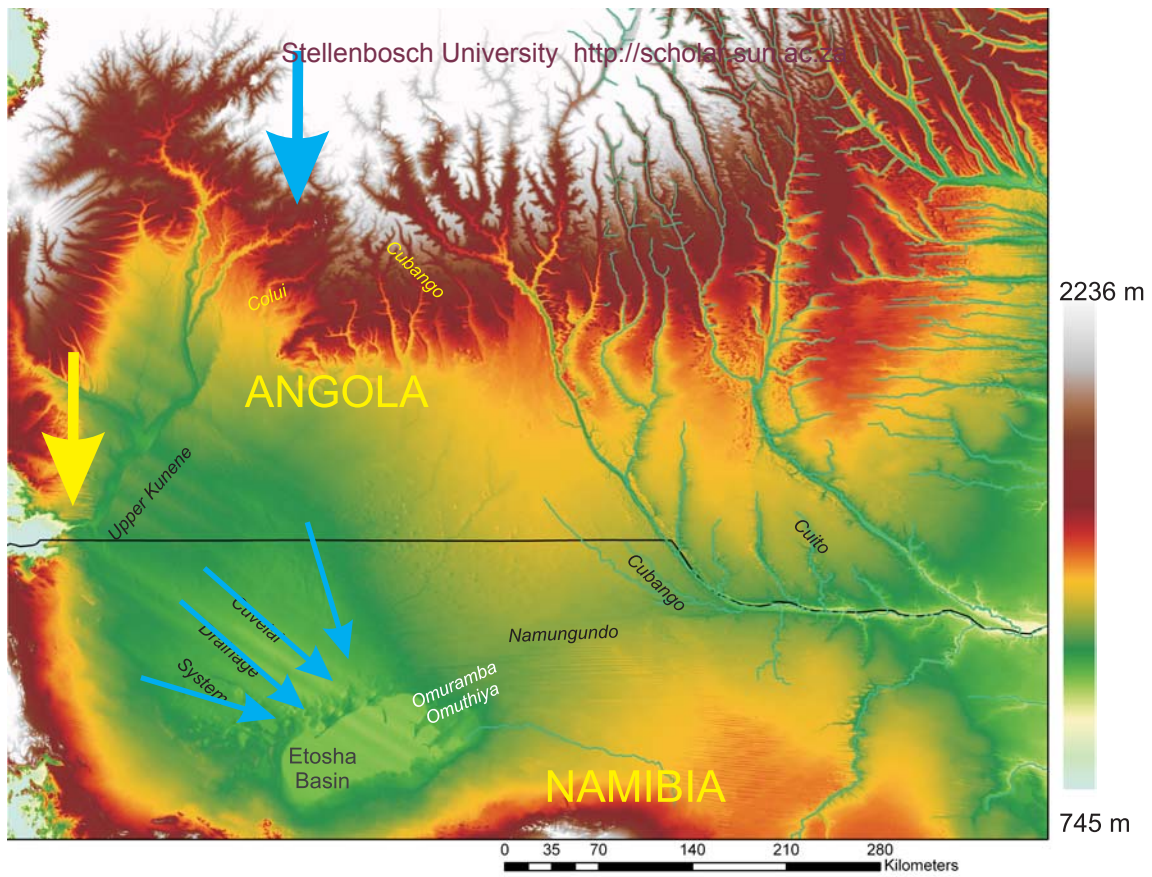


Figure 4.10a. [Top] Topology of drainage systems of southwest Angola and northern Namibia, with respect to the Owambo depression, which contains the Etosha basin. The connection suggested by Moore & Liken (2001) between the Cubango and the Colui rivers is indicated by the blue arrow. The yellow arrow depicts the site, near the town of Calueque, where the Upper Kunene was diverted in the late Pliocene to flow into the Atlantic Ocean (as concluded by Hipondoka 2005). Historical evidence (Earl of Mayo 1883; Section 2.4.6) confirms that lechwe antelope occurred upstream of Calueque, along the floodplains of the Upper Kunene river.

Figure 4.10b. [Bottom] Detail of the eastern margin of the Owambo depression to illustrate the possible connection between the Namungundo (an east-flowing tributary of the Cubango) with the Omuramba Omuthiya, which today drains westwards into the Etosha Pan complex. Hipondoka (2005) concluded that this link between the Okavango graben and the Owambo basin was extant during the late Pleistocene, and it has possibly existed more recently.

4.10b). This would have provided a route for fishes and aquatic antelopes to disperse between the Owambo depression and Upper Kunene floodplains. In wet periods, it is likely that the headwaters of the Cuvelai drainage would have allowed aquatic organisms to disperse between the Owambo depression, and the Upper Kunene. Another possible route involved drainage rearrangement in the Cubango headwaters. Moore & Larkin (2001) suggested that the Colui River in western Angola was originally a much longer river, as a major southwest flowing tributary of the Upper Kunene. The Colui headwaters were then pirated by the Lower Cubango (Fig. 4.10). This event would enabled dispersal of Okavango fishes into the Kunene.

4.11 BIOTIC SIGNATURES OF LANDSCAPE EVOLUTION: CONGRUENCE AND ANOMALIES IN BIOGEOGRAPHIC PATTERNS

4.11.1 Background: Indicator Taxa and Biogeographical Methodology

This second part of the Chapter builds on the framework established in the overview of landscape evolution. As the focus of this study, the relevance of lechwe antelopes as biotic signatures of landscape evolution has already been emphasized. Their tight dependency on floodplains is suspected to underlie their disjunct distributions (Chapter 2). This section expands this approach, and describes and summarizes distributions of fishes across the Katanga-Chambeshi region. Provenance and sources of the data are described in Section 4.2.3. These biogeographical patterns represented among different taxa of fishes are inferred to reflect either past dispersal events, and/or vicariance. These inferences serve to identify past connections between drainage systems, and so infer how their topologies have changed. Barnard (1936) demonstrated how distributions of certain extant organisms can reflect ancient influences of geological history, as exemplified in the Cape Fold Belt, South Africa. Ichthyology provides a wealth of examples of how landscape evolution has controlled distributions of fishes in both aquatic and marine habitats (Bishop 1995). Extant fish distributions are intricately related to hydrographic history (Skelton *et al.* 1991; Reid 1996). So it is not surprising that geological history constitutes the overwhelming signal in macroecological patterns among west African assemblages of freshwater fishes (Hugueny 1989; Hugueny & Paugy 1995). For example, Hocutt (1979) summarized how drainage evolution has controlled speciation of fishes across the Appalachian Mountains of North America (Mayden 1988).

Recent phylogeographic studies confirm this strong geomorphological control over the evolution of fishes (e.g. Waters & Wallis 2000; Waters *et al.* 2001; Sullivan, *et al.* 2002, 2004), and also aquatic salamanders (Jones *et al.* 2006). The phylogeographic history of a cyprinid fish provided support for

existence of an ancient fossil river, the Tethys, in eastern North America (Berendzen *et al.* 2003). Hrbek *et al.* (2004) demonstrated how evolution of cyprinid fishes (Genus *Pseudophoxinus*) can be explained by drainage rearrangements driven by plate tectonics. Certain phylogeographic studies have also generated surprising insights; notably dispersal of a cichlid fish from equatorial Africa into the middle East, possibly through the Nile drainage system (Werner & Mokady 2004). In contrast to Africa's Great Lakes (Salzburger *et al.* 2005), there appear to have been very few, if any, phylogeographic studies of the fishes of the Katanga-Chambeshi region. The recent report on cichlids (Joyce *et al.* 2005) is the singular exception. Moreover, molecular dating of divergence events between sister taxa can delimit timings of key geological events such as river captures and prevailing geomorphological conditions. (This subject is explored in more detail when discussing phylogeographic patterns (Chapter 6).) Nevertheless, it is important to acknowledge that extant ecological structure of some assemblages of freshwater fishes, as in parts of Australia, may reflect equally strong control by fluctuating climates (Unmack 2001).

Debates and controversies surrounding methods of biogeographical reconstruction deserve some consideration here. Knowledge of distributions of African freshwater fishes has advanced immensely since the first reviews of the group's diversity and evolution (e.g. Boulenger 1905). As of December 2005, the authoritative online source, Fishbase (www.fishbase.com), listed an incomplete total of 389 species as occurring within the political limits of Zambia. Teugels & Guégan (1994) estimated at least 1000 freshwater species occur in the Congo basin and its tributaries. Yet, this region has been very sparsely studied. Indeed, inventories of fish faunas in many African wetlands are very incomplete. As importantly, micro- and macrotaxonomies are in flux. It is important to acknowledge that robust phylogenies are important to reconstruct accurate biogeographical signals (Greenwood 1983; Vari & Weitzman 1990; Reid 1996), which handicaps applying syntheses of published knowledge to identify biogeographic patterns with confidence (Lundberg *et al.* 2000; Stiassny 2002). This unfortunately applies to drainage systems of the Katanga-Chambeshi region. Nevertheless, I have collated information for species complexes, which appear to be monophyletic, and whose selected taxa are considered morphologically distinct by taxonomic specialists in the respective groups.

The long standing debate over dispersal versus vicariance has often been discussed with respect to fishes (Croizat *et al.* 1974), in arguing that vicariance has been the dominant process in the evolution of regional and continental biota (Nelson 1978). Bell-Cross (1982) provided ample evidence that both processes contributed equally to sculpt the ichthyofauna of south-central Africa (Skelton 1994). The

burgeoning discoveries from phylogeographic studies confirm this. In fact, a phylogeographic study of south-central African cichlids (Joyce *et al.* 2005) revealed that wholesale dispersals have occurred across the rivers of south-central Africa, as concluded by Bell-Cross (1982). This is not to say that vicariance has not been important! The composite signal in all these data affirm an interplay between vicariance and dispersal.

Insufficient knowledge, most critically the general lack of phylogenies for African fishes, precludes applying the methods of cladistic biogeography (Humphries & Parenti 1999), or parsimony analysis of endemism (Cisci *et al.* 2003) to the overall goal of this study. For example, the seminal study by Mayden (1988) employed seven cladograms to analyse 34 major rivers within North America. Nonetheless, controversy still persists over the most appropriate research programme that should ideally structure such biogeographical analyses. The tension between Cladistic Biogeography versus Phylogenetic Biogeography hinges on adherence to *a priori* in place of *a posteriori* assumptions and of how taxon relationships and geographic distributions reflect control by historical processes, respectively. Phylogenetic Biogeography bases its argument for scientific rigour on being grounded in a philosophy of Popperian falsification, and is proposed to minimize *a priori* prescriptions on speciation processes (Van Veller *et al.* 2003). Nevertheless, an inductive process of discovery – accumulating independently compiled patterns of facts – to reveal common patterns can be especially powerful, where such evidence can culminate in sufficient consistent signal (see Conclusions to Chapter 5).

A recent example is illustrated in the recent study of aquatic biodiversity across the Mexican Transitional Zone, by Huidobro *et al.* (2006), which based a Parsimony Analysis of Endemicity on identified generalized tracks (as modified from a panbiogeographic framework, Morrone 2001). It is exciting to look forward to the insights that can be revealed by accurate studies of speciation of fishes and other aquatic taxa in tandem with their parasites. Collation of such data will provide considerable scope to apply event-based biogeographical methods (Cisci *et al.* 2003). Such insights should reveal finer details of the histories of archipelagoes, with respect to phylogenetic and phylogeographic patterns of surrogate taxa. Any quantitative analysis of the distributional data, accumulated for this thesis, would ideally need to consider entire ranges of all taxa compared. More rigorous revision of biogeographic patterns across the Katanga-Chambeshi region would be better informed if framed in a larger study area to include the total ranges of widespread aquatic taxa, such as *Hydrocyon vittatus* and *Hepsetus odoe*.

4.11.2 Speciation of Vertebrates in Katanga

In addition to high species richness, the Kamalondo depression – together with the associated Upemba horst - possesses a significant endemism of amphibians (Brooks, *et al.*, 2001), reptiles (Broadley & Cotterill, 2004) and birds (Cotterill 2006). A close relationship between two sister species of terrapins suggests a past connection between the Kamalondo depression and the Upper Zambezi-Okavango system. The endemic Upemba terrapin, *Pelusios upembae* Broadley 1981 and its sister species, *P. bechuanicus* Fitzsimons 1932 (endemic to the Upper Zambezi and Okavango drainages) suggests relatively recent vicariant speciation. It is unclear which species is the more derived lineage, but their close affinities testify to recent links between the two drainage systems (Broadley & Cotterill, 2004). Numerous endemic fishes have evolved in the Kamalondo depression, including the lungfishes *Polypterus katangae* Poll 1941 and *P. meridionalis* Poll 1941 (Malaisse, 1997). Combined, the biotic signatures of the many ichthyofaunal indicators within and around Katanga reveal important aspects of drainage evolution. These are reviewed in more detail below.

In what were preliminary attempts to review this complex history, three reviews revealed how certain vertebrates reflect a dominant control by landscape evolution. One paper highlighted examples of large mammals (Cotterill 2003c). A second reviewed speciation in complexes of weaver birds (*Ploceus* spp) and Swamp flycatchers of the *Muscicapa aquaticus* complex: all confined to large swamps. All these birds are described as arundiphyllic (reed-loving) in their predilection for large permanent wetlands. Swamp flycatchers are also members of a guild of Afrotropical birds dependent on very large swamps of papyrus, *Cyperus papyrus* (Cotterill 2004). These papyrus specialists have evolved adaptations to their specialized niches in papyrus swamps (Leisler & Winkler 2001).

Equally, on going research on bathyergid molerats (Faulkes *et al.* 1997, 2004) revealed strong geomorphological controls on both cladogenesis and genetic evolution with interesting patterns in what is here termed the Katanga-Chambeshi region. In particular, these results revealed that several endemic species, characterized by extensive karyotypic evolution, have diversified in the *Cryptomys mehowi* clade (reclassified into the genus *Fukomys* by Kock *et al.* (2006) not *Coetomys* Gray 1864 as in Ingram *et al.* 2004). Most recently, Van Daele *et al.* (2004) argued the Plio-Pleistocene model of drainage evolution centred on Zambia (Moore & Larkin 2001; Cotterill 2003c) accounts for the vicariant evolution of geographically isolated molerat populations across Zambia. These burrowing rodents are represented by 17 karyotypically distinct populations (Van Daele *et al.* 2004).

4.11.3 Aquatic Molluscs of Katanga and northeast Zambia

The assemblages of freshwater molluscs in the Upper Congo drainage systems of northeast Zambia and Katanga are dominated by Congo basin species, and are significantly richer than the comparatively depauperate fauna of the contemporary Zambezi system. Aquatic mollusc faunas in Katanga also exhibit high endemism, notably in the Thiaridae and Unionidae. The fauna of both the Chambeshi-Luapula and Upper Lufira systems totals 77 species, with 19 endemics (Mandahl-Bath 1968; Brown 1994; Dudley 2000). Specific endemism within each system comprises: Upper Lufira (4/42) Upper Chambeshi-Bangweulu (3/43); and Lower Luapula-Mweru (11/29). In addition, two endemics are shared between the latter two systems.

The principal drainage systems of Katanga have been enriched by faunal mixing. Of the six Unionidae endemic to Katanga, the distribution of *Coelatura luapulaensis* (Preston 1913) constitutes an illuminating biogeographic signal. *C. luapulaensis* occurs in both the Upper Lufira and Bangweulu-Chambeshi systems, which points to their recent connection. Furthermore, three species recorded in the Upper Lufira and Bangweulu-Chambeshi are absent from Lake Mweru and the Lower Luapula River, but occur in the Zambezi drainage (Dudley 2000). Overall, these data point to vicariant speciation in these molluscs. This recent pulse of evolution contrasts with the gastropod mollusc fauna of Lake Tanganyika, where speciation rates appear to have been relatively low within the lake over a period of 10 million years. Biogeographical comparisons reveal that Lake Tanganyika has in fact conserved gastropod diversity lost from surrounding drainage systems (Wilson *et al.* 2003).

4.11.4 Vicariant Speciation of Arundiphyllid (Reed-Loving) Birds

Recent speciation in two groups of arundiphyllid birds (in *Muscicapa* and *Ploceus*, respectively), illustrate a most interesting congruence. The vicariant distribution of Swamp flycatchers of the *Muscicapa lualabae* complex comprises at least three species. The nominate population is restricted to extensive papyrus stands in the Upemba Swamps, with an entirely isolated population around Lake Bangweulu, from where it occurs along the Luapula River to Lake Mweru. The closely related *M. grimwoodi* Chapin 1953 is restricted to the Lukanga Swamps in central Zambia (Cotterill 2004).

Distributions of arundiphyllid weavers of the *Ploceus reichardi* group (defined by Louette & Benson 1982) closely approximate those of the *Muscicapa lualabae* complex. *P. reichardi* is confined to the Rukwa rift and southern margin of Lake Tanganyika; while *P. ruweti* is known only in the Lufira swamps, with *P. upembae* in Upemba, and *P. katangae* restricted to Bangweulu and the Luapula

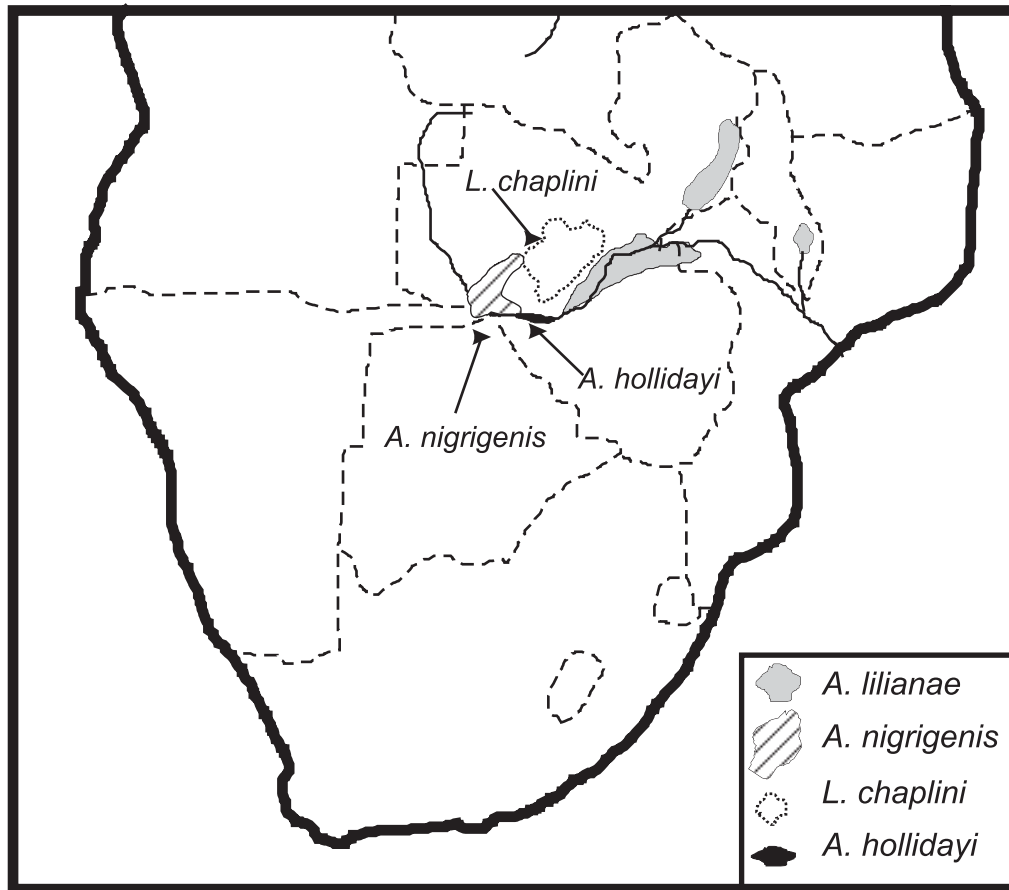


Figure 4.11. Distributions of four species of birds with localized distributions centred around the inferred fossil drainage of the Palaeo-Chambeshi and Zambezi rivers. The distributions of the Katanga-Chambeshi endemics are arrowed: Chaplin's Barbet *Lybius chaplini*. and Black-cheeked Lovebird, *Agapornis nigrigenis*. Note the vicariant distributions of the latter with respect to *A. lilianae*, isolated in low altitude river valleys (Middle Zambezi, Luangwa and Lower Shire). The Batoka Black Swift, *Apus hollidayi*, a local endemic, is confined around its roosts in the Batoka Gorge. Modified from Cotterill (2004, 2006).

(Cotterill 2004, 2006). The congruent zoogeography of these weavers and Swamp flycatchers is explained as dichopatric speciation of formerly widespread ancestor, associated with vicariance of the Bangweulu, Lufira and Upemba depressions. Overall, the realm of their speciation extends from the Lukanga Swamps north to the Kamalondo and Lake Mweru, and east to rift valleys in southern Tanzania. The latter wetlands border the headwaters of the Chambeshi in the northeast. There are also swamp-dwelling weavers around Lakes Dilolo (Fig. 4.5). These birds appear to be confined within the Cameia depression, but their relationships to taxa comprising the *P. reichardi* group have yet to be elucidated (Louette 1984). They are currently identified as *P. velatus*, which is unlikely (see Dean 1996). It is possible that these weavers in the Cameia depression share affinities with arundiphylic weavers endemic to the Upemba and Lufira wetlands in Katanga.

4.11.5 Speciation of Birds associated with Evolution of the Upper Zambezi River

The formation of the Batoka Gorge by the Upper Zambezi focuses Chapter 5, where the history of the erosion of Batoka is discussed in detail. This is, however, the appropriate place to describe the significance of two interesting cases of speciation. One is the Black-cheeked lovebird, *Agapornis nigrigenis* which populated the mopane woodlands of the Machili Flats only after major drainage events broke up the Palaeo-Chambeshi system. Dessication of the delta of the Palaeo-Chambeshi (or Palaeo-Kafue) was the initial event in the sequence of landscape evolution where mopane woodlands came to populate the clay sediments (Cotterill 2004, Section 4.8). The second is the Batoka Black Swift, *Apus hollidayi* Benson & Irwin 1960 traditionally treated as a subspecies of Black Swift, *A. barbatus*. It is geographically isolated from the latter, where its breeding sites are wholly confined to the basalt cliffs of the Batoka Gorge (Irwin 1981). This is interesting, because the erosion of this western section of the Batoka Gorge, populated by *A. hollidayi*, has occurred entirely within the Pleistocene. So, *A. hollidayi* represents a rich avifauna (Hartley 1993; Leonard 2005), with its species assembled very recently across a very young landform (Chapter 5).

4.11.6 Overall Patterns of Fish Biogeography

Totals for species richness within each drainage system of south-central Africa were summarized by Skelton (1994) following on Bell-Cross (1982). These statistics are all likely underestimates, because fish taxonomy has advanced significantly over the decade since Skelton's (1994) review, with numerous discoveries of new taxa and revisions. Nonetheless, these overall patterns remain instructive in how ichthyofaunas of neighbouring drainage systems differ and also share similarities. Pairwise similarity coefficients are the principal, and useful, indicator of these patterns, where a faunal similarity index

compares two drainage systems. Reflecting summed effects of complex historical processes, these statistics quantify how many common species compared faunas share. Each of these extant assemblages has inherited elements from at least one proto-drainage system, and has been complemented by recent dispersals into the system. A pertinent example is the Upper Kafue with a total richness of 64 species of fishes, of which only two are absent from the Upper Zambezi, which has a richer ichthyofauna. Particular species and certain species complexes comprising these faunas provide valuable data that reveal where (and also when) key events in geomorphological evolution determined modern patterns (Bell-Cross 1982; Skelton 1994).

In a landmark study, Skelton (1994) demonstrated how aspects of landscape evolution, since early in the Cenozoic, can explain principal features in the evolution of the freshwater fishes of southern and central Africa. River captures have mixed previously isolated assemblages, and also aided dispersals. For example, a relevant biotic signature of landscape evolution is the close similarity between the assemblages of the Upper Kafue, Okavango and Upper Zambezi River (Bell-Cross 1972, 1982; Skelton 1994), which is explained by these systems sharing a previously persistent link, that only changed recently. Moore and Larkin (2001) incorporated Skelton's ichthyological evidence to help reconstruct how drainage systems have evolved across south-central Africa, beginning in the Mesozoic. Northward dispersal of Zambezi elements in the Upper Congo fish fauna appear to have been contained by the Luvua cascades north of Lake Mweru (Jackson 2001). Further north, the Gates of Hell (Portes d'Enfer) on the Upper Lualaba have been invoked to divide many elements of the Upper and Lower Congo ichthyofaunas (Malaisse 1997).

Skelton's (1994) review revealed that the first significant events in the evolution of the Zambezi ichthyofauna tracked hydrographic changes that modified endoreic drainage systems through the Oligocene and Miocene. This means that extant fish faunas of "High Africa" did not evolve from dispersant species from the north (contra Boulenger 1905; Roberts 1975). Skelton concluded their endemism rather reflects geological determinants since the early Cenozoic. Skelton's model builds on that of Bell-Cross (1982). This distinguished western and eastern theatres of ichthyofaunal speciation within south-central Africa. Bell-Cross (1982) termed these the WETBID (Western End Tertiary Basin of Internal Drainage) and EETBID (Eastern End Tertiary Basin of Internal Drainage), respectively. Following Bell-Cross (1968, 1972, 1982), Jackson (1986) and Skelton (1994) emphasized the affinities of the Zambezi and Upper Congo fish assemblages. Phylogenies of neoboline cyprinid fishes (Howes 1984) and soft-shelled turtles of the genus *Cycloderma* both point to a former connection between the

faunas today isolated in the western Zambezi drainage basin and the Lake Victoria basin. This congruence is also supported by the modern distributions of several, better known, central African fishes (Skelton 1994). I begin the following review of these taxa with perhaps the most illuminating example (Bell-Cross 1982; Skelton 1994).

4.11.7 The Remarkable Biogeography of the Tigerfish, *Hydrocyon vittatus*, in south-central Africa

The absence of tigerfish, *Hydrocyon vittatus* Cuvier 1819 from certain drainage systems in the Zambezi region (notably the Upper Kafue and) was highlighted as an interesting anomaly by Jubb (1952). Bell-Cross (1967) proposed that tigerfishes invaded southern Africa from the Congo basin after the Kasai captured an Upper Zambezi tributary, and subsequently studied geomorphological aspects of this river piracy event in some detail (Bell-Cross 1982). Thus, the timing and routes whereby tigerfishes dispersed, across south-central Africa, are potentially informative to decipher whether topologies of certain drainage systems changed before or after this initial invasion. Such anomalies could refine relative timings of drainage rearrangements across the Palaeo-Chambeshi system.

As judged by its widespread distribution across several drainage basins, *H. vittatus* has been highly dispersant. Its range includes nearly all the Congo basin as well as the larger Nilo-Sudanian system; and rivers flowing into Lake Tanganyika including the Ruaha. South of the South Equatorial Divide, tigerfish occur throughout the Upper Zambezi-Okavango, middle and lower Zambezi systems. It is also occurs throughout the Luapula-Chambeshi system; and in the Lufira and Upper Lualaba systems in Katanga. Nevertheless, glaring gaps in its distribution stand out. Tigerfish are absent from the Upper Kafue, Lake Malawi, and also the Cuanza and Kunene systems (Bell-Cross 1965a) Waterfalls with a vertical drop of 3 m are considered sufficient to contain dispersals of central African fishes (or at least upstream dispersants). The Buckenham and Avumba Menda Falls on the Lower Kafue were invoked as containing tigerfish from the Upper Kafue (Bell-Cross 1965a). And rapids and waterfalls across the Shire River have similarly contained tigerfish downstream of Lake Malawi (Tweedle *et al.* 1979). It is also significant that tigerfishes have failed to invade the Upper Kafue across the watershed from the Upper Lufira and Luapula headwaters (Fig. 2.1 & 4.3).

It is equally interesting to contrast the distribution of another predatory fish, *Hepsetus odoe*, the African Pike, with *Hydrocyon vittatus* (Wine-Miller & Kelso-Winemiller 1994; Skelton 2001). African pike occur in the Upper Kafue as well as the Okavango and Upper Zambezi systems. They are absent from the Zambian Congo system, upstream of the Luvua cascades; yet, they occur through the Lufira and

Upper Lualaba systems across Katanga, but have presumably failed to disperse out of the Luvua into Lake Mweru and its feeder rivers. It is further revealing that the Northern Barred-Minnow, *Opsaridium zambezense*, is widespread through the entire Zambezi basin. It also occurs in the Upper Chambeshi and Bangweulu Swamps, but is conspicuously absent from the Upper Kafue basin (Skelton 2001). I suggest these dispersal events have some bearing on when the Trans-Katanga drainage existed.

Table 4.3. Diversity of three species complexes of Killifishes (*Nothobranchius*) across south-central Africa within the Palaeo-Chambeshi archipelago. Data collated from Valdesalici & Waldekamp (2004, 2005).

Species Complex	Caprivi	Kafue Flats	L. Luapula	U. Luapula	Lufira
<i>N. brienii</i> group	-	-	<i>N. brienii</i>	-	<i>N. hassoni</i>
<i>N. malaissei</i> group	-	-	<i>N. symoensi</i>	<i>N. rosenstocki</i>	<i>N. malaissei</i>
<i>N. polli</i> group	<i>N. "caprivi"</i>	<i>N. kafuensis</i>	-	-	<i>N. polli</i>

4.11.8 Killifishes (Cyprinodontiformes: Nothobranchiidae)

A signature of Palaeo-Chambeshi vicariance is the killifish, *Nothobranchius kafuensis* - known only from the Kafue Flats and Lukanga basin; and it is separated from an undescribed sister species of *N. kafuensis* is restricted to the Chobe-Linyanti system (Skelton 2001). The closest relative of these sibling species is *N. polli*. This *N. polli* species complex is complemented by two other complexes, whose respective species exhibit congruent ranges across Katanga and northeast Zambia. It appears that more species await discovery considering the relatively poor inventories of the region (Valdesalici & Waldekamp 2004, 2005). I suggest this killifish fauna was enriched after fragmentation of an antecedent, contiguous drainage system. The diversity of three species complexes of *Nothobranchius* across Katanga and Zambia is invoked to reflect vicariance of the Palaeo-Chambeshi and Trans-Katanga drainage systems (Table 4.3). The absence of Killifishes from the Owambo basin is surprising (especially considering the extensive system north of the Etosha basin). So perhaps their presence has been overlooked there, because they appear to have occurred throughout the Palaeo-Chambeshi system, which held intimate links with both Palaeo-Lake Etosha and the Upper Kunene.

4.11.9 The Principal Piscine Indicators of Landscape Evolution

The restricted distributions of selected species of fishes are tabulated in Appendix 3. The taxonomy of the river sardines, Genus *Mesobola*, is problematic (Seegers 1997); nevertheless, their vicariant distribution across the south-central African plateau suggests vicariance of a formerly contiguous Palaeo-Chambeshi distribution. This explains how *M. brevianalis* (Boulenger 1908) and *M. moeruensis* (Boulenger, 1915) are now restricted to the Upper Zambezi and Chambeshi-Luapula systems, respectively (Skelton 1994). Howes (1984) suggested that *M. moeruensis* is restricted to Lake Mweru only; such that specimens of river sardines from Lake Bangweulu and the Upper Chambeshi represent an undescribed taxon. Their divergence would obviously postdate dispersal downstream from the Chambeshi system. Equally interesting is the distribution of the Lufira tilapia, *Tilapia ruweti* (Poll & Van der Audenaerde 1965). It occurs in the Upper Lualaba-Lufira, is absent from the Upper Kafue, yet is widespread in lower reaches of the Upper Zambezi-Okavango system (Skelton 1994; Malaisse 1997). Resolution of this anomaly is probably handicapped by taxonomic error (Type II error, see Chapter 3), from using the BSC to classify geographically isolated populations; and so obscures important biogeographic signal. A representative of *T. ruweti* is absent from the Barotse floodplain, and also remains unknown in the Upper Kafue. Moreover, the poorly known *T. baloni*, restricted to the Luongo River, appears to be the vicariant sister taxon of *T. ruweti*. Given that at least two species are likely involved, their modern dichoptry likely reflects vicariance of the Palaeo-Chambeshi across the Katanga Pedicle.

4.11.10 Dispersal and Vicariance of Fish Faunas in Katanga and northeast Zambia

Malaisse (1997) compared fish faunas of the three principal drainage systems in Katanga (Upper Lualaba-Lufira, Kamalondo and Luapula, Fig. 4.3). Patterns in species richness illustrate their previous connection with both the Lower Congo and Upper Zambezi. Complements of both faunas have elevated the species richness of Katanga's wetlands. Their contributions of Upper Zambezian elements are, respectively: 21%, 11%, and 21%. Concomitantly, complements of Congo fishes in the Upper Lualaba-Lufira, Kamalondo and Luapula are 38.3%, 25.1% and 13.7%, respectively. Equally importantly, dispersals have interspersed with isolation. In each region, a significant proportion of endemics contributes to total species richness: Kamalondo (47/183); Upper Lualaba-Lufira (12/87); and Luapula (39/146). These high levels of endemism contrast against the Kasai-Bushimaie-Lulua (2/77). This overall endemism points to isolation of these drainage systems in Katanga as discrete and persistent geomorphological entities. Their vicariant history entailed separation from each other, as equally from the Lower Congo and Zambezi fish faunas. This vicariance was sufficiently prolonged (exemplified by the Kamalondo) that many endemics have

evolved; and it is noteworthy that the high endemism of Kamalondo fishes constitutes the most reliable evidence for existence of a Palaeo-Lake Upemba (Sections 4.6.1 & 4.6.4).

We also cannot discount the possibility that variation in Pleistocene climates also controlled links between drainages (and equally different erosion rates). These effects certainly accompanied, and perhaps even exceeded, the impacts of tectonic activity. Thus, the drier Pleistocene interpluvials likely magnified isolation of these drainage systems, pertinently the Kamalondo, in Katanga. Remarkable sandy landforms - the dilungu - on the plateaux of Katanga are interesting signatures of such dry episodes. These dilungu represent more arid episodes that alternated with mesic periods, significantly wetter than the modern climate (De Dapper 1981, 1988). Barham (2000, 2001) has emphasized the importance of expansions of the Mega-Kalahari sandsea through the Pleistocene, when the aeolian sediments of the world's largest contiguous sandsea were reworked during arid glacials represented in the Marine Isotope record (Chapter 5). Alternating contractions and expansions of xeric vegetation, which paralleled expansions of the Mega-Kalahari, most likely explain allopatric speciation in many birds, isolated today in western Angola, Barotseland and on Katanga's plateaux. Many of these are grassland specialists, but also include forest birds, such as the warblers, *Phylloscopus eustacei* and *P. laurae* within western Angola (Mt Moco) and northern Zambia, southern Katanga and eastern Angola, respectively (Cotterill 2006).

4.11.11 Dichopatric Speciation of Endemic Vertebrates and Evolution of the Luongo River

Bell-Cross (1982) and Balon & Stewart (1983) suggested that the Luongo River in northeast Zambia (today a tributary of the Lower Luapula) was originally connected to the Upper Zambezi system. Thereafter, its capture by headwaters of the Lower Luapula created the modern river comprising two discrete units: the senile Upper Luongo and the youthful lower reaches. These authors invoked this hypothesis to explain both the unusual topographic profile of the Luongo River, and the Upper Zambezian complement identified in the fish fauna of the Upper Luongo.

Comparison of the fish faunas of Katanga with the Luongo is revealing. An interesting endemic is *Kneria paucisquamata* Poll & Stewart 1975 with a sister species, *K. katangae*, endemic to the Lufira system (Poll 1976; Balon & Stewart 1983). Furthermore, the Luongo, Kalungwishi rivers, and Lake Mweru each possess an endemic species of *Orthochromis*; which in the case of *O. kalungwishiensis* and *O. luongoensis* suggest a recent link between these two rivers (Appendix 3). Subject to active taxonomic revisions of the Cichlidae, a significant level of endemism of *Orthochromis* has evolved across the Upper Congo drainage

systems. No less than four endemics are confined in the Lower Luapula, with *O. torrenticola* in the Lufira system (Greenwood & Kullander 1994).

In addition to the Upper Kafue, this disparity between two parts of one river, typified by the Luongo, is also seen in no less than three other rivers in the Zambezi region. The upper reaches of the Kalomo contain exclusively Upper Kafue species; as do upper sections of the Lunsemfwa and Malungwishi in central Zambia. All exhibit an analogous senile character. Yet the youthful, lower sections of all three rivers (namely the Kalomo, Lunsemfwa and Malungwishi) have typical fish faunas of the Middle Zambezi into which they flow (Bell-Cross 1972, 1982; Balon & Stewart 1983). All are delimited by either the Gwembe, or Muchinga, escarpment, which explains how sharp biogeographic distinctions, similar to the Luongo system, have evolved in each of these rivers (depicted on Fig. 4.2b).

4.11.12 Western Angola

A high component of endemism in the Kunene ichthyofauna stands out (Skelton 1994, 2001; Appendix 3). But as discussed above, uncertainties over phylogenetic relationships decree that these biotic signals (especially involving cichlid fishes) need to be assimilated judiciously into biogeographic syntheses. Nevertheless, the diversity represented among the Kunene endemics does not represent spurious signals. They are interpreted to represent a former connection of the Kunene drainage with the OKZ (Okavango, Upper Zambezi and Upper Kafue drainage systems), through two routes. One entailed a headwater capture of the Cuito river by the Kunene (Moore & Larkin 2001; Fig. 4.10); and the second suggests a former role of the Owambo basin when linked to wetlands in northern Botswana, and thus the Palaeo-Chambeshi system. Bell-Cross (1982) concluded that the Upper Cuanza River holds strong ichthyofaunal links with the OKZ drainage systems. Evidence for southward advance of the Upper Cuanza reveals multiple drainage capture events of Cubango - Cuito headwaters. I suggest this is the mechanism that directly facilitated faunal exchanges across these systems (Section 4.9.2; Fig. 4.6). This pattern and proposed process is equally significant to explain how lechwe antelopes dispersed north to reach floodplains along the Upper Cuanza (Chapters 2 & 6, Figs 2.2, 4.5 & 4.6).

4.12 THE CICHLID SPECIES FLOCK IN SOUTH-CENTRAL AFRICA

The serranochrome cichlids have also speciated widely across south-central Africa. Apart from two species in south Africa, the zone of their recent evolution extends from Katanga across the Upper Kafue, and Upper Zambezi systems to the Okavango and Kunene (Greenwood 1993). The *Oreochromis*

endemics in the Rufiji and Pangani basins in east Tanzania (Trewavas 1983; Skelton 1994) also underwent a wave of recent speciation, similar to these cichlids across south-central High Africa.

Vicariant distributions of two cichlids, *Sargochromis greenwoodi* (Bell-Cross 1975) and *Serranochromis altus* Winemiller & Kelso-Winemiller 1990 suggest they are artefacts of a formerly contiguous distribution. These fishes are restricted to slow-moving water and deep channels on the Kafue Flats, and lower reaches of the Upper Zambezi-Okavango (Skelton 2001). Their congruent ranges include the Upper Kafue, Okavango and Upper Zambezi, and point to a contiguous distribution formerly linked by palaeo-lakes in northeast Botswana, which involved the lower reaches of the Palaeo-Chambeshi system.

The rivers of south-central Africa harbour a high species richness of cichlid fishes, especially in the genera *Chetia*, *Serranochromis* and *Sargochromis*. These cichlids are a dominant component of the fish assemblages in the Upper Zambezi-Okavango, Upper Kafue and Chambeshi-Luapula drainage systems (Marshall 2000; Skelton 2001). A phylogeographic study (99 individuals, 31 south-central African taxa) revealed that their speciation has been remarkably recent. It has manifested in an adaptive radiation (Joyce *et al.* 2005). Joyce *et al.* (2005) hypothesized that these south-central cichlids are the extant representatives of a radiation that took place in Palaeo-Lake Makgadikgadi. Geochemical dates from calcretes (C^{14}) and TL dates of fossil shorelines (Section 4.8.2), were cited in support of an hypothesis that this radiation occurred from the late Pleistocene to Holocene. This hypothesis has yet to reconcile with inherent problems in these dates, and especially with the preservation of ESA artefacts knapped from silcretes which formed in the desiccated lake bed near the 945m shoreline (Cotterill *et al. unpublished ms*, Chapter 5).

The phylogeographic database compiled by Joyce *et al.* (2005) reveals six principal clades. These represent a very recent radiation when compared in the overall context of a phylogeny of African cichlids (Salzburger *et al.* 2005). It is interesting that speciation of the Schwetzochromini likely occurred after a lake-dwelling ancestor dispersed into the Malagarasi River, where most of the known species have only become known to science within the past decade (De Vos & Seegers 1998). The origins of this very recent Congo-Zambezi radiation are more obscure. It is difficult to reconcile with the hypothesized origin in Palaeo-Lake Makgadikgadi, that Joyce *et al.* (2005: 92) suggested has "...a minimum age of 52,000 yr BP"; and furthermore persisted into the Holocene. This evolutionary scenario is difficult to reconcile with evidence presented in this chapter, and synthesized through Chapter 5.

Revealing signals in the phylogeographic sequence data of Joyce *et al.* (2005) await formal recognition. One is the geographical structuring of their six mtDNA clades, which points to earlier vicariance of drainage systems across the Palaeo-Chambeshi archipelago. This could possibly reflect primary cladogenesis induced vicariance during the Early Pleistocene. Cotterill *et al.* (unpublished ms) rejected the PLM hypothesis for two reasons. Radiocarbon dates cited by Joyce *et al.* (2005) have no scientific credibility (Watchman & Twidale 2002; Section 4.8.2), and bioturbation has yet to be explained away with respect to TL dating of fossil shorelines (Macfarlane *et al.* 2005, Section 4.8). Overall, errors in geochemical dating of LPM (and indeed all palaeo-lakes in the Okavango graben to date) has fostered misunderstandings, not least in biogeographic scenarios built around hypothesized tenures. Above all, the detailed revision of the region's prehistory suggests that PLM is even older, and had dried out before the end of the ESA, possibly by early in the Middle Pleistocene, before ~700 Ka (Chapter 5). The alternative explanation for the origin of the south-central species flock is that their speciation occurred in concert with complex dynamics across an archipelago of palaeo-lakes, pertinently Lake Patrick, and Palaeo-Lakes Bulozzi and Thamalakhane (Cotterill *et al.* unpublished ms; Chapter 5).

Subject to complete sampling (especially to remedy lack of data for Katanga), a complementary phylogeographic study of a species complex of riverine cichlid (*Pseudocranilabrus philander*) reveals strong influence of vicariance between populations isolated across the Zambian Congo system, with distinct populations in three drainage systems: Lake Mweru, the Bangweulu-Upper Chambeshi and the Lunzua river (south of Lake Tanganyika, bordering the Chambeshi headwaters). A separate clade, attributable to *P. philander s.s.*, is widespread in the Upper Kafue system, from where it invaded the Upper, Middle and Lower sections of the Zambezi river (Katongo *et al.* 2005). I interpret the genetic structure and speciation in *P. philander* to reflect strong control by vicariance of the Palaeo-Chambeshi drainage system through the Pleistocene.

4.13 COMBINING THE EVIDENCE: SYNTHESIS OF BIOLOGICAL AND GEOLOGICAL DATA

The first part of this chapter has revealed that the wetlands emplaced during the Quaternary and Neogene across the Katanga-Chambeshi region are indeed nascent landforms that existed on an ancient landscape. This principally comprises the African erosion surface, which owes its protracted existence (characterized by senile topographies) to relative quiescence of the underlying craton rich lithosphere. High Africa has prevailed despite considerable episodes of diastrophism since before Gondwanaland broke up. These upheavals latterly involved the rifting across the eastern half of the continent through the

late Cenozoic. This is not to say that uplift of High Africa has not modified the Katanga-Chambeshi region, because warping and faulting has changed its landscapes in subtle, yet profound, ways.

The case of the late Pliocene uplift event exemplifies how prevailing hydrographic conditions are intimately linked with the physiognomy of the encompassing landscape. It cannot be overemphasized how Africa's unusual topography has framed and controlled the evolution of drainage across a range of spatial scales. The most encompassing is the distinct hypsometry of Africa's drainage basins on a continent uplifted persistently within its passive plate margins. This explains how, through much of the Cenozoic, Africa's drainage was dominated by endoreic drainage systems centred around basins, vaguely partitioned across gently sloping swells. This large scale structure of basins and swells reflected underlying uplift and warping of the lithosphere, driven by thermal dynamics in mantle plumes. Thus, the latter has multiple effects. It caused Cenozoic doming and also forged the characteristic basin and swell topography of the African continent (Doucouré & de Wit 2003; Goudie 2005).

I begin this conclusion by revisiting the interesting anomalies in dispersals of tigerfishes. *Hydrocyon vittatus* reached the Upper Chambeshi relatively recently from the Congo system, after the Kamalondo and Mweru depressions, had been severed from the Upper Kafue and its associated floodplains (Kafue Flats and Lukanga). Similarly, *H. vittatus* only invaded the Upper Zambezi after disruption of the Palaeo-Chambeshi. Otherwise, tigerfishes would have gained access into the Upper Kafue, by dispersing northeast across the Machili Flats. This means piracy of the Upper Kafue by the mid-Zambezi occurred before tigerfishes dispersed through the Upper Zambezi. Given that the likely route of dispersal of this voracious predator into the Upper Zambezi headwaters was from the Kasai; then the associated capture events appears to have occurred comparatively late in the Pleistocene, and equally occurred after isolation of the Cuanza from the Kunene; and the Kunene from the Okavango-Kafue graben (Section 5.8).

4.13.1 Drainage Links from Katanga to the Atlantic Coast

A shared, or rather partially shared, history between the Zambezi and Upper Congo fish faunas was first argued by Jackson (1962, 1986) and Bell-Cross (1968, 1972, 1982). The evidence assembled above (Table 4.3, Appendix 3) reveals this history is more complicated than previously considered.

Collectively, congruent zoogeographic patterns assembled in the previous section confirm that a period of unequivocal isolation followed on links between Upper Zambezi-Okavango drainage systems with those in Katanga. This was when each of Katanga's principal drainage systems (notably the Kamalondo) existed in isolation for a protracted period. Previously, long rivers were linked within the Kalahari basin by their

deltas. This has had notable biogeographical consequences, because aquatic organisms could potentially disperse between otherwise remote areas across a vast subcontinent. Dispersant species could reach the watersheds abutting east Africa's rift valleys from those bordering the Atlantic coast along the headwaters of the Cuanza and Kunene systems, and vice versa. This period existed (probably with intermittent breaks) through the period when these rivers deposited considerable sediments in the Kalahari basin. The period began in the Neogene, if not earlier, and persisted until quite recently in the Quaternary.

4.13.2 Possible Extents of Palaeo-Chambeshi Catchments

The Palaeo-Chambeshi not only drained part of the northeast Zambia plateau, but also much of southeast Katanga for at least some period during its tenure. Precursors of rivers that today flow north into Lake Mweru and the Lualaba system, formerly flowed south. This antecedent system included the proto-Upper Luongo, the Palaeo-Kafila, and perhaps part of the present Kalungwishi River (Figs 4.3 & 4.4). Patterns of speciation exhibited in aquatic organisms within these systems, pertinently the Lufira and Kamalondo, underscores past links with wetlands south of the Upper Congo drainages. This arena of faunal exchange extended from Katanga across Zambia across the Kalahari basin. The combined signal in the biogeographical dataset suggests that drainage evolution has controlled speciation and dispersals in the aquatic biodiversity across the south-central African plateau.

4.13.4 The Palaeo-Chambeshi and Palaeo-Lakes in the Kalahari Basin

The evidence summarised above reveals that Palaeo-Lake Makgadikgadi attained its highest levels when interconnected as the terminus within a endoreic drainage systems. This occurred sometime during the Pliocene and/or Quaternary, and inundated a vast part of the Okavango-Kafue graben (60 000 km² - perhaps as large as 120 000 km²). Its 945 m shoreline covered a large area of northeast Botswana and southwest Zambia (Fig. 4.7a). Evidence further suggests that the PLM stage in south-central Africa was followed by the existence of two smaller lakes in the Barotse and Kafue basins, respectively. The 17 000 km² Lake Patrick filled the Kafue Flats for a significant period during the Pleistocene, but had ceased to exist before ~250 Ka. The existence of a Palaeo-Lake Bulozzi does not appear to have been posited previously.

Persistence of each of these palaeo-lakes entailed a complex interplay between drainage, tectonics (and thus topography) and palaeo-climates – especially given the extensive catchment necessary to supply inflows of ~ 88 km³/annum to maintain PLM. The fossil shorelines testify that Palaeo-Makgadikgadi persisted for a considerable period despite large evaporative losses and fluctuating climatic regimes (Shaw

et al. 1997; Moore and Larkin 2001). Alongside the Upper Zambezi, Cuando and Okavango, the Palaeo-Chambeshi system, with its headwaters situated on the Rukwa – Rungwe highlands, is invoked to have contributed significant inflow (Cotterill 2003c, 2004, 2005, Table 4.2). The robustness of a successful reconstruction of the tenure of any one of these palaeo-lakes can benefit from coeval conditions that must have manifested in critical topologies – reflected in coeval landforms that existed together around the Okavango-Kafue graben. For example, the persistence of PLM, in fact its very existence, hinged on inflows of large, perennial rivers (to provide the minimum inflow of 88 km³), so it follows that the dating of its tenure must concur with analogous datings of related landforms: pertinently, the Upper Zambezi River, and the Palaeo-Chambeshi as represented by its Machili delta. Where evidence permits, this tactic of historical reconstruction is applied in Chapter 5.

Pressing questions pertain to when PLM existed. Geomorphological evidence for a complex relationship between the Palaeo-Chambeshi and PLM includes: a delta preserved as the Machili Flats; alluvium (namely OG II) along the upper Zambezi; and the deep clays that underlie the Machili Flats.

Furthermore, gravels contemporaneous with OG II underlie both the Kafue and Machili Flats lacustrine clays. Evidence for their contemporaneity is based on the late ESA artefacts they share in common. These insights need to be reconciled with the evidence for impoundment of the Upper Zambezi in the Kalahari Basin after OG II had been aggraded. Complex interrelationships between these sediments and the events that formed them are discussed in Chapter 5, where I evaluate this, and allied, archaeological evidence in more detail.

4.13.5 The Biogeographical Significance of the Palaeo-Chambeshi Drainage System

The Cuando and Okavango were and remain important tributaries into the northeast Kalahari basin, as was the Upper Zambezi until comparatively recently, and still is linked (via the Chobe) near its Mambova-Simalaha floodplain. With its headwaters abutting the Rungwe-Rukwa highlands, the extent of the Machili alluvium attests to the sustained volume of discharge from the Palaeo-Chambeshi River into the Kalahari basin. Lechwe antelopes can be expected to have occurred widely along the Palaeo-Chambeshi system, as they did along floodplains of the Upper Zambezi-Okavango system across Angola, until extirpations in the 20th century (Cotterill 2005, Chapter 2). The extant distribution of Springhare, *Pedetes capensis* (Forster 1788) reaches its northeast limit in the Katanga Pedicle, abutting the Mukuku Hook (Ansell 1978), geographically distinct from the east African *P. surdaster* Thomas 1902, with the latter's southern distributional limit abutting the Rukwa graben (southwest Tanzania). A plausible explanation to explain the northeast limit in range of *P. capensis* invokes vicariance of the Palaeo-Chambeshi in the Katanga Pedicle,

in tandem with palaeo-climatic controls on Africa's arid corridor (Chapter 6). Further south, modern limits in distributions of several large mammals are most plausibly explained by a common restriction on dispersals by the Palaeo-Chambeshi (including the Proto-Kafue River), and more recently Lake Patrick and the modern state of this landform as the Kafue Flats. The modern, albeit historical, distribution of White Rhinoceros, reached its northern limit along the Upper Zambezi River (Shortridge 1932; Smithers 1983); and it is interesting that this species appears to have occurred in the vicinity of the Kafue Flats in the Middle Pleistocene at the Middle Stone Age site of Twin Rivers (Clark & Brown 2001; Chapters 5 & 6).

The former course of the Palaeo-Chambeshi forms a congruent boundary dividing the ranges of several sister species of terrestrial vertebrates. This suggests the drainage system formed a significant biogeographical barrier, which contained dispersals of terrestrial faunas between northern and southern Zambia. These patterns constitute additional evidence for relatively long persistence of what was once one of Africa's principal rivers (Cotterill, 2003c, 2004). Judging from prevailing topography, the Palaeo-Chambeshi appears to have been a wide, shallow river. This possibly characterized its lower reaches, southwest of the Bangweulu depression. One can expect that its course was especially broadened, if not anastomosed, where it graded gravels across the Kafue graben. River flow obviously declined greatly after scission of the Palaeo-Chambeshi (creating the modern configurations of the Kafue and Luapula-Chambeshi rivers), nevertheless broad floodplains can be expected to have persisted as wetlands of considerable extent, especially when seasonally inundated along much of its former channel(s). Thus, their relevance as continued aquatic habitat, pertinently to lechwes, perhaps persisted after scission of the Palaeo-Chambeshi. This exemplifies how an inductive lag in geomorphological causation can influence biota over a relatively protracted period. In fact, today, this obsolescent wetland continues to contain north-south dispersals of terrestrial organisms, including particular mammals, and several birds (Table 4.4). It is notable that the ranges of two locally endemic birds of conservation concern in southwest Zambia, namely the Black-cheeked Lovebird, *Agapornis nigrigenis* and Chaplin's Barbet *Lybius chaplini* coincide remarkably closely with habitats that owe their existence to (and are directly descendent from) the lower reaches of the Palaeo-Chambeshi (Cotterill 2004; Table 4.4, Fig. 4.11).

4.13.6 The Significance of the Trans-Katanga Drainage and its Vicariance

Clearly, Katanga's wetlands have undergone intervening periods of links with, and isolation from, the Lower Congo and Upper Zambezi. Equally, each has been isolated in its own right as a discrete and

Table 4.4. Species of terrestrial vertebrates where selected pairs of species of birds and mammals with parapatric distributions divided by (and abutting on) the former course of the Palaeo-Chambeshi River in Zambia. See Cotterill (2003a) for further details of mammalian examples. Modified from Cotterill (2003c, 2004).

	Northern-Northwest Zambia	Southern - southeast Zambia	Comments
<i>Camaroptera brachyura intercalata</i>	White 1960	<i>C. b. sharpei</i> (Zedlitz 1911)	Bleating Warblers (maps: Hall & Moreau 1970:191)
<i>Calamonastes undosus cinereus</i>	Reichenow 1887 and <i>C. u. katangae</i> Neave (1909)	<i>C. stierlingi</i> (Reichenow 1901)	Wren-warblers (maps: Hall & Moreau 1970:191; Sinclair & Ryan 2004)
<i>Eremomela atricollis</i>	Bocage 1884	<i>E. usticollis rensi</i> Benson 1943	Burnt-necked, and Black-necked Eremomelas (maps: Hall & Moreau 1970:196)
<i>Papio kindae</i>	Lönnerberg 1919	<i>P. griseipes</i> Pocock 1911	Kinda and Gray-footed Baboons (Ansell 1978: Map 85). Yellow baboon, <i>P. cynocephalus</i> (Linnaeus, 1766) in the Luangwa valley has a complementary relationship to <i>P. griseipes</i> with respect to <i>P. kindae</i> in northeast Zambia (Ansell 1978; Rogers <i>et al.</i> 2004)
<i>Cercopithecus opisthostictus</i>	Sclater, 1894	<i>C. moloneyi</i> Sclater, 1893	Blue and Moloney's Monkeys (Ansell 1978: Map 82)
No representative of the <i>G. camelopardalis</i> complex occurs		<i>Giraffae camelopardalis infumata</i> Noack 1908	Angolan Giraffe is confined west and south of the Upper Zambezi river. Blue Wildebeest is confined west and south of the Upper Zambezi river, with what appears to be an isolated population in central Zambia confined between the Zambezi and Upper Kafue rivers. The Zambian endemics <i>G. thornicrofti</i> Lydekker 1911 and <i>C. cooksoni</i> Blaine 1914 are confined to the Luangwa valley (Ansell 1978; Cotterill 2003c)
<i>Connochaetes taurinus</i> cf <i>taunmus</i> (Burchell 1823)		<i>Connochaetes taurinus</i> cf <i>taurinus</i> (Burchell 1823)	Crawshay's and Common Waterbucks (Ansell 1978: Map 135)
<i>Kobus crawshayi</i>	P. L. Sclater 1894	<i>K. ellipsiprymnus</i> (Ogilby 1833)	

persistent geomorphological entity. Durations of this vicariance were sufficiently prolonged (exemplified by Kamalondo and Mweru), that their faunas gained a significant component of endemics. Brown (1994) concluded that the distinct mollusc fauna of Lake Mweru evolved in a formerly much deeper lake. Independently, Dixey (1944, 1955a) arrived at the same conclusion using geological evidence fifty years earlier. The occurrence of Zambebian fishes in Katanga's rivers confirms northward dispersals, perhaps across the contemporary Congo-Zambezi watershed, as suggested by Bell-Cross (1965b, 1982). The expanded biogeographic dataset in this study suggests these dispersals were relatively recent. These likely represent the most recent event that has enriched the biodiversity of Katanga's wetlands. Thus, three stages ensued. In the first, dispersals through the Trans-Katanga and Palaeo-Chambeshi presumably mixed faunas via connected drainages. Thereafter speciation elevated endemism in these isolated drainage systems. The most recent biogeographic event entailed range expansions of contemporary Zambebian and also Lower Congo species into Katanga's rivers.

Only further research can decipher precisely when these hydrological links existed. The model sketched out by Moore & Larkin (2001) and Cotterill (2004), while heuristically useful, could only guess at timings of hypothesized events. This especially applies to the history of the proposed Trans-Katanga drainage which interfaced closely with tenure(s) of Palaeo-Lake Lufira. Nonetheless, this study has advanced somewhat to identify principal patterns and mechanisms to explain these interesting facets of the late Cenozoic history of Africa. The Katanga Pedicle centred around the Itawa Dambo and Kafulafuta - Muniengashi rivers constitutes a zone of vibrant geobiotic dynamics. Across this zone, rearrangements of landforms involved the Bangweulu and Mweru depressions, the Palaeo-Kafila and the Luongo-Kalungwishi drainage system. Detailed studies of these extant landforms should reveal missing details sorely needed to refine the narrative of biotic and landscape evolution. These details should tell us a great deal about where and when the ancestors of the Upemba, Black and Roberts lechwes could have dispersed.

4.13.7 Coeval Landforms and Timings of Geomorphical Evolution

Ebinger & Sleep (1998) suggested that Cenozoic magmatism resulted from the impact of a single plume under east Africa. This has also been associated with repeated faulting and uplift in separate events across the EARS. It is interesting that far reaching effects ramified from these pulses, and created coeval landforms whilst significantly altering existing relief

(such as the Upemba horst). Radioisotopic dating constrains these events fairly tightly, thanks to the volcanic formations interbedded within alluvial and lacustrine sediments. These eruptions of ash and lava coincided closely with significant diastrophism; thus lavas and tuffs are interbedded with lacustrine sediments displaced along faults.

The evidence for regional effects following on single geological agencies are difficult to prove conclusively. Nevertheless, evidence along the Albertine rift strongly suggests that lacustrine sediments were uplifted in a series of discrete, coeval events through the Pleistocene. These can be dated from the Virungas, southwards above Lake Tanganyika, to the northern margins of Malawi. Haldemann (1969) described Pleistocene sediments, in northeast Zambia, uplifted up to 300 m along the southwest margin of Lake Tanganyika. On the Rungwe plateau, Delvaux *et al.* (1992) showed that two volcanic eruptions delimit initiation of a significant pulse of faulting to between 560 ± 10 and 420 ± 30 Kya. Sedimentation was terminated within the Rungwe region after this episode of tectonic activity. The focus of volcanic activity in the Rungwe highlands lies at a triple junction between the Malawi, Usangu and Songwe basins, all under stress of radial extension. It is logically assumed that the Katanga and Mweru rifting events can be correlated with this diastrophism. Furthermore, their effects can be expected to have propagated west and southwest into the Kalahari basin, and perhaps even further west. As far as the evidence permits, this subject is explored in the next chapter (Section 5.8).

4.14 CONCLUSIONS

"From the presence of large stone implements of very primitive type in certain of the gravel terraces of the Gwaai system, it follows that the upheaval took place just before the advent of man, and hence somewhere about the close of the Pliocene epoch" A. L. Du Toit (1933: 14)

4.14.1 Buffered Landforms in Ancient Landscapes

Landscapes exhibit a spectrum of responses in how rapidly they react to perturbations. Buffered landscapes are those characterized by slow changes, so they persist under a regime of frequent, repeated disturbances from exogenous agencies; and these contrast starkly against how reactive landscapes change rapidly when disturbed (Allen 2005; Allen & Allen 2005). The majority of landforms, if not the encompassing landscape, of Africa's hinterland appears to be dominated by buffered landforms. And they dominate the topography of the Katanga-Chambeshi region. As argued by Twidale (2005), such

buffered landforms can be recognized as lineages because they have survived many millions of years of extreme disturbances, where tectonism and erosion worked in tandem to destroy many other continents and landforms. An important theme emerging in this thesis is that lechwe antelopes represent a species complex in a biota that has evolved recently on ancient landscapes.

Remarkably extensive vestiges of ancient landscapes testify to the geomorphological antiquity of High Africa. High Africa has existed for tens of millions of years. Many of its original landforms have survived uplift and warping since long before the break up of Gondwanaland (127 Mya). The factors responsible for its persistence have acted in synergy. These include peculiarities of the geometry of the African plate. The latter's unusual stability has greatly facilitated protracted weathering, which, under tropical conditions, etched landscapes through the Cenozoic. This accretive action ultimately etched regoliths to great depths. Together, deep regoliths and ancient architecture of the African erosion surface underpin this buffering capacity of High Africa. The extant properties of these extensive portions of the African erosion surface, and younger landforms, represent how landscapes have accommodated repeated warping and faulting of the hinterland.

Drainage networks have been central players in this theatre of geological evolution across the Katanga-Chambeshi region. Because these hydrographic systems are dominated by shallow basins (supporting floodplains and shallow lakes) even slight epeirogenic changes tended to exercise radical effects on hydrology. This is seen where minor uplift and downwarping affected the Upper Zambezi and Bangweulu systems in radical ways. Only very late in the Cenozoic has runoff from Katanga and northeast Zambia flowed northwest, through the Congo, to ultimately reach the Atlantic Ocean. Likewise, only recently did the Upper Zambezi, Upper Kunene, Chobe, Upper Kafue (and ultimately the Okavango!) become parts of exoreic drainage systems. Alongside many other organisms, the distributions of lechwe antelopes appear to have been affected greatly by these intricate dynamics of late Cenozoic landscape evolution.

4.14.2 Landscape Evolution and Biogeographical Patterns

Patterns in the diversity and endemism of aquatic biota in Africa's rivers and lakes testify to the adage, favoured by panbiogeographers, that life can be conceptualized as the fourth geological layer. The congruence of biogeographic signals amongst extant fishes points to how basins have been previously linked. The significant endemism of the principal hydrographic basins in northeast Zambia and Katanga testify that these landscapes also persisted as isolated entities. As exemplified by the Bangweulu,

Kamalondo and Mweru graben, their vicariance was sufficiently protracted that numerous endemic fishes and molluscs have evolved. These patterns structure hypotheses to test how these episodes of geological history affected populations of the *Kobus leche* complex. This principal aim structures Chapter 6.

The spectrum of geological, climatic and biological evidence, available to this synthesis, has revealed a complex history of landscape evolution. It is abundantly clear that the region's biodiversity has been changed inexorably by dynamics in hydrographic systems. Nevertheless, it is far from clear when important events occurred in these biological and geological realms. This is an important weakness that decrees further study, and especially weakens our understanding as to when antecedent drainage configurations changed into the extant hydrographic networks of the Katanga-Chambeshi region. Tighter constraints on timings of capture events of the major rivers are especially relevant to reconstruct when key events occurred in the evolution of biota and landforms.

4.14.3 The Importance of Robust Dating Constraints on Evolutionary Events

Considerable uncertainty surrounds when palaeo-lakes existed in northeast Botswana before the Holocene. This review has concluded that radiocarbon dates of Kalahari landforms have no scientific applicability – especially toward framing biogeographical explanations. These problems mean that their application is no longer tenable to delimit tenures of the Palaeo-Lake Makgadikgadi, as well as the inferred Caprivi and Thamalakhane palaeo-lakes.

Analogous uncertainties are attached to thermoluminescent (TL) ages determined for certain Kalahari group sediments. Nevertheless, great faith continues to be placed on their purported dating of significant geomorphological events, notably tenures of aeolian and lacustrine landforms in the Kalahari basin. It remains to be established how much these statistics represent effects of burrowing by soil-dwelling organisms (especially termites) instead of larger scale processes caused by palaeo-climates and palaeo-drainage. This problem is complicated, where weaknesses in these TL dates (and, surprisingly even radiocarbon dates of calcretes) continue to escape critical scrutiny by editors and peer-reviewers; such that prominent journals have featured far reaching reconstructions of biogeographical and climatic patterns founded on shaky geomorphological reconstructions about the Kalahari basin. It appears that dogmatic beliefs can be hard to overturn, especially where they support attractive hypotheses. These uncertainties suggest that a more scientifically responsible tactic is to place all TL dates in quarantine, until compounding effects of bioturbation can be discounted.

Weaknesses in the applicability and reliability of geochemical dating methods dictates that alternative evidence must be sought to refine the chronology delimiting Plio-Pleistocene evolution of the Katanga-Chambeshi region. By definition, such a narrative of landscape evolution is challenged to delimit timings of the key events that saw landforms change, disappear and appear. This bears directly on understanding important patterns of biotic evolution across south-central Africa. In terms of their aetiological impacts, the dynamics intrinsic to Neogene and Quaternary palaeo-environments had far reaching effects. Palaeo-climates are repeatedly invoked as having caused a spectrum of patterns. In addition to a wealth of biogeographical patterns (some summarized in this chapter), palaeoanthropology and archaeology reveal how radically hominids across Africa were affected by dynamics of past climates and landscapes through the late Cenozoic. The next Chapter mines this fascinating wealth of data residing in the literature of palaeoanthropology and archaeology. Knowledge gained in these intensively researched fields can be applied, surprisingly as it may seem, to answer key questions as to when and where lechwe antelopes evolved.

Despite the paucity of hominid fossils so far excavated within the Katanga-Chambeshi region, a relatively detailed knowledge exists about where and when Stone Age industries existed. It is most convenient that so many known Stone Age sites are situated close to principal rivers. In fact, many are sited within key landforms of Quaternary vintage flagged as critical to answer pressing questions of this study. Remarkably, hominid lithics came to be preserved in revealing abundance within sediments of palaeo-lakes and extinct rivers that dominated the evolution of the Katanga-Chambeshi region! A wealth of archaeological evidence has been documented along the edges of the Upper Zambezi around Victoria Falls, and is complemented by important sites in Angola, Botswana and Zambia. The tenures of all these sites relate directly to key events during the Quaternary that saw drainage changed radically across the Katanga-Chambeshi region. My objective is to review pertinent data, compiled in this chapter, in the context of the archaeological record. Compared against uncertainties attached to purported ages of Kalahari sediments, far more reliable ages are delimited for hominid cultures, with their tenures delimited by panoplied dating. What we know about when these successive Stone Age cultures existed rests on different sites, in far-flung locales, whose tenures have come to be interlinked closely by intensive research - dated by a combination of geochemical techniques. So it turns out that the archaeological record is of great relevance to refine the narrative of landscape evolution, compiled in this study. Its precision is further reinforced when correlated against the record of Pleistocene climate change. Synthesis of all these data is the task of Chapter 5, with its geographical focus on the Batoka

Gorge eroded by the Victoria Falls. This synthesis is the logical progression to sift key evidence, laid out above, toward refining the model of drainage evolution presented at the end of Chapter 5.

“Perhaps the best model for what is going on, and should be going on, is the emergence of plate tectonics in the second half of the 20th century. With new instruments, new techniques and new theories, it was possible to understand the forces that shape the evolving earth, to reconstruct the movements of plates, continents, *and other individuals* over vast periods of geological time, and to tell the story of the earth as it really happened.” M. T. Ghiselin (2005b: 102 *italics his*)

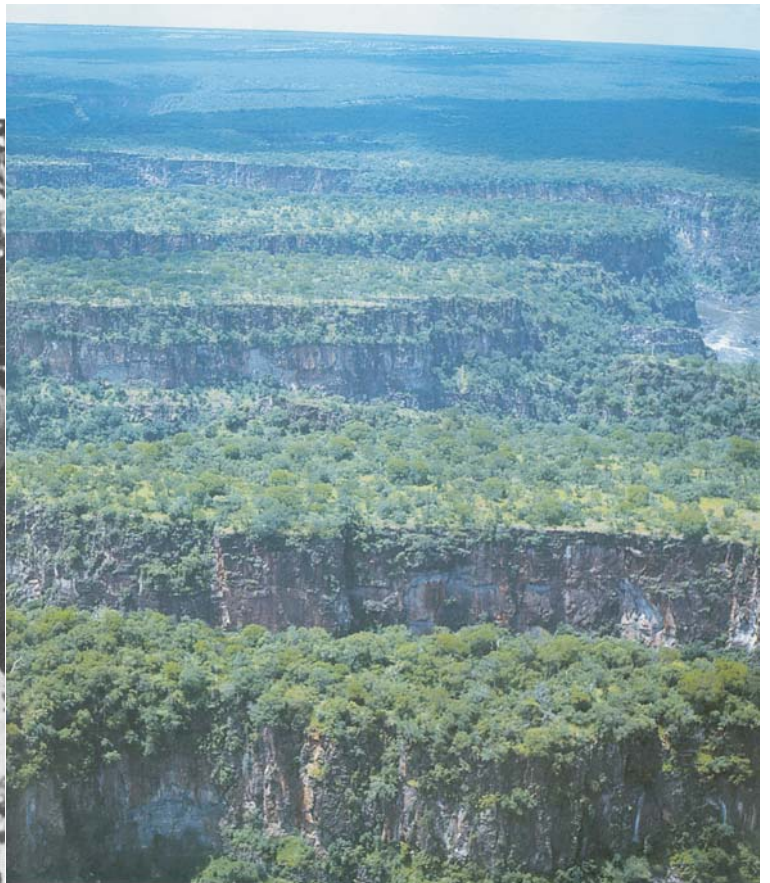
CHAPTER 5



View north west across the Victoria Falls and the Upper Zambezi River
Photograph: Jan and Fiona Teede

View east, downstream of Victoria Falls, of the western Batoka Gorge incised by the Zambezi River through the Pleistocene
Photograph: Jan and Fiona Teede

Sangoan handaxe (early Middle Stone Age) indurated in ferricrete at N'gonye Falls, Upper Zambezi River
Photograph: Northern Rhodesia Information Department



CHAPTER 5. DATING THE BATOKA GORGE, AND CONSTRUCTING A MODEL OF DRAINAGE EVOLUTION OF THE WETLAND ARCHIPELAGO

"The finding of primitive stone implements in the old agate-bearing gravels on the Zambezi at Victoria Falls, which were laid down before the lip of the cataract had, under headwater erosion, retreated to its present position, points to the immensity of time since Palæolithic man first dwelt in that neighbourhood." A. L. Du Toit (1933: 19)

5.1 INTRODUCTION

The evidence collated through Chapter 4 still awaits the justice of being structured into a narrative of evolutionary history. The final section of this chapter presents this interpretation of late Cenozoic landscape evolution of the Katanga-Chambeshi region. The previous chapter left unfinished the task of stitching all the combined evidence together into a refined narrative of landscape history. The precision of such a synthesis depends entirely on how well one can estimate when key events occurred. If they can be delimited with improved precision, then it follows that a greatly resolved understanding of their respective tenures will be conferred as to when significant wetlands in the region appeared, disappeared, and changed. These major palaeo-lakes existed within vast drainage systems, and evidence further suggests they were altered by cotemporaneous events, especially episodes of tectonic activity that ramified through the EARS. With respect to localized, well studied areas, this connectivity allows application of chronological insights, admittedly with reservation, to landforms elsewhere across the Katanga-Chambeshi region that await direct dating.

Although Barham (2000) placed great credence on a chronology of Kalahari sediments reliant on luminescent dating (collated by Stokes *et al.* 1998), severe problems with their reliability were not considered. Uncertainties attached to dates of Kalahari sediments obtained by radiocarbon and luminescent methods have been emphasized, and remain a problem in more recent studies (e.g. Bateman *et al.* 2003; Ringrose *et al.* 2005). Most unfortunately, accretional growth patterns of calcretes, and bioturbation of aeolian and lacustrine sediments obviate their respective reliabilities. So, one must seek other means to date critical events in the evolution of the Katanga-Chambeshi region (Section 4.9.2). Fortunately, alternative chronological indicators exist. Where correlations permit, reconstructions of Quaternary landscape evolution in Africa can benefit greatly from the relatively well resolved chronology of Stone Age prehistory.

The previous chapter also did not pay deserving attention to the relatively recent evolution of the Upper Zambezi river. So, a summary of its history, since late Neogene times, is presented below; and this review describes in detail the evolution of an interesting region of this long river. This is that

portion of the Zambezi's channel (and valley) between the Barotse basin (Bulozi floodplain) and the Gwembe Trough. Close scrutiny of its late Cenozoic evolution in fact serves to focus the aims and content of this chapter. My aim is to derive critical, and much needed, chronological insights through the scrutiny of the history of a complex of landforms. They are all confined along the Upper Zambezi river, downstream of the Okavango graben. Geographically, this intensive study area straddles the international border shared between Zambia and Zimbabwe, west of the Gwembe trough (Fig. 5.1). I specially focus on the sediments comprising the Victoria Falls Formation (VFF), whose evolution, and modern context, interrelates with the Batoka Gorge incised by the Zambezi. This study area lies squarely at the centre of the Four Corners Trans-Frontier Conservation Area linking some of Africa's largest protected areas in Angola, Botswana, Namibia, Zambia and Zimbabwe (Cotterill 2003d; Moore 2003).

Rich deposits of hominin artefacts in the Zambezi's sediments provide unique insights into the late Cenozoic history of the region. Detailed studies of the region's archaeology (Clark 1950; Dixey 1950) revealed that a succession of Stone Age cultures are preserved in the VFF. Since then, major gains in knowledge have rendered the terminology of these VFF data obsolescent. So, a key task in this chapter entails updating names of Stone Age cultures and their palaeo-environmental contexts. Here I pay special attention to refined reconstructions of Pleistocene climatic variation, toward updating the stratigraphy of the VFF.

Where these archaeological signals can delimit ages within the Quaternary history of the wetland archipelago; they can, ultimately, contribute to understanding biogeographical problems - pertinently to establish when key events occurred in the evolution of the *K. leche* complex. It turns out signals in the VFF are critical to date formative events across the Machili and Kafue Flats. My strategy is to first describe important details of the archaeological evidence; then, based on a revised stratigraphy of the Victoria Falls Formation (VFF), reassess the erosion history of the Batoka Gorge. Particular attention is placed on dating each hiatus when erosion by the Zambezi river ceased. Moore & Larkin (2001) suggested this break in river flow through the Batoka Gorge reflects its diversion into northeast Botswana to maintain Pleistocene palaeo-lakes, notably PLM. An important discovery in this Chapter is that there were in fact two, and not just one, period when the Zambezi did not flow through the VFF.

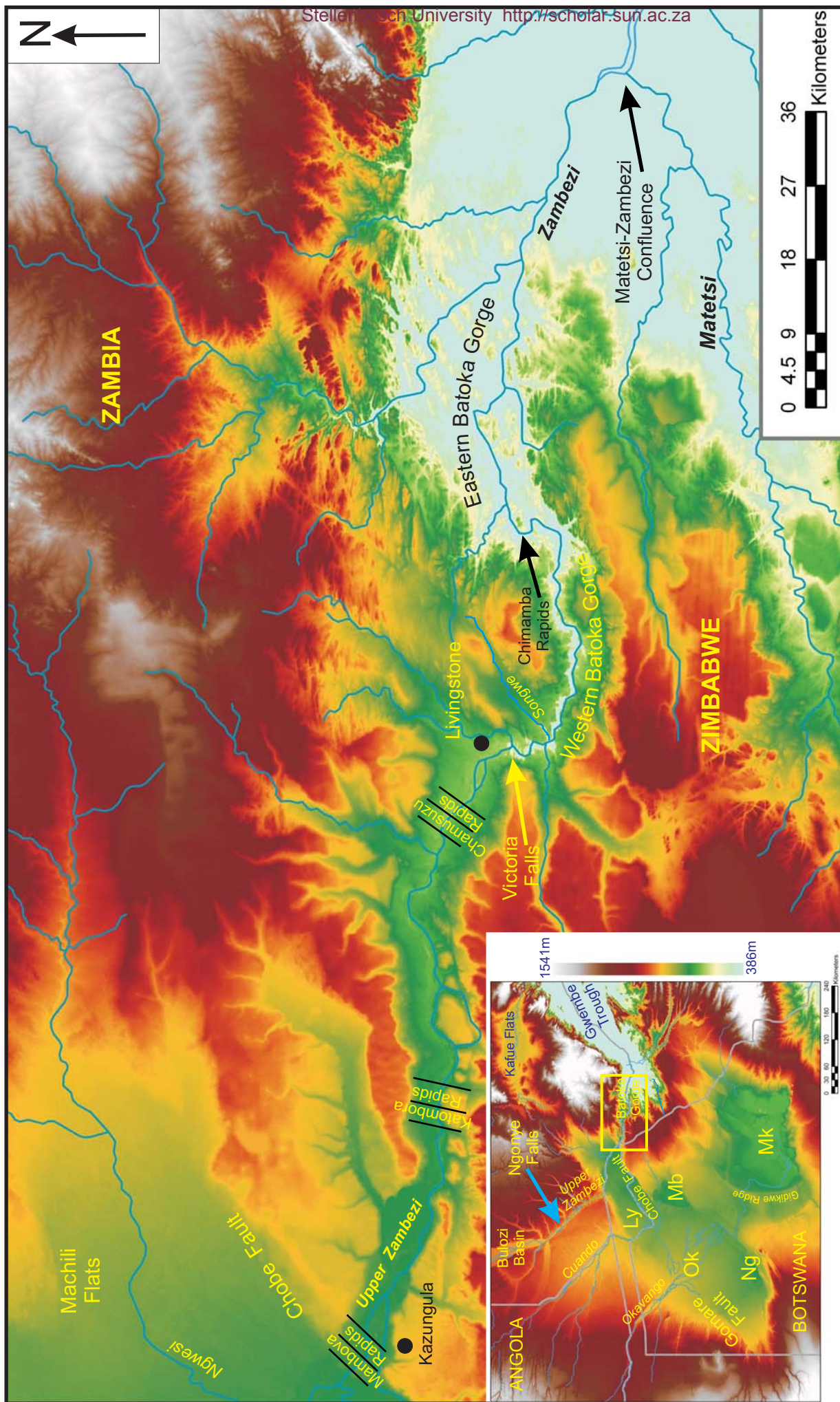


Figure 5.1. Overview of a portion of the “Four-Corners” region of south-central Africa, centred on the international border shared between Angola, Botswana, Namibia, Zambia and Zimbabwe. Details of the Upper Zambezi valley are the focus of the review of landscape evolution in this chapter. Principal rapids in this chapter are labeled. The Batoka Gorge, approximately 100 km in length, is situated between the Victoria Falls and the Matetsi-Zambezi confluence. Neogene and Quaternary sediments formed by the erosion of the Upper Zambezi (downstream of the Mambova rapids to the eastern end of Batoka Gorge) are termed the Victoria Falls Formation (VFF), and are interrelated with the Batoka Gorge. Through their evolution, particular landforms in the Barotse basin and Okavango-Kafue graben have interacted closely with that of the Upper Zambezi river, and are labeled on the smaller, inset map. The abbreviated labels of the drainage basins in northeast Botswana follow Fig. 2.2.

Thus pertinent evidence collated in this chapter delimits two interrelated sets of events in the Pleistocene. One is to reconstruct when the Zambezi river eroded the Batoka Gorge. The second is to employ this refined history, where applicable, to constrain when key events in drainage evolution occurred. It turns out that the archaeological record provides the best available evidence to build a chronology.

In toto, the insights obtained in this chapter also provide hitherto unavailable constraints on timings of key events in landscape evolution across the Katanga-Chambeshi region. The rich archaeological record of the VFF is a most fortuitous asset, given its geochronological functions. And its geographical situation is equally fortuitous; because it abuts the Okavango-Kafue graben, and evolution of its sediments has been intimately related with that of the Batoka Gorge. Moreover, all three landforms can be seen to form a critical node. They all lie in a zone where principal drainage networks, with farflung catchments, have experienced a long and complex history of links. Suffice to say, the chronology delimited in the VFF has surprisingly broad application, wherever the history of a landform can be correlated to palaeo-hydrological conditions in the Okavango-Kafue graben and the Batoka Gorge. As depicted on Fig. 5.1, the interlinked events of key interest comprise:

- tenure of palaeo-lakes, pertinently: Palaeo-Lakes Makgadikgadi (PLM) and Thamalakhane (PLT) in northeast Botswana; and Lake Patrick in central Zambia.
- the timing of scission of the Palaeo-Chambeshi river from the Upper Zambezi river and other endoreic tributaries including the Upper (Proto-) Kafue, with these periods all interlinked with tenures of significant palaeo-lakes.
- scission of the Palaeo-Chambeshi headwaters (from the Proto-Kafue river) that isolated the Upper Chambeshi and Bangweulu basin, when drainage around the Mweru rift system was changed radically;
- delimiting when the trans-Katanga drainage existed, and so connected wetlands in the Kamalondo and Lufira depressions with major wetlands to the south.

5.2 DATA SOURCES AND TERMINOLOGY OF THE ARCHAEOLOGICAL RECORD

Pioneering efforts (Lamplugh 1906, 1907, 1908; Du Toit 1933; Armstrong & Jones 1936; Dixey 1944, 1950; Clark 1950; Wayland 1954) demonstrated the potential of dated stone age artefacts to

reconstruct when certain Quaternary landforms existed in south-central Africa. Pertinently, archaeological evidence in alluvial sediments revealed that the Zambezi river had incised the Batoka Gorge not only rapidly but also recently (Clark 1950; Derricourt 1976). Analogously, Stone Age artefacts constrain ages of palaeo-lakes in northeast Botswana (Grove 1969; McFarlane & Segadika 2001). One challenge in this chapter is to revise these archaeological archives in the context of reappraised dates for when complementary prehistoric cultures existed. New dates and archaeological excavations from Kenya (McBrearty 2001; Deino & McBrearty 2002) and Zambia (Barham 2001, 2002) underwrite significant revisions in the timing of critical episodes in human evolution. Most importantly, these reveal that key events occurred far earlier in the Pleistocene than traditionally believed. Together with refined, and deeper resolution of climatic reconstructions, I apply these revised insights to establish when key geomorphological events occurred in the Katanga-Chambeshi region.

Publications pertaining directly to the archaeological record of the Katanga-Chambeshi region first appeared in 1905. Given that one has to be careful to update their now obsolescent terminology, when relating it with current geological and archaeological evidence, I follow Barham (2000, 2001, 2002) and McBrearty & Brooks (2000) in their archaeological terminology of the Early, Middle and Late Stone Age cultures: hereafter the ESA, MSA and LSA, respectively. An alternative, and useful, rendition of this terminology was proposed by Clark (1968), updated by Lahr & Foley (2001). This equates early ESA (Oldowan) to Mode 1; late ESA (Acheulian) industries to Mode 2; early and mid MSA (Sangoan and Lupemban, respectively) to Mode 3; with later middle to late MSA (Still Bay, Tshangulan, Howieson's Poort, respectively) assigned to Mode 4; and Late Stone Age (Wilton) to Mode 5. The terminology of MSA cultures is indeed confusing, and has been somewhat mired in controversy. Fortunately, the Pan-African nomenclature was recently refined by McBrearty & Brooks (2000), with further resolution obtained by Barham (2000) and Wurz (2002) in Zambia and South Africa, respectively. The affinities of what Clark (1950) termed the Magosian in the VFF is discussed in detail below.

It is important to emphasize that monikers for prehistoric cultures bracket segments in what was a continuous progression in human evolution. This is well demonstrated in late MSA sequences studied by Harper (1997), who cautions against placing too great an emphasis on named cultures. Equally, Wurz (1999) cautions against delimiting cultural successions into typological assemblages. Many of the issues at stake in archaeological classifications parallel those challenging systematists' efforts to classify biodiversity into microtaxonomic entities. So the arguments detailed in Chapter 3 apply to each

of the unique tools preserved in the archaeological record; each a product of human ingenuity. It may appear extreme to argue that stone tools constitute a human's extended phenotype. Yet, in important respects, they would have had inherent consequences for fitness, whether products of learned or inherent behaviours in Plio-Pleistocene hominids. This applies to MSA and LSA humans especially. To conclude, the classifications of Stone Age cultures serve as heuristic guides to complex, continuously changing cultures, which do nonetheless (and most fortunately) present us with discernable characters. So their occurrences can be correlated across different sites across Africa.

5.3 THE TRANSITION FROM THE EARLY STONE AGE (ESA) TO MIDDLE STONE AGE (MSA)

Archaeological evidence is preserved in the sediments associated with several of the larger wetlands in the Katanga-Chambeshi region. Many of these are of Middle Pleistocene antiquity. Latterly, they have received great interest, because their artefacts figure centrally in the ESA-MSA transition. This subject has attracted unprecedented attention from archaeologists and palaeoanthropologists over the past two decades. Considerable attention and research has focused on this transition from the ESA to MSA. New evidence (especially refined geochemical dating) reveal that this significant cultural change occurred in the Middle, and not as recently as the Late Pleistocene. As importantly, the weight of evidence now reveals that tropical Africa has been the theatre where this ESA-MSA transition occurred. A fresh look at this old evidence reveals that behavioural innovations, characterizing the early MSA, centred around the southern and eastern edges of the Congo basin, and extended to east Africa. This revokes traditional beliefs that the origins of symbolism were confined to the Palaeartic quite late in Late Pleistocene Europe (Barham 2002; Henshilwood & Marean 2003; Marean & Assefa 2005). Nevertheless, it has proved most challenging to date these older African deposits confidently, which has led to this period being labelled the “Muddle in the Middle” (Brooks 2003). A major reason is the chronology, relating to their Middle Pleistocene occupancy, lies beyond the application of radiocarbon dating and requires refinements of relatively new Radioisotopic and Electron Spin Resonance technologies (Schwarcz 2001). Nevertheless, important insights have been gained over the past decade. Understanding where, how and why the ESA-MSA transition occurred is a major challenge in palaeoanthropology. The answers will tell modern humans a very great deal about what is presently an obscure, yet critical, event in our evolutionary history (Tattersall 1991; Johanson & Ellery 1996; McBrearty & Brooks 2000; Henshilwood & Marean 2003).

So what exactly characterizes the ESA-MSA transition? A relatively rapid transition in hominin behaviour occurred during the Middle Pleistocene. It manifested rapidly in novel ways of

manufacturing stone tools. Middle Stone Age lithics reflect a shift in reliance from hand held to hafted implements. So, this transition entailed a shift from large Acheulian handaxes and cleavers (and also small flakes) to smaller, more finely knapped blades that could be hafted onto wooden handles. Furthermore, ochre (of universal symbolic significance) began to be used for the first time in central and east Africa in the early MSA (McBrearty 2001; Henshilwood & Marean 2003; Marean & Assefa 2005). Over the past decade, refined isotopic dating methods, together with new evidence, have revised dates for late ESA and early MSA sites downwards, in time, back into the Middle Pleistocene, to reveal these living sites are much older than traditionally believed.

An initial impetus for this revision of prehistoric dates, and recognition of African origins of the human revolution was the demonstration through the 1980s that the late MSA in the southern Cape (South Africa) was much older than then generally believed. In this respect, a key indicator is the Howieson's Poort culture - dated between 70 000 - 50 000 yrs BP (Deacon 1989) and subsequently confirmed by a combination of dating methods (Wurz 2002, 2005; Jacobs 2005; Tribolo *et al.* 2005). These revisions revoke established archaeological lore, and have been only grudgingly accepted by the archaeological community (Henshilwood & Marean 2003; Deacon 2004). They not only overturn the original postulation that the ESA-MSA transition occurred recently in the Late Pleistocene (~50-100 Kyr BP); but endorse the antiquity of symbolism in Africa. Dated artworks from South Africa's Cape Province further confirms that symbolism evolved in the Middle Pleistocene (Henshilwood *et al.* 2002; McBrearty 2002). We now have to reconcile with a scenario that places the ESA-MSA transition around 250 Kya, in the Middle Pleistocene - in tropical Africa. McBrearty & Brooks (2000) concluded that late Acheulian and early MSA sites cluster between 200 - 300 Kyr and then disappear from the archaeological record. Twin Rivers in central Zambia is one of the very few securely dated MSA sites, with earlier MSA tools (Lupemban) and also ochre. It is constrained between 300 and 265 Kya (Barham & Smart 1996; Barham 2002). Faunal associations at Twin Rivers confirm a Middle Pleistocene palaeo-environment (Clark & Brown 2001; Avery 2003), as does scattered evidence associated with early MSA (Sangoan lithics) around 400 Kya, and perhaps even as old as ~500 Kya in Kenya (McBrearty & Brooks 2000; McBrearty 2001; Barham 2002).

On the basis of these dates, it is reasonable to infer that the ESA to MSA transition in south-central Africa occurred before 200-300 Kya, and perhaps as early as 500 Kya. The scant evidence makes it unclear whether or not this transition was diachronous across east and south-central Africa. Recent $^{40}\text{Ar}/^{39}\text{Ar}$ dating of volcanic sediments delimited early MSA (Sangoan) tools and ochre deposits with hominin fossils at Kapthurin, East Africa to 510 - 512 Kya (McBrearty 2001; Deino & McBrearty

2002). This constraint has far reaching implications for the antiquity of the early MSA in Zambia, but more especially to constrain dates of geomorphological events relevant to this study. Following McBrearty (1988) and Barham (2001, 2002), these early MSA artefacts in the VFF are called Sangoan, although some authorities have equated them with late ESA (Kuman *et al.* 2005), and they are equivalent to the Charaman industry of Zimbabwe (Cooke 1966, 1978). Unfortunately, Barham (2000) chose to ignore valuable evidence (Clark 1950) for the Sangoan in the VFF, and treated the Lupemban as the oldest MSA culture recorded in central Africa.

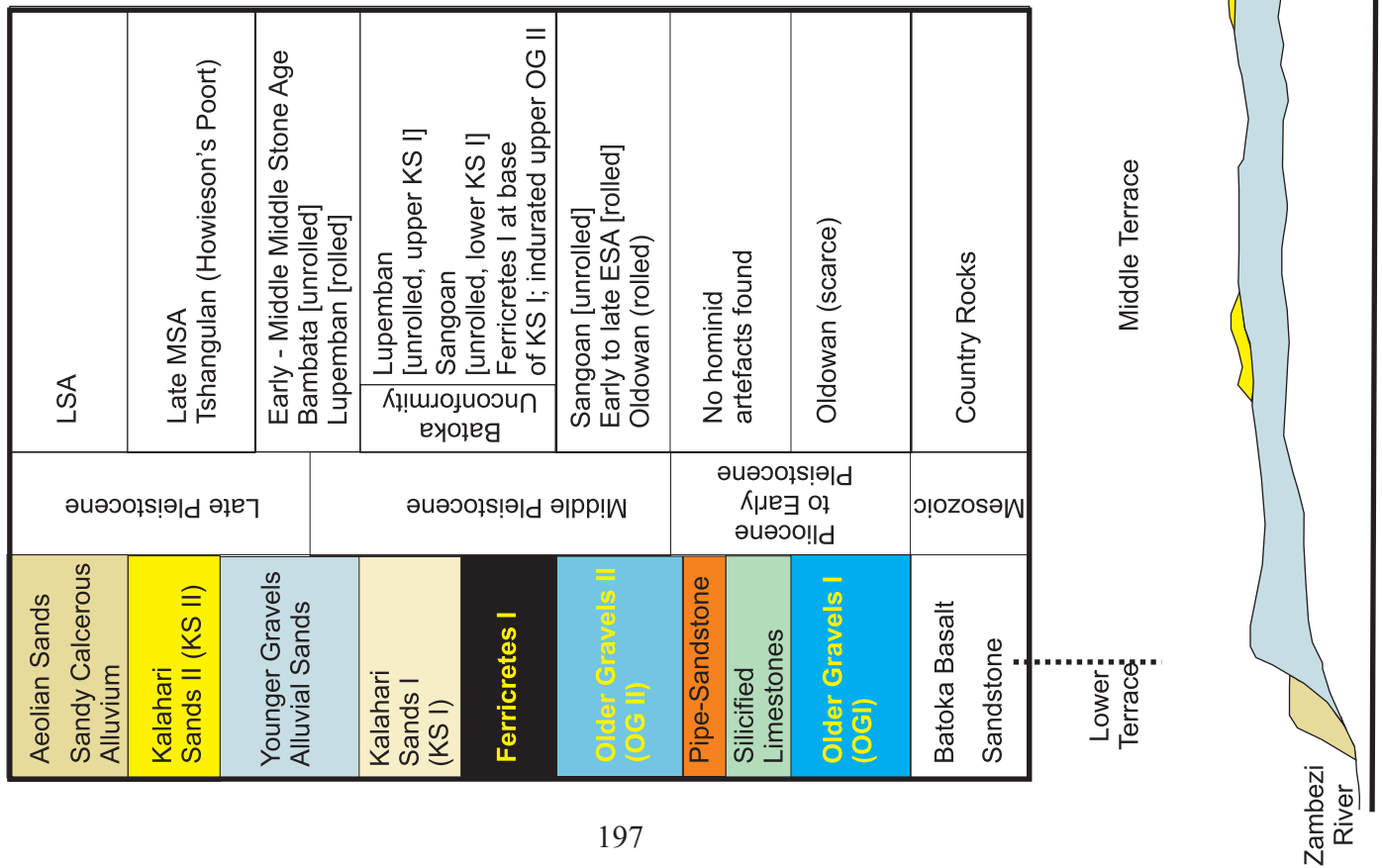
5.4 EVOLUTION OF THE ZAMBEZI RIVER

“The Zambezi, its tributaries and streams no longer part of the system provide a copybook example of the formation of a modern river from several ancient water-courses. In the past, the Zambezi has experienced river capture, watershed migration, continental warping and confluence across floodplains. Each event has contributed to the fauna, and differences along the river are explainable in these terms. In addition, the relationship between Zambezi stocks and those of adjacent systems, notably the Congo, becomes easier to understand.” P. N. B. Jackson (1986: 269)

The extant configuration of the Zambezi river is geologically recent, from two very different sections conjoined recently into a novel topology. This event was related intimately to more regional geomorphological changes, which influenced landforms across and outside the Zambezian region. The evolution of the Zambezi has been a research focus by geologists for several decades, and its heterogeneous nature (the two different sections) was suggested by Du Toit (1933). Principal events in its evolution are now fairly well understood (Moore & Larkin 2001; Moore *et al.* 2006), but major uncertainty centres on the erosion history of the Batoka basalts. Here, the Victoria Falls testifies to how the Zambezi has incised ~100 km of gorge. This formation is of special interest, because this is where the Middle Zambezi has captured the Upper Zambezi in at least two discrete events, represented by a least one break in erosion of the Batoka Gorge. The Upper Zambezi was probably first pirated late in the Pliocene, and then again in the Pleistocene. It has proved very difficult to decipher more precise constraints around these events. One contribution to these uncertainties relates to ages of lacustrine sediments in northeast Botswana, and tenures of associated palaeo-lakes. Erroneous signals from calcretes (see Shaw 1988a,b) and latterly the TL dates presented by Ringrose *et al.* (2005) constitute false signals that are better ignored for reasons discussed in Chapter 4.

Resolving these problems is difficult to carry out in isolation, because all evidence points to tectonic activity in the Okavango-Kafue graben as the ultimate control over landscape evolution in this region. It follows that river piracy and tenures of palaeo-lakes share interwoven histories, most pertinently

Figure 5.2. Schematic transect of the three principal terraces within the wide valley of the Upper Zambezi river (only north bank depicted) above Victoria Falls, to illustrate stratigraphic relationships among alluvial and aeolian sediments. Stone Age artefacts preserved in respective sediments are listed in the legend. In this region of the river, YG I is confined to the Middle Terrace, with Older Gravels II (OG II), capped by Ferricretes I and KS I, confined to the Upper Terrace. The Batoka Unconformity represents a break in alluvial deposition, when KS I covered the entire valley. Much of KS I has been eroded subsequently from valleys. Deposition of Kalahari Sands II (KS II) is inferred to have occurred between 71 - 57 Kya in Marine Isotope Stage (MIS) 4. Vertical axis exaggerated, not to scale, and distances and heights are approximate estimates. This diagram was compiled from illustrations and descriptions in Clark (1950) and Dixey (1950).



with the events entailing formative river captures that centred on sequential piracy events by the Middle Zambezi river (Moore & Larkin 2001). Clearly, understanding the more recent history of the Zambezi's evolution dictates attention to several interrelated phenomena. In their own right, complex bodies of evidence relate to each of these landforms. The best place to begin is with a review of the stratigraphy of the Victoria Falls Formation, and only then reconsider cotemporaneous events in geomorphological evolution elsewhere. It turns out that the timing of formation of the Batoka Gorge provides invaluable insights into aspects of Quaternary history applicable across the Katanga-Chambeshi region.

5.4.1 The Victoria Falls Formation (VFF)

International scientific attention was first attracted to the antiquity of human evolution in Africa, when the Stellenbosch culture (ESA) was publicized by Peringuey in 1900 (Deacon & Deacon 1999). This was followed very soon after by discoveries of abundant stone artefacts along the Upper Zambezi around Victoria Falls by Feilden (1905) and Lamplugh (1906, 1907, 1908). This attracted international interest. Later, detailed studies revealed an archaeological record in the vicinity of Victoria Falls extending from early ESA to late LSA (Armstrong & Jones 1936; Clark 1950; Dixey 1950).

From the outset, Lamplugh (1906, 1907, 1908) recognized that the older artefacts in upper gravels deposited along the original broad river channel (formed by the meandering Zambezi) predated the river's incision of the spectacular Batoka Gorge (to culminate in the modern position of the Victoria Falls). These early reports all discuss how a prehistoric chronology could be used to reconstruct when the Zambezi river eroded the Batoka Gorge. The first calculations, toward unraveling this geomorphological history (by Clark 1950, 1963) overestimated erosion rates. This is understandable, given the underestimated ages placed on archaeological cultures. The most recent reconstruction (by Derricourt 1976), albeit also wanting in precision, was employed to reconstruct when the mid-Zambezi pirated the Upper Zambezi (Nugent 1990; Moore & Larkin 2001).

Recent refinements gained in archaeological dating (especially for the ESA-MSA transition) have yet to be applied to revise the VFF and erosion history of Batoka Gorge. Such a reconstruction also stands to gain enhanced resolution from greatly resolved reconstructions of palaeo-climates. Here, I employ these data to reevaluate key events in the evolution of the Upper Zambezi. Furthermore, it turns out that contemporaneous evidence can be applied to antecedent drainages (forged by the Palaeo-Chambeshi system). This refined reconstruction of the erosive history of the Batoka Gorge confers unprecedented insights into aspects of human evolution around Victoria Falls. Not least, it provides a

tighter constraint on when the ESA - MSA transition occurred. This revision updates the stratigraphy of Upper Zambezi sediments (Clark 1950) in light of current archaeological terminology, and what is now better understood about vicissitudes of Pleistocene climates.

The stratigraphy of the Victoria Falls Formation (VFF) is summarized in Fig. 5.2. Its sequence of landforms are most comprehensively preserved across the wide valley of the Upper Zambezi above the Victoria Falls. Dixey (1950) and Clark (1950) emphasized that the relative positions of these sediments varies downstream where the river narrows, and erosion has removed older deposits. Archaeological evidence revealed that antecedent, braided flow regimes through the Zambezi's channel laid down the Older Gravels in two discrete levels; such that the Older Gravels I (OG I) at higher levels only contained ESA Acheulian artefacts. Older, eroded Oldawan tools also occur more rarely in OG I. Older Gravels II (OG II), at ~6m below OG I along the Middle Terrace, contain artefacts of middle to late ESA antiquity. These Older Gravels are capped by Ferricretes I. The timing of this cementation of these river sediments is interesting, as these ferricretes preserve Sangoan tools. By contrast, any ESA tools present in Ferricrete I had been rolled. All more recent MSA artefacts lie above Ferricretes I, with Lupemban artefacts preserved in Kalahari Sands I (KS I).

The most recent formations in the VFF are the Younger Gravels I (YG I), which represent persistent grading of the Upper Zambezi. Microliths of the most recent MSA culture (termed the Tshangula culture, Cooke 1966), are preserved in Kalahari Sands II, and are in turn superseded by LSA artefacts (Clark 1950, 1963; Derricourt 1976, Figs 5.3 & 5.4). Based on descriptions of the VFF (Clark 1950; Dixey 1950), I infer that this key archaeological evidence was not been redistributed by bioturbation, principally because KS II and the gravels lie directly on solid basalt. Nevertheless, activities of soil organisms may have buried some Sangoan and Lupemban tools to the base of KS I to overlie OG II. As discussed in Section 4.9.2, several studies have demonstrated that artefacts have been redistributed over several metres, vertically, through sediments (Cahen & Moeyersons 1977), which is attributed principally to burrowing termites (McBrearty 1990).

5.4.2 The Evolution of Batoka Gorge

Clark (1950, 1963) paid close attention to the relative positions among the strata comprising the VFF, with respect to key landforms in the Batoka Gorge (Figs 5.2 & 5.3). Based on Clark's fieldwork, the following relationships between sediments and hominin artefacts constitute chronological estimates. Delimited times of their formation allow one to calculate rates of erosion. And it is these statistics that

can be related to geomorphological events further afield. Ages can then be estimated for the different sections that make up the ~100 km long Batoka Gorge:

1. The Kalahari Sands II (KS II) capping the gently sloping terraces along the vertical edges of the upper Gorge characteristically preserve late MSA, Tshangulan artefacts. This sediment only extends up to the beginning of the 4th Gorge, because it was eroded by the wide river that then occupied the valley at this point. Thus the gorges upstream have been incised since the deposition of KS II. Derricourt (1976) calculated this distance at 2.96 km, which closely approximates the retrogressed route taken by the eroding Zambezi since the formation of KS II.
2. Invariably preserved as a distinct upper terrace, the Younger Gravels (YG I) extend above the gorge for at least 20 km downstream of the Victoria Falls. They demarcate the margins of an abandoned channel of the Zambezi, formed prior to its incision of the western Batoka Gorge (Clark 1950, 1964). With no justification, Derricourt (1976) restricted his estimate for the extent of YG I only to its confluence with the Songwe. He calculated this distance at 6.75 km, to closely approximate the route eroded by the retrogressing river back to the lower end of the 3rd Gorge, bordering the 4th Gorge.
3. The Chimamba Rapids is the only example of any significant waterfall across the Zambezi below Victoria Falls, within the entirety of the Batoka basalts. Here, the river channel, constricted to a total width of 18 m, drops 6 m vertically. This landform also contains the upstream limit of a degradation terrace at the base of the eastern Batoka. The sloping sides, bounding this eastern gorge, contrast against the near vertical, deep trenches of the western gorges. Clark (1950: 125) concluded "...that the erosion of the western and upper section of the gorge above the Chimamba Rapids was a much more recent event than that of the lower 35 miles (56 km) below these rapids."
4. Clark (1950) and Derricourt (1976) mentioned that "Older Gravels" had been deposited by the Zambezi along the entire valley, upstream of the Matetsi confluence, before incision of the eastern gorge. They did not distinguish whether these were OG I or OG II. This uncertainty can only be resolved by further fieldwork, I present a testable hypothesis as to their respective locations.

5.4.2 Factors that have Controlled Retrogression of Victoria Falls

Applying any average erosion rate to the Neogene and Quaternary history of the Zambezi must accord with influences that caused erosive capabilities of the river to vary through the Quaternary. Clark (1950) and Bond (1964) emphasized that erosion of the Batoka basalts has been characteristically saltational, where excavation of shatter-joints proceeded much faster than erosion of the much harder, unjointed, sheets of basalt. Wellington (1955: 391-399) concluded that local and regional differences in erosion resistance of the Batoka basalts could explain differences in the geomorphology along the Zambezi's channel. Moreover, erosion intensity can be expected to have fluctuated in concert with unprecedented pluvial periods and droughts, as river volume varied. It is further possible that episode(s) of uplift may have accelerated the rate of incision, because Dixey (1950) postulated that portions of the Zambezi's channel have been tilted by crustal movements. These possibly coincided with events of tectonic activity focused along the Okavango-Kafue graben. The evidence lies at the points where distinct rapids partition the long, quiescent stretches of the Upper Zambezi river. These rapids, delimiting these tilted river-sections, represent a series of lineaments that parallel the Chobe fault. This late Cenozoic tectonism appears important. Tilting of the Zambezi's bed controlled textures of sediments graded by the river above Victoria Falls, especially YG I, with the deepest deposits along these quiescent stretches of the Upper Zambezi (Dixey 1950). Additional uncertainty, and a topic of critical relevance, relates to the tenure of the Palaeo-Chambeshi (Sections 4.6-7). The stratigraphy of the Kafue Flats reveals that Lake Patrick formed during the late ESA, Early Pleistocene (Section 4.9.3). So, the Palaeo-Chambeshi River may in fact have contributed the major catchment, which eroded a significant portion of the Batoka Gorge.

5.4.3 Kalahari Sands II and the Late Middle Stone Age

Derricourt (1976) concluded that the Zambezi had regressed 2.96 km since the Last Glacial Maximum (MIS 2), and then assumed that Kalahari Sands II (KS II) formed at ~20 000 yr BP. Constraining the age of KS II hinges on the affinities and age of what Clark (1950) called Magosian artefacts, which reveal this stratum's contiguity above the Zambezi's banks. A precise estimate of when KS II formed is critical to all subsequent extrapolations. The name, Magosian, is not applicable to these south-central African artefacts representing the final industry of the MSA, antecedent to the LSA; and so Tshangula is used here as previously applied to local variants of the late MSA in west and north Zimbabwe (C. K. Cooke 1966, 1979; Walker 1995). Moreover, the mixture of larger blades with smaller points, illustrated and described by Clark (1950), is further reminiscent of the Howieson's Poort industry in the southern Cape Province, which is reliably dated between 70 - 50 Kya (Deacon 2001; Wurz 2002). Northeast of Victoria Falls, the late MSA artefacts at Mumbwa (central Zambia)

and Mumba (northwest Tanzania), discussed by Barham (2000) appear contemporaneous with what is here termed Tshangula in the KS II along the Upper Zambezi. The late MSA in northwest Botswana dated at 77 Kya (Brooks *et al.* 1990) is also considered contemporaneous (McBrearty & Brooks 2000).

Clark (1950) emphasized that the few LSA sites around Victoria Falls can be clearly distinguished from the older culture (his Magosian) in KS II, on which LSA microliths had accumulated. As confirmed by new dates, the Howieson's Poort culture approximates MIS 4. All these South African sites preserve evidence of a widespread gap in occupancy in the latter part of MIS 4 (Wurz 2002, 2005; Jacobs 2005; Tribolo *et al.* 2005). The end of the MSA is also represented by a gap in occupancy of Zimbabwean shelters throughout the Matobo Hills (Walker 1995) and at Redcliff, near Kwe Kwe (Cooke 1978). Barham (2000) describes a corresponding vacation of Mumbwa Cave, in central Zambia, after the end of the MSA, until it was colonized by LSA people. So the combined regional evidence suggests that human densities were very low through this period, until populations expanded in the following interglacial, through MIS 3 (Deacon 2001, Fig 5.3)

Thus, it is the LSA that manifested during the LGM through MIS 2 (Marean & Assefa 2005), dated at ~27 to ~21 Kya (Partridge *et al.* 1997; Partridge *et al.* 1999; EPICA 2004), when mean annual precipitation across south-central Africa (around Batoka) is estimated at 30-60% below modern levels (Partridge 1997; Partridge *et al.* 1999). So, revised evidence points to mobilization of aeolian sands over the antecedent arid glacial (MIS 4) to bury Tshangulan artefacts in KS II of the VFF. Furthermore, this revision places a useful, previously unavailable, constraint (57 000 - 71 000 yr BP) delimiting the age of KS II across the region. This date can be contrasted against TL-based estimates of 173 - 78 Kya in northwest Zimbabwe (Munyikwa *et al.* 2000), and 115 - 95 Kya for linear dunes in Namibia, which constitute the oldest dates for deposition of aeolian sediments in the region under an arid palaeo-climate(s). All other TL dates of KS dunes in the region range across a spectrum of ages since 48 Kya into the Holocene (Thomas *et al.* 2000; Shaw & Goudie 2002). Deposits of KS II in western Zambezi contained what are here termed Tshangulan lithics. A similar industry (Late Tshilotan) was also described in KS II in northeast Angola (Clark 1950, 1964). Nonetheless, the applicability of these lithic indicators to date deposits of KS II, elsewhere, is contingent on their containing Tshangulan artefacts. One also has to be vigilant of bioturbation, wherever KS II overlies non-lithified strata.

Therefore, it follows that the Victoria Falls have regressed 2.96 km from the end of the 3rd Gorge to their present position at a rate of 0.042 - 0.052 m/yr: within delimiters of 57 000 and 71 000 years BP,

respectively (set within MIS 4). Erosion possibly increased concomitantly with higher rainfall prevailing in MIS 3. (This average rate is nearly three times slower than the erosion estimate of 0.15 m/yr calculated by Derricourt 1976.) Thereafter, Derricourt bracketed the early MSA at 110 000 - 90 000 yr BP. This can now be recognized as a serious underestimate. Moreover, his arbitrary downstream limit on the extent of YG I (i.e. the distance of 6.75 km below the start of the 4th Gorge to the Songwe-Zambezi) also requires correction (Fig. 5.4).

5.4.4. The Age of the Batoka Gorge

One can employ three different erosion statistics to calculate the age of the western Batoka Gorge, between the Chimamba rapids and the 4th Gorge. An additional variable centres on the actual extent of YG I along the edge of the abandoned river channel, paralleling the incised gorge. Derricourt's delimitation restricts the extent of YG I to upstream of the Songwe, yet Clark (1950) emphasized YG I extends 20 km downstream of Victoria Falls:

1. The revised erosion rate (0.042 - 0.052 m/yr) recalculates the age of YG I, based on Derricourt's erroneous delimitation of the distribution of these gravels to the Songwe, to 130 - 161 kyr. This then suggests the Zambezi eroded 6.75 km upstream from the Songwe confluence to the start of the 4th Gorge in this time. The translated age of 187 - 232 Kya (to erode 9.71 km from the Songwe-Zambezi confluence to Victoria Falls) would then require simultaneous formation of YG I and its fresh Lupemban tools. Given the Lupemban was well established by ~260 Kyr BP at Twin Rivers (Barham & Smart 1996), this age is likely an underestimate.
2. According to this Twin Rivers constraint, a more realistic, maximum, age of deposition of YG I is 300 - 250 Kyr BP, which translates to an erosion rate between 0.067 - 0.080 m/yr to incise 20km of the western Gorge downstream of Victoria Falls. This then is taken as the maximum age for YG I.
3. Conversely, the erosion rate based on MIS 4 dates YG I between 384 - 476 Kyr. If the antiquity of the ESA-MSA transition (suggested from dates in East Africa) is indicative, this might well be a revealing statistic. These gravels preserve Sangoan and early Lupemban tools, both rolled and glazed, which obviously means they were graded along the Zambezi after use. One can speculate these were made even earlier in the Middle Pleistocene. It would then follow that fresh Lupemban artefacts became associated with YG I after the latter's deposition.

The principal tenure of these Lupemban tool-makers in the Zambezian region is hypothesized to approximate semi-arid conditions during MIS 8 (301 - 241 Kyr), on the basis of the Twin Rivers dating constraint cited above. It then follows that, subsequently, these MSA artifacts would have buried deeper by bioturbation into KS I (see Section 4.9.2).

Calculations employing these maximum and minimum rates of erosion, translate into two scenarios for the time in which the Zambezi incised the entire western section of the Batoka Gorge of 40.71 km, from Chimamba Rapids upstream to Victoria Falls:

The rate of erosion, calculated from deposition of YG I between 300 - 250 Kyr (0.067 - 0.080 m/yr), is most likely too rapid. Nevertheless, it estimates erosion of the western gorge from the Chimamba rapids commenced at 509 - 608 000 years BP;

If the YG I did indeed only form 187-232 Kya (from which an erosion rate of 0.0862 - 0.107 m/yr can be derived), then it corresponds that the western gorge only began to erode from Chimamba rapids around 380 - 472 000 years BP.

It more likely took 970 - 783 Kyr to erode the entire western gorge (40.71 km). This calculation employs the more tightly constrained estimate of erosion rate, derived from late MSA (Tshangulan) artefacts buried in KS II during MIS 4.

5.4.5 The Chimamba Rapids and the Batoka Unconformity

Based on these erosion rates, the eastern Batoka Gorge (~60 km) took as long as 1 429 – 1 154 Kyr (0.042 - 0.052 m/yr), or 750 – 896 Kyr (based on 0.067 - 0.080 m/yr) to erode: applying erosion rates estimated for the Western Batoka. We must also consider the caveat that erosion of the eastern gorges was possibly more rapid, if basalt layers are and perhaps less resistant to erosion in the eastern Batoka. Increased erosive force from the Palaeo-Chambeshi would also have increased the rate of incision of the Eastern Batoka; and evidence suggests it was indeed the principal tributary of the Zambezi system flowing to the Indian Ocean for some period of the Pliocene to Early Pleistocene. And its potential length, and catchment, approximated that of the Upper Zambezi (Section 4.8, Table 4.2). This would perhaps equate to a period of 696 – 561 Kyr (based on 0.107 - 0.0862 m/yr) to erode 60 km of the eastern Batoka's basalt. Any such estimate must also recognize the significant period corresponding to impoundment of the Upper Zambezi (represented at the Chimamba rapids). The oldest, and most recent, estimates correspond to 2 037 – 1 663 or 1 168 – 941 Kya for initiation of erosion from the

Matetsi-Zambezi confluence, respectively. Correspondingly, these statistics bracket the age of the entire 100 km of the Batoka Gorge. Refinement of these estimates can only follow on detailed fieldwork to quantify the heterogeneity of the Batoka basalts and then refine estimates as to their susceptibility to erosion.

The Chimamba rapids represent a significant period, when the Zambezi did not erode the Batoka Gorge (Clark 1950; Derricourt 1976). Secondly, the deep deposits of Kalahari Sands I, under which Ferricretes I indurated the older gravel beds, is named the Batoka Unconformity. Exact details of the pedogenic origin of these ferruginous sediments in the Zambezi valley awaits deserving research. Their classification is complicated by the many different processes that have formed the wide diversity of the sediments variously termed ferricretes and laterites, and discussed by Bourman & Ollier (2002). Until the details of the origins of Ferricretes I is revealed, this nomenclature follows Clark (1950).

In combination, the Chimamba rapids and Batoka Unconformity in the VFF point to two discrete, and remarkable, palaeo-environmental situations that affected the Upper Zambezi severely during the Early and Middle Pleistocene, respectively. These terminations in river flow resulted from first-order geomorphological control – namely tectonism. This epeirogeny likely exercised widespread effects on landforms across the region, not least drainage systems. Above all, these events raise pressing questions about causal efficacy. How does the erosion history of Batoka relate to counterfactual influences of climatic change with respect to tectonism expressed within and along the margins of the Okavango-Kafue graben.

Moreover, the Chimamba rapids represent a significant change in the gradient of the Zambezi through the Batoka. This reflects either structural control by the basalt on erosion, a genuine cessation of river flow, or - previously not considered - a radical change in erosive power reflecting a substantial alteration in river catchment. Critical questions pertain to how the break in river flow, represented by the Chimamba rapids, relates to that represented in the induration of Ferricretes I under Kalahari Sands I. It is reasonable to question whether these landforms testify to a single, or two separate, cessations of river flow. Furthermore, the diversion of drainage into northeast Botswana of a river with a Pleistocene catchment approximating (if not exceeding) that of the Upper Zambezi today (Table 4.2) would have maintained a large palaeo-lake. It follows that two discrete river impoundments (upstream of Batoka) would then account for two major lacustrine stages in the Okavango-Kafue graben.

Toward resolution of this geomorphological puzzle, I propose a novel hypothesis. Is it possible that two very different drainage systems were responsible for erosion of the Eastern versus Western sections of the Batoka gorge. Whilst the Western section can be plausibly explained as erosion by the Upper Zambezi alone; might not the deeper, wider expanse, downstream of the present day Chimamba Rapids, reflect erosion by a much larger discharge? This logically required large tributaries debouching into the Upper Zambezi river. It is plausible to invoke the Palaeo-Chambeshi, or at least the Palaeo-Kafue (prior to the latter's impoundment as an endoreic tributary, which maintained Lake Patrick). Based on estimated hydrological budgets (conservative given the annual rainfall of 450mm/yr, Section 4.9, Table 4.2), these extended catchments would have contributed at least 27 and 12 km³/yr over and above the 35km³/yr of the Upper Zambezi. Their erosive power would have been far higher under relatively mesic climatic conditions, which characterize the rainfall gradient across these catchments. This extends from ~450mm/yr over northeast Botswana to >1 000mm/yr over Katanga and northeast Zambia. Only tighter constraints on tenures of respective drainage topologies, in relation to precise dating of representative landforms in the Batoka gorge, and the VFF, can delimit more precise narrative of Plio-Pleistocene history.

I suggest the initial break in erosion, suggested by the Chimamba Rapids, reflects the tenure of PLM in the Early Pleistocene; albeit it possibly also reflects a radical change in drainage topology upstream. The latter either entailed a distinct event or corresponded to the tenure of PLM. Thereafter, the Batoka Unconformity represents a more recent impoundment. This occurred later, after the Zambezi had begun to incise the western gorge. It enabled ferricretes to form under Kalahari Sands I across dry river valleys, and this more recent impoundment of the Zambezi was likely of shorter duration in the Middle Pleistocene. It is less clear how it relates to tenures of a palaeo-lake in northeast Botswana, but the ferricretes, at Ngonye Falls, convincingly testify to the tenure of a palaeo-lake upstream in the Bulози floodplain. Might this later event, associated with a lower lake stage, explain the 936 m fossil shorelines in northeast Botswana (Figs 4.7a,b & 5.5)? This would place a Middle Pleistocene tenure on the Palaeo-Lake Thamalakane stage (936m), originally proposed by Shaw (1988b) as Late Pleistocene or early Holocene (albeit on suspect radiocarbon datings of calcretes). PLT covered at least 7000 km², of northeast Botswana, and also inundated the Makgadikgadi basin to the 936 m shoreline (Thomas & Shaw 1991; Fig. 5.5).

The weight of evidence points to tectonic control over the Upper Zambezi's flow downstream of the Okavango graben, with uplift across the Chobe fault (Thomas & Shaw 1991; Moore & Larkin 2001). Apart from mentioned above, there has been little consideration of possible controls by palaeo-climates

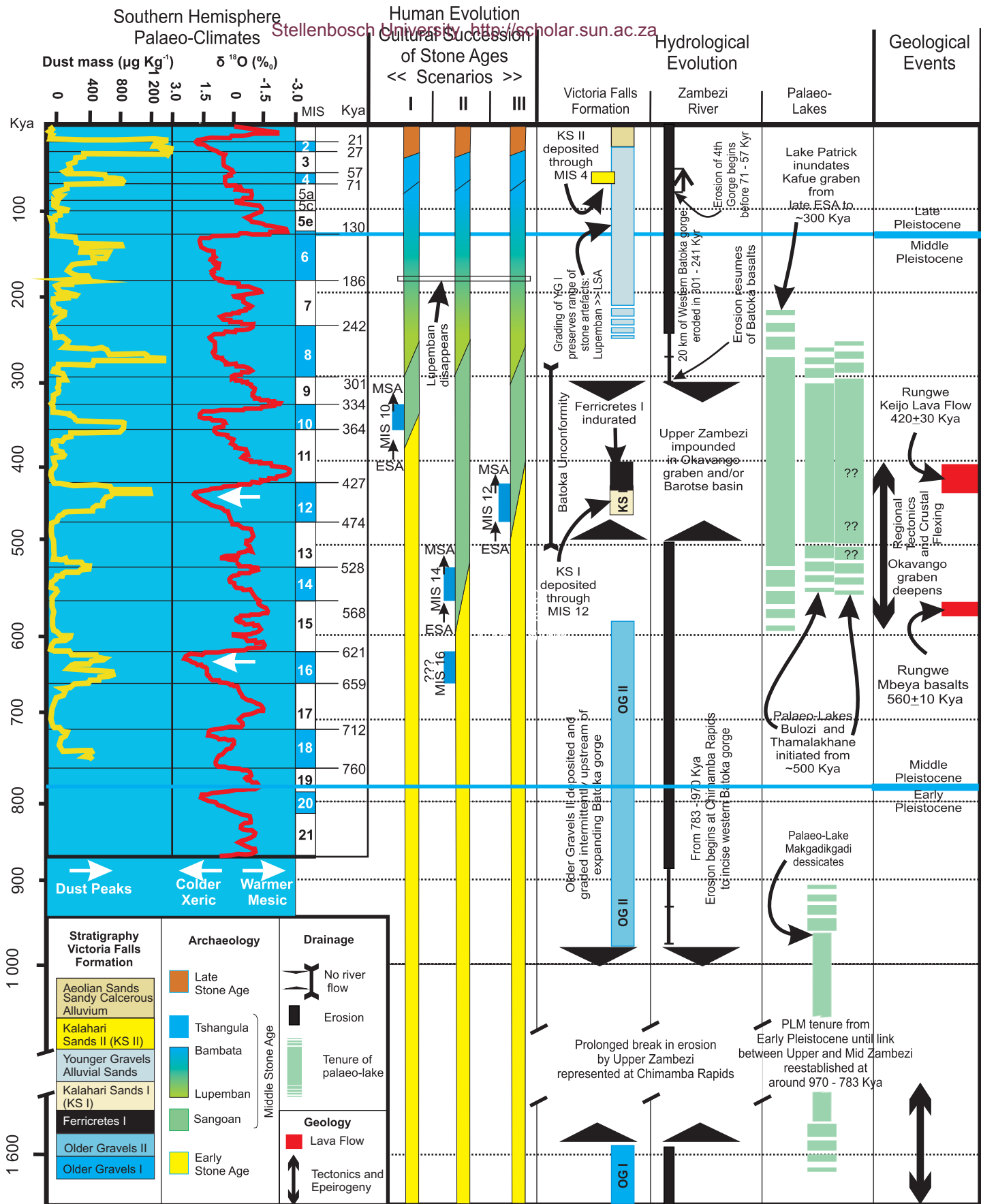


Figure 5.3. Comparison of how three contrasting reconstructions (Scenarios I-III) explain the origin of the stratigraphy of the Victoria Falls Formation (VFF), with respect to history of erosion of the Upper Zambezi across the Batoka basalts. Important events include the breaks in erosion of the Batoka gorge, and the transition from the Early (ESA) to Middle Stone Age (MSA). Archaeological data are collated from Clark (1950) and Dixey (1950), and revised as described in the text. Representation of the Marine Isotope Stages (MIS) depict palaeo-climates, and are adapted from Denton (1999), Zachos *et al.* (2001), EPICA (2004) and Lisiecki & Raymo (2005). The white arrows denote especially cold conditions during cryospheric expansions, which also coincided with pronounced dust peaks as preserved in the EPICA Antarctic ice core (EPICA 2004). Dates for volcanicity obtained from Delvaux *et al.* (1992).

on the hydrological regimes that formed the VFF and sediments in the Okavango-Kafue graben. It is tempting to speculate as to what climatic contexts were associated with cessations and reunions of flow through the Zambezi's channel at Batoka. It might only be coincidence that estimates for the earliest break (in the Zambezi's erosion of Batoka) corresponds to the mid-Pleistocene revolution (MPR) at around 900 Kya (see Section 4.4, pg 118); although, this correlation is obtained by calculations based on slower erosion estimates. This switch in climate manifested in an overall increase in global ice volume, and the change in periodicity from 41 to 100 kyr cycles (Ravelo *et al.* 2004). The weight of evidence points to deposition of deep sands (KS I), under which the Older Gravels were indurated with Ferricretes I, during a glacial period that preceded Termination V (the transition between MIS 12 and MIS 11 ~430 kyr BP). The new Antarctic ice-core confirms that the two coldest glaciation events are reflected in MIS 16 and MIS 12, when sea levels were particularly low. Peaks in the dust profile also correspond to these glacial expansions (EPICA *et al.* 2004, Fig. 5.3). So an important task in this revision is to pin down which glacial period fostered deposition of KS I. Did it occur quite early in the Middle Pleistocene (MIS 16, 621 - 659 Kyr BP), or more recently, perhaps in MIS 12 (427-474 Kyr BP)?

The paucity of artefacts found in KS I appears to mirror a genuine absence of people from around the Batoka through the early Middle Pleistocene; and so it might indeed reflect a genuine chiasma in the archaeological record. Nevertheless, by 384 - 476 (or less likely 300 - 250) Kyr, sufficient Sangoan artefacts had accumulated across the Zambezi valley to impart a distinct signature after their aggradation into OG I. This reconstruction points to Sangoan *Homo* living on KS I (not the Older Gravels II before they were indurated with ferricrete forming under KS I), after the overburden had been stripped off. So, the question remains that the contemporary location of Sangoan tools – abutting OG II - could reflect their burial by bioturbation into KS I.

5.5 ADDITIONAL EVIDENCE

5.5.1 Tectonics, Palaeo-Environments and Ferricretes: Impounded Rivers and Palaeo-Lakes

The chronological significance of Ferricretes I, in the VFF, appears to hold broader geographical relevance in the prehistory of south-central Africa. Several sites have been described where contiguous expanses of ferricrete cap gravels along valley floors. In areas that have escaped erosion, Ferricrete I still remains buried where it first formed - under deep deposits of Kalahari Sands I (Clark 1950, 1963, 1964). It could possibly delimit strata elsewhere, but such an application requires caution; even though the ferricretes representing this formation appear to occur widely across south-central Africa. Their formation followed on an intense Middle Pleistocene glacial expansion, when substantial depths of KS

I covered these regions. Nevertheless, Clark (1950) considered the formation of Ferricrete I to be an exception in the Zambezi valley, where ferricretes are uncommon. This was presumably because more arid climates (even during inter-pluvials), predicated against their formation. Ferricretes (presenting as extensive duricrusts) are more common across the Congo basin, including Katanga (DRC) and Lunda (NE Angola) invoking seasonal mesic climate as a key determinant of their formation (Clark 1950, 1963; Alexandre & Alexandre-Pyre 1987; McFarlane 1991).

At no less than three scattered localities (Barotseland and Victoria Falls, and northeast Angola) late ESA Acheulian and Sangoan artefacts are entombed in Ferricrete I. In contrast, Lupemban tools lie scattered - free - on the indurated surface, buried under Kalahari sands. A similar pattern was described as characteristic along certain rivers in Angola (Clark 1963) as at Victoria Falls (Clark 1950). It logically follows that these ferricretes, preserved in these three scattered localities, represent coeval landforms. They indicate widespread climatic conditions, which affected deep, contiguous deposits of Kalahari sands in valleys.

The ferricretes exhumed by the Zambezi eroding across the Ngonye (=Sioma) Falls preserve entombed early MSA (Sangoan) artefacts (see Frontispiece to this Chapter). A ferricrete bar is also preserved in the bed of the Upper Zambezi above the Victoria Falls; which confirms the Zambezi was not flowing when this induration occurred. It was the discoverer of both these remarkable sediments, J. D. Clark, who first pointed out that both these formations reveal that the Upper Zambezi was not flowing when these ferricretes formed (Clark 1950). So, it logically follows the Zambezi was impounded upstream of both these points. Disruption of river flow (represented by the ferricretes) was initiated before expansions of Kalahari Sands I in the severe glacial. Equally, the ferricretes in the VFF reveal that no flow can be attributed to the Palaeo-Chambeshi at this time. This deduction confers with stratigraphic evidence from the Kafue Flats, where lacustrine sediments postdate late ESA artefacts in alluvial gravels attributed to the Palaeo-Chambeshi river. So I conclude that a mini-archipelago of no less than three palaeo-lakes existed in the Bulozzi, Kafue and Okavango depressions through at least part of this period. (Obviously, the palaeo-lake in the Okavango depression would have been much smaller than PLM; and it is tentatively attributed to P-L Thamalakhane Stage) Initiation of their tenures is delimited by the late ESA artefacts in OG II. Following Simms (2000), the termination of Lake Patrick possibly occurred earlier than ~300 Kya, and certainly had ceased to exist by 200 Kya. Moreover, the estimated age of YG I (~300-200 Kyr, Section 5.6.4) sets the upper limit to Palaeo-Lake Bulozzi, and the latter's complex interplay with the Palaeo-Lake Thamalakhane stage in northeast Botswana.

Figure 5.4. [Following Page] Reconstruction of the sequence of events that emplaced, abraded and eroded strata along the Zambezi through the Plio-Pleistocene to incise the Batoka Gorge and form sediments of the Victoria Falls Formation (VFF). Stratigraphic designations follow Clark (1950) as depicted in Figs 5.2 & 5.3.

a. **Late Pliocene, or beginning Pleistocene.** The broad channel of the Zambezi across the Batoka basalt was established during the Pliocene. Incision of the steep Gorge had been initiated from the Matetsi confluence by at least 1.35 - 1.67 Ma, and more likely in the late Pliocene. Associated alluvial conditions prevail upstream, where the Palaeo-Chambeshi laid down similar gravels across the northeast reaches of the Okavango and Kafue graben.

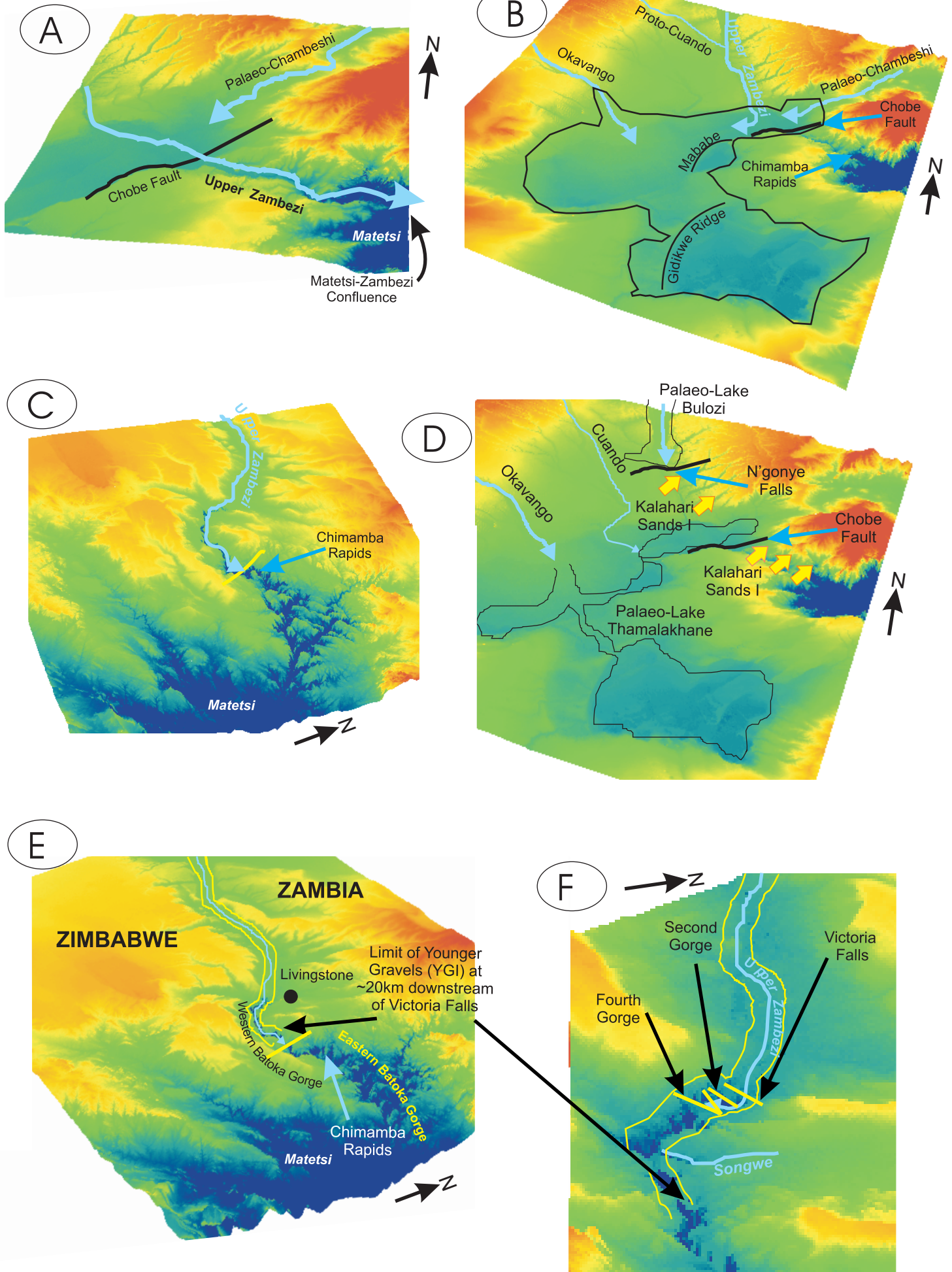
b. **Early Pleistocene.** Around 970 - 783 (or perhaps 608 - 509) Kya, the major nick point in erosion of the Zambezi is roughly 40 km downstream of the position of the modern Victoria Falls. This position approximates that of the Chimamba rapids today. Uplift along the Chobe fault deepens the Okavango graben to impound the Upper Zambezi, and divert its entire catchment into the Kalahari Basin. River flow ceases across the Batoka basalts. Late ESA people, living throughout these valleys, populate sediment surfaces with Acheulian tools. Palaeo-Lake Makgadikgadi persists in the Kalahari basin at its 945 m asl shoreline, and the Mambova limestones probably formed at this time along its northeast shoreline.

c. **Beginning of the Middle Pleistocene (738 - 597 Kyr).** The Zambezi reestablishes its course, and extensive erosion is ensuing. This event followed either on crustal warping, and/or local erosion of the barrier at the Chobe fault. Palaeo-Lake Makgadikgadi (PLM) desiccates in the northeast Kalahari basin. The eroding Zambezi exploits faults and shatter joints in Batoka basalt to incise the deep trenches of the Western gorge. Possibly, makers of Sangoan artefacts settled the Zambezi valley in the Middle Pleistocene during Inter Glacials, where their tools accumulate on exposed laterites, perched sediments and erosion resistant basalt blocks.

d. **Middle Pleistocene Glacial (MIS 16 or MIS 12)** Low sea levels, with colder conditions at lower latitudes follow from cryospheric expansion, which is associated with arid climates across the African subcontinent. Widespread activation and deposition of aeolian Kalahari sands occurs from southern Africa, extending north of the Congo river. Hominins may have been absent from the Zambezi valley in this glacial period. Zambezi river is not flowing, following on its impoundment in Barotse land. Sangoan *Homo* populate the region during the following interglacial, living on the surface of the Kalahari sands. Their tools are subsequently bioturbated to the underlying gravel bed. The prevailing climate across the Zambezian region switches to markedly warmer temperatures. Increased rainfall ensues, with distinct seasonality, such that Ferricretes I form unconformably across the valley floor. Conditions were possibly similar to those across the southern Congo basin today, with mesic savannas. Ferricretization entombs Acheulian artefacts in OG II, with early Sangoan artefacts on these gravels. It is likely that reunion of the Zambezi occurs during a period of pluvial conditions (Fig. 5.3) that breached the barrier (previously imposed by tectonism). While this may in turn reflect climate, it is difficult to prove. Large loads of stripped-off Kalahari sediments initially increases erosion downstream of Chimamba rapids. Accelerated erosion further sculpts eastern gorges; such that this time lag in erosion of the western basalts upstream magnifies Chimamba Unconformity. Erosion slows once the river reaches bed rock (including the duricrusts comprising indurated laterites).

e. **Middle Pleistocene: 476 - 384 (less likely 300 - 250) Kyr.** Aggrading river conditions lay down gravel beds (YGI), including redeposited early MSA tools of Sangoan and early Lupemban industries. The Zambezi is continuing to retrogress westwards, exploiting structural weaknesses in the Batoka basalt. Lupemban tool makers populate the region soon after aggradation of YG I, and their populations persist through the ensuing arid (MIS 8) and interglacial (MIS 7) periods.

f. **Late Pleistocene (MIS 4: 71 - 57 Ka).** Erosion by the Zambezi had recently incised the 4th Gorge; when Kalahari sands are remobilized during MIS 4, burying late MSA Tshangulan tools. By the start of the Last Glacial Maximum (~ 27 000 yr BP in MIS 2), the Zambezi had regressed to approximately halfway along the 2nd Gorge. This was when LSA cultures were evolving across Africa.



5.5.2 Geochemical Dates for the ESA to MSA Transition

As summarized above (Section 5.3), the consensus - admittedly from patchy data - is that the transition to MSA cultures from Acheulian (late ESA) occurred in the Middle Pleistocene. Barham (2001, 2002) and Marean & Assefa (2005) have argued this occurred within central Africa, where xeric savannas expanded to dominate the landscape under an arid palaeo-climate during a major cryospheric expansion. And they further hypothesize that this transition correlated with MIS 8 or MIS 9. So this period can be tentatively delimited to around 242 - 301 Kyr or 334 - 364 Kyr. The latter constraint is more plausible, because the Sangoan predated the Lupemban; and the Lupemban was already in existence at Twin Rivers during MIS 8 (Barham & Smart 1996; McBrearty & Brooks 2000; Barham 2002). The $^{40/39}\text{Ar}$ dates of 510 - 511 Kyr for two archaic *Homo* skulls at Kapthurin, Kenya are especially noteworthy, because they underlie sediment horizons that preserve the oldest evidence for abundant use of red ochre and Sangoan artefacts (Deino & McBrearty 2002). This evidence reveals that the key innovations, represented in the Sangoan culture, were already evolving when mesic conditions prevailed in East Africa through MIS 13 (474 - 528 Kyr).

The sandy calcereous alluvium (YG I, Figs 5.3 & 5.4) along the Upper Zambezi represents a period of prolonged flow of the Zambezi River, because the poorly defined bedding of YG I testifies to grading conditions persisting over a prolonged period. Here a continuous sequence of stone industries are preserved in YG I, from late Lupemban (MSA) at the base through to LSA at the top. As pointed out by Dixey (1950), this represents a continuous process where river flow persisted through at least one drier glacial period. Moreover, after the Batoka Unconformity, the Zambezi's flow does not appear to have declined markedly during glacial periods, notably MIS 4 (Fig. 5.3).

A significant constraint is provided by Uranium Series (Ur-Th) dates on tufa associated with Twin Rivers on the northeast edge of Kafue Flats. Between 300-200 Kyr, the Lupemban culture existed in Zambia, with no traces of Sangoan, let alone Late Acheulian, artefacts. So, at its very youngest, the Sangoan industry predates at least MIS 8. This provides support to constrain deposition of Younger Gravels I (YGI) to before MIS 8 (hypothesized 384 - 476 Kyr). Thus, Sangoan, but not Lupemban tools, were rolled within these gravels. For fresh Sangoan tools were preserved in OG II alongside late Acheulian tools, where after these representatives of both industries were indurated under Ferricrete I. It appears that at least three glacial cycles are represented in the sedimentary history of the Zambezi through grading of YG I (Fig. 5.3). The significance of this evidence sets the stage to reconstruct detailed scenarios centred on the ESA-MSA transition. These dating constraints manifest in

discrepancies, which in turn foster alternative reconstructions to delimit when the Zambezi eroded the Batoka Gorge in concert with tenures of palaeo-lakes in Zambia and northeast Botswana.

Further evidence from northeast Angola relates to these uncertainties, where Lupemban and Sangoan living sites were studied in detail (Janmart 1953; Clark 1963). Without precise dates, and only with these published data, it is difficult to constrain ages of ESA and MSA artefacts in deep gravel beds along major rivers (draining the southern Congo basin in Dundo Province, northeast Angola). The chronology of their deposition appears to be close, if not contemporaneous. This greater antiquity implied for the MSA in central and east Africa antedates more recent MSA (Stillbay) sites on the highveld and coastal margins of South Africa (McBrearty & Brooks 2000; Barham 2002; Tribolo *et al.* 2005). Here, an MSA site pertinent to this study is Florisbad. The age of the fossil hominin, recovered from Florisbad sediments, was revised by Electron Spin Resonance dating to 259 ± 35 Kyr (Grun *et al.* 1996).

5.6 RECONSTRUCTIONS OF MIDDLE PLEISTOCENE SCENARIOS

5.6.1 Evolutionary Dynamics between the Upper Zambezi and mid-Zambezi rivers

Moore & Larkin (2001) concluded that links between the Upper and mid-Zambezi have been established repeatedly, (following discrete disruptions) since the late Pliocene. Reappraisal of the VFF in this chapter endorses a late Pliocene timing for this initial piracy event. These constraints can then be inferred to place approximate dates on initial events in the Zambezi and neighbouring landforms. The uncertainties surrounding these tentative dates can be addressed from alluvial and aeolian sediments accumulated on the Batoka basalts. So I reconstruct the erosion history of the Zambezi in the form of three contrasting scenarios, two of which represent outerlying extremes in uncertainty, for the oldest and youngest approximations that can be reasonably placed on the VFF. Two key uncertainties structure these scenarios. One is when the Sangoan Industry existed in relation to the age of OG II. The second relates to the tenure of the Lupemban culture, and the age of YG I.

Three axioms also govern reconstructions of these scenarios, and serve to delimit approximations. One is that periods of aridity can be constrained to particular glacial periods, when finite episodes of cryospheric expansion are reflected in the ^{18}O marine record. Two, I invoke the persuasive agreement (Brain 1981, 1985) that arid conditions, across much of Africa, were correlated tightly with expansions of the cryosphere. Moreover, dust peaks in Antarctic ice cores can be invoked as proxies when arid conditions prevailed over landmasses to the north. Three, severe ecological constraints, driven by episodes of global cooling, provided the impetus for the evolution of behavioural and technological

innovations in hominids, including *Homo* during the Pleistocene (Barham 2000, 2001, 2002, McBrearty 2001; Potts 2001; Marean & Assefa 2005).

As reviewed above, there are few reliable dates constraining tenures of the late ESA and early MSA (Sangoan); so their begins and ends straddle broad timeframes. When considered in the context of all available evidence, a narrow array of windows appear within this jigsaw puzzle of Quaternary history. And they likely coincide with the particular arid glacial, when innovations represented in the Sangoan industry actually evolved. On the assumption that this technical revolution evolved under the impetus of nutritional stress, during a severe dry palaeo-environment; then the search to delimit a refined timing on the ESA-MSA transition should focus on the severest glacials during the Middle Pleistocene. Combined evidence from palaeoanthropology and palaeoecology suggests these technical innovations were invented in a particular population of *Homo*, subject to adverse ecological stresses (Barham 2000, 2001). This was during drier conditions when Kalahari sands were reworked by aeolian agencies across much of south-central Africa, and xeric habitats covered much of the region. These conditions coincided closely to where deep Kalahari sands had expanded across south-central Africa (as in the Zambezi valley. The KS I, represented in the VFF, represent the most conclusive evidence for such an extreme arid period. Subsequently, ferricretes indurated these aeolian sediments (KS I) and OG II (Figs 5.2 & 5.3). Excavation of plant tubers in deep sands would have benefited greatly from the innovation of hafting stone picks on to wooden handles. (This suggestion expands the Underground Storage Organ (USO) hypothesis of Laden & Wrangham (2005).) It is reasonable to hypothesize that Sangoan hominins learnt to knap and haft stone picks during such an extreme period of regional aridity. Digging picks would have greatly improved foraging efficiency of Sangoan *Homo*, and enhanced their access to critical food resources.

So, based on the archaeological evidence available, the windows within the Middle Pleistocene that framed the ESA-MSA transition coincided with the inclement, arid conditions of either MIS 16, 12 or 10. Thus three scenarios appear most plausible. In the next section, I sift all this evidence to evaluate these candidacies, and refine which of these three scenarios best fits the criteria, and so accommodates a realistic interface between patterns and events represented in colligations of databases (archaeology, palaeo-climate, palaeo-hydrology, and geomorphology).

5.6.2 Scenario I - the ESA / MSA Transition approximates MIS 8 (301-242 Kya) or MIS 10 (334 - 364 Kya)

Marean & Assefa (2005) restricted the ESA-MSA transition to MIS 8. There are two inconsistencies in this suggestion. Although MIS 8 was one of the longest among all the cooler, drier periods (that prevailed over much of High Africa, through the Pleistocene), it was by no means the severest! This hypothesis glosses over the subtle, but critical, distinction that the older Sangoan culture anteceded the Lupemban; such that these two industries might well reflect sequential innovations that originated under prolonged, but subsequent, periods of ecological stress. Delimiting the ESA-MSA transition to MIS 8 is as difficult to reconcile with evidence that the Lupemban culture already existed around the Kafue Basin (Twin Rivers) at least 260 Kya.

Munyikwa *et al.* (2000) constrained KS I dunes, south of Victoria Falls overlying Ferricrete I, to 173 - 78 Kyr; but admitted their thermoluminescent (TL) date is an underestimate. This is indeed much younger than the Uranium series date (~260Ka) at Twin Rivers placing the Lupemban Industry (that postdates Ferricretes I) in MIS 8. It fits even less well against the Sangoan artefacts preserved at the base of KS I. Two explanations can be invoked. One is that close stratigraphic proximity of Sangoan above Acheulian artefacts in OG II might represent a misleading association caused by bioturbation, after their burial from initial positions on top of KS I. The second explanation is that this paucity of artefacts in the upper levels of KS I reflects a genuine gap in the archaeological record, when hominids were absent from the region. Perhaps, lack of surface water, with upstream impoundment of the Zambezi, mitigated against occupation of the dry valley by *Homo* through this arid period. This scenario also means the progression from origin of the Sangoan industry, in MIS 10, to more refined Lupemban industries was achieved in tens of thousands of years (applying Twin Rivers chronology for the Lupemban, Section 5.5.1).

5.6.3 Scenario II - the ESA / MSA Transition approximates MIS 14 (568 - 528 Kya)

Before evaluating MIS 14, possible candidacy of MIS 16 needs to be considered. All evidence points to the antecedent Sangoan culture, predating the Lupemban, even earlier in the Middle Pleistocene. Amongst possible arid periods, MIS 16 is the oldest candidate, given the earliest Sangoan artefacts reach back to ~ 500 Mya at the very earliest. Alternatively, Sangoan *Homo* lived in the dried out Zambezi valley through the interglacial preceding formation of KS I, which explains how their artefacts accumulated, unrolled, on OG II. No evidence has been found that points to any population of *Homo* inventing technologies associated with the initiation of Mode 3 stone tools from a time approximating MIS 14. Nonetheless, if Scenario II is realistic, it suggests the Sangoan persisted for

over 200 Kyr before Lupemban artefacts appeared. Nevertheless, all the reliably dated living sites throughout Africa (approximating MIS 16 - 14) are attributed to advanced Mode 2 industries. They are characterized by large, symmetrically knapped, Acheulian tools characterizing the late ESA (McBrearty & Brooks 2000; Deino & McBrearty 2002). Pertinently, the majority of such ESA sites discovered on the dried-out floors of palaeo-lakes, in northeast Botswana, contain such artefacts in abundance (Fig. 5.5, see below). Furthermore, no discernable dust signature corresponds to MIS 14 (unlike other major Pleistocene glacials). Yet, MIS 16 (marked by queries on Fig. 5.3) does coincide with major peaks in the circulation of atmospheric dust, but there is no hard evidence for any early MSA culture this early in the Middle Pleistocene. A scenario in which KS I formed as early as MIS 14 or 16, would mean correspondingly earlier impoundment of the Upper Zambezi; so scenario II translates into an unrealistically rapid erosion of the western Batoka Gorge, thereafter. So I conclude the combined evidence suggests MIS 14 is not a likely candidate for the glacial period, which framed initiation of the ESA-MSA transition.

5.6.4 Scenario III - the ESA / MSA Transition approximates MIS 12 (427 - 474 Kya)

This scenario suggests KS I was deposited during the following intense arid conditions driven by the glacial expansion during MIS 12. I assume contemporaneity for the Sangoan and Lupemban, respectively, across equatorial Africa (on both sides of the EARS). So, its climate effects were presumably widespread across central and east Africa. The Kapthurin archaic *Homo* in Kenya, at 510 Kya, sets the oldest limit, currently known, on appearance of the Sangoan culture. So one might assume the transition to the MSA had already begun by the start of MIS 12, when both late Acheulian and early Sangoan artefacts had been aggraded into OG II. Thus, this cultural transition in hominin populations under ecological stress occurred under the arid conditions during MIS 12 (an exceptionally cold glacial, EPICA 2004). It is also likely their densities were relatively low in arid landscapes, then characterized by acute ecological scarcities and constraints for hominids across the Zambezi region.

To pursue this historical reconstruction further, one can presume that during consequent mesic conditions (with marked annual seasonality) bioturbation buried Sangoan artefacts into the lower levels of KS I, before the base of this sediment was then indurated into Ferricretes I. This logically occurred during the following interglacial: in MIS 11 when the Zambezi was still impounded upstream maintaining Palaeo-Lake Bulozzi. One can further speculate that the sharp peak in global temperature, at just over 400 Kya would account for the seasonal tropical conditions, required to foster widespread ferricretation across the Zambezi region (Fig. 5.3). I conclude that Scenario III, centred around an ESA-MSA transition in MIS 12, provides the best fit to the disparate evidence.

Furthermore, a major episode of faulting modified the Rungwe highlands between 570 - 390 Kya; and Delvaux *et al* (1992) revealed this pulse of diastrophism is constrained by dated Rungwe lavas (Figs 4.1 & 5.3). This pulse of tectonic activity in the Middle Pleistocene appears to have been of considerable pertinence; especially if it propagated west across Katanga, and southwest into the Kalahari basin. Thus, important landforms in these regions can be hypothesized to be coeval with the Rungwe horst, which was uplifted ~300m during the Pleistocene (as evidenced southeast of Lake Tanganyika, Haldemann 1969). This event correlates well with KS I emplaced during MIS 12, after the Zambezi has been impounded at two points in its channel. So, such a regional pulse of tectonics explicates significant phenomena additional to the Upper Zambezi's impoundment in the Okavango graben. For if regional tectonism (that affected much of the Katanga-Chambeshi region) did indeed correspond to pronounced uplift along the EARS (between 570 - 390 Kya), then great resolution follows. It delimits initiation of the Batoka Unconformity, and thus initial tenures of palaeo-lakes in the region, including perhaps the Thamalakhane stage at the 936-920 m shorelines in northeast Botswana.

5.7 THE AGES OF THE PALAEO-LAKES - MAKGADIKGADI AND THAMALAKHANE

To reiterate, the VFF, as constrained by archaeological data, provides the only reliable evidence, presently available, to constrain tenures of palaeo-lakes within the Okavango graben, notably PLM. Moreover, it illuminates aspects of Lake Patrick; and it provides convincing evidence for a Palaeo-lake Bulozhi. As dated by early MSA artefacts, the Ngonye ferricretes preserve convincing evidence for Palaeo-Lake Bulozhi. As discussed in detail (Section 4.9.2), major anomalies and significant errors have yet to be accounted for in purported TL dates of aeolian and lacustrine sediments, which reflect profound bioturbation (MacFarlane *et al* 2005). Equally, radiocarbon ages purported to date calcretes cannot be applied (Watchman & Twidale 2002). With chemical conditions associated with increased acidity, silcretes precipitated from dwindling lake waters as PLM dessicated to create layers > 50 cm thick. Subsequently, these dried out sediments were exploited as tool material to knap handaxes, cleavers and other artefacts from chunks of silcrete. It is important to note that several such ESA sites are located at altitudes below the 945m shoreline, which is attributed to the Acheulian industry of the ESA (MacFarlane & Segadika 2001; Fig. 5.5).

Moreover, MSA sites have been discovered at several sites in fossil lake beds delimited by 936 m shorelines, which must then postdate the Palaeo-Lake Thamalakhane stage. Helgren (1984) describes several sites (mapped in Fig 5.5 across the Makgadikgadi depression) with artifactual debris around 920 m level attributed to MSA living sites. This combined evidence points to colonization of the dried

out lake bed (obviously after PLM had dried up) by Acheulian tool makers most likely before the ESA-MSA transition. At least one site (Ngxaishini Pan) was occupied continuously. Here, artefacts extend from the late ESA, through the MSA to Holocene LSA. Considered in toto, this archaeological evidence points to MSA people living around the margins of smaller palaeo-lakes that formed the 936m and lower shorelines. Several of these MSA sites lie below not only the 936 m, but also the 920 m fossil shorelines of the youngest palaeo-lake stages (Robbins & Murphy 1998; McFarlane & Segadika 2001, Fig. 5.5). Furthermore, it logically follows that this distribution of late ESA sites across the Okavango graben postdates the tenure of PLM. This conclusion is contingent on more detailed and comprehensive studies of archaeological sites, in tandem with more precise dating of unperturbed (i.e. non-bioturbated) fossil lake sediments.

The estimation that the Upper Zambezi resumed erosion 970 - 783 Kya (and began to incise the western Batoka Gorge) explains how ESA *Homo* came to make their Acheulian tools out of the silcretes formed in the dessicated lake floor of PLM (Fig. 5.5). It will be especially interesting to test whether the uplift/warping (followed by incision) of limestone sediments near Mambova was contemporaneous with induration of OG II with ferricrete, or the older Chimamba break. Precise dates for these limestones and other sediments will further constrain the timings as to when rivers were flowed into the Okavango graben.

The largest palaeo-lake that might have filled the Okavango graben is a fascinating subject for conjecture. As mentioned in Section 4.9, Thomas & Shaw (1991) mentioned that less well defined evidence suggests that an even larger lake formed above the 945 m isogram attributed to the tenure(s) of PLM (when it formed a lake of ~65 000 km²). Topographic details revealed in the DEM (hitherto unavailable) supports this possibility (Fig. 5.5). Nevertheless, such suggestions remain conjectural in the absence of physical evidence of fossil landforms, attributable to lacustrine processes, especially boulder beds eroded by the strong wave action of such a vast water body. In this respect, it is revealing that no other offshore fossil sandbars complement the massive Gidikwe and Mababe ridges, attributed by Thomas & Shaw (1991) to the strong wave-fetch across PLM, with over 300 km of open lake waters exposed to prevailing winds. The northeast extension of alluvial sediments does, nonetheless, reach an altitude of ~ 1 000 m asl, which most likely corresponds to fluvial deposits across the delta of the Palaeo-Chambeshi River. Nevertheless, to illustrate this conjectural idea, the contour highlighted in Fig. 5.5 depicts the extent of a palaeo-lake that would occupied the 970 m level, with its principal endoreic delta in the northeast, where the Palaeo-Chambeshi debouched into the Okavango graben.

Such a palaeo-lake would have covered at least 250 000 km² (Fig. 5.5)! Alternatively, the shoreline of PLM might have expanded and contracted intermittently to form a much broader shoreline.

5.8 REVISED MODEL OF LANDSCAPE EVOLUTION FOR THE KATANGA-CHAMBESHI REGION THROUGH THE PLIO-PLEISTOCENE

The remainder of this chapter will now apply these chronological constraints to the total evidence available. Synthesis of all these data reveal numerous facets of consilient evidence to refine how landforms have evolved across south-central Africa; where drainage has indeed undergone radical rearrangements. The diagrammatic details of the key events and stages in this late Neogene and Quaternary history can now be summarized. The scope of this model also extends to dynamics of purely terrestrial landforms (notably Katanga's Kundelungu plateau). The synthesis of Chapters 4 & 5 confirms hypotheses for landscape evolution proposed first by Dixey (1943, 1944, 1955): with notable corrections and additions. It also expands the scope and details of the broad-scale narrative of Moore & Larkin (2001).

The evidence supporting these conclusions resides in consilient synthesis of archaeological, biological and geological datasets, in this and the previous chapter. Fig. 5.6 attempts to bring together the principal threads, and summarize key events as to when major landforms evolved across the Katanga-Chambeshi region. Within the bounds of inherent uncertainties, it seems that Scenario III (based on the history of the VFF) underpins the most plausible reconstruction of landscape evolution, especially with respect to when tectonics changed drainage systems. It is not surprising that uncertainties prevail, which will only be rectified by precise dating of key sediments.

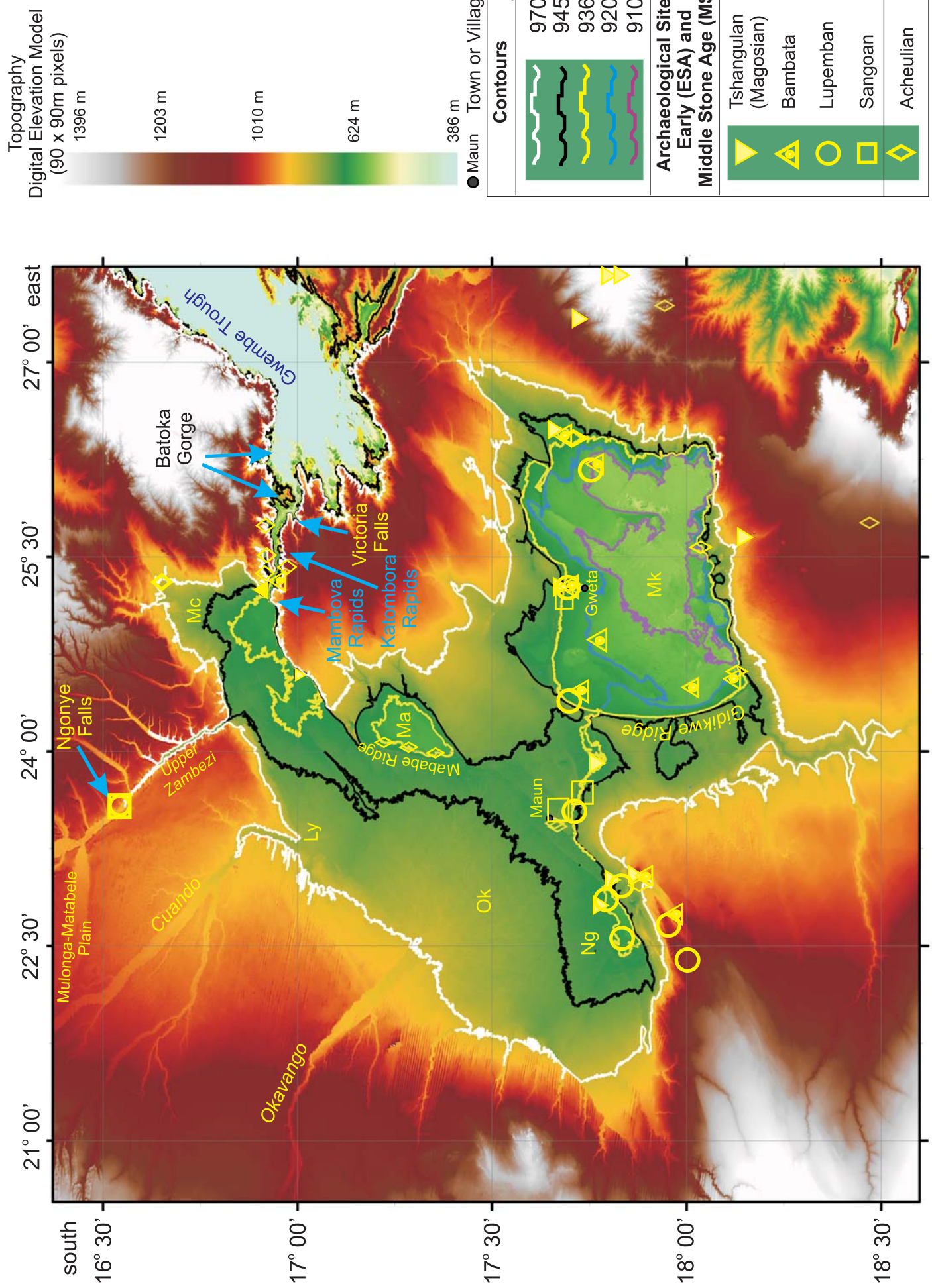
The final model accounts for previously unrecognized links among drainage systems across the Katanga-Chambeshi region. These include connections of wetlands in Katanga and Angola, with those centred on the Okavango and Kafue depressions. These links likely existed before Palaeo-Lake Makgadikgadi attained its maximum extent. Thereafter, in addition to its headwaters in southeast Katanga, the Palaeo-Chambeshi drained a larger portion of northeast Zambia than the modern Chambeshi does today. These former tributaries likely included the Luongo, linked in turn with the Kalungwishi (Figs 4.3 & 4.4). Recent speciation in fishes and aquatic birds within subprovinces of the Katanga drainage system, (pertinently the Lufira and Kamalondo depressions), reveals that these connections were followed by periods of isolation (Section 4.11). Thus, complex interactions between these drainage systems entailed links following on scissions. I suggest these dynamics facilitated

Figure 5.5. [Following page] Detail of the extent of inundations of the northeast portion of the Kalahari basin (Okavango graben) in relation to recorded living sites of *Homo* of Early (ESA), Middle (MSA) and Late Stone Age (LSA). The principal fossil-lacustrine formations in northeast Botswana are indicated by altitudes of shorelines formed by fluctuating palaeo-lakes: Lake palaeo-Makgadikgadi (LPM), 945m maximum (a); Lake-palaeo-Thamalakhane, 936m (b); and smaller lakes at 924m (c); 920m (d); and 910m (e) in the Chobe (C), Linyanti (L), Mababe (Ma), Makgadikgadi (Mk) and Ngami (N) sub-basins (after Thomas & Shaw 1991). Majority of the stone tools, preserved in these living sites, were mainly knapped from silcretes that comprise fossil lake floors. It is further noteworthy that these artefacts extend from the late Early Stone Age (ESA) through the Middle Stone Age (MSA). The spatial extents of palaeo-lakes is delimited by contours calculated in ArcGIS Spatial Analyst from DEM topography (delimited by 1 800m² pixels). Locations of these landforms conform with that in earlier mapping by H. J. Cooke (1979), Cooke & Verstappen (1984), and Thomas & Shaw (1991) from 1:50 000 Ordnance topographic maps, augmented by directly quantified altitudes. ESA living sites are labelled: 1. Metsemasweu River, just N of Serowe, being 5.5km NW of point 22 25'S, 26 45'E. Acheulean axes (Ebert *et al* 1976); 2. Gweta (6km NE of) between the 945m and 920 m fossil shorelines. 3. Ngxaishini Pan (=Makawe Pan) ~12km N of Gweta site (Robbins & Murphy 1998). There is evidence for a continuous living sequence from the ESA, through Middle Stone Age (MSA) to Late Stone Age (LSA) at Ngxaishini Pan (McFarlane & Segadika 2001). 4. Nwetwe Pan basin (1), along edge of Karroo sandstone platform near 945 m shoreline - above the basin of Nwetwe Pan, ca 21° 07'S, 25° 34'E (Helgren (1984). 5. "Well-made hand axes (ESA) fashioned from silcrete are especially common finds along the Boteti river, near Maun where silcrete outcrops in the river bed..." (Robbins & Murphy 1998: 53). 6. MSA artefacts from the delta of the Nata river; almost identical to Lupemban artefacts in Younger Gravels around Victoria Falls. This site is located below the 920m shoreline (Bond & Summers 1954). 7. Kudiakan Pan with late MSA tools, which appear similar to the Bambata industry. These were knapped from abundant nodules of silcrete, which is abundant in the surface of the pan. It is pertinent to the age of the palaeo-lake stage that these MSA artefacts are manufactured from silcrete and lie close to the edge of the 910 m shoreline (Robbins 1988).

periods of dispersal that alternated with vicariance of aquatic biodiversity across the south-central African plateau.

5.8.1 Formation of the Luapula-Chambeshi Drainage System

Bell-Cross (1968, 1982) concluded that the lack of faunal exchange between the Luapula-Mweru and Upper Kafue systems means that the link between Lakes Bangweulu and Mweru was established after the Palaeo-Chambeshi had been disrupted. This is invoked to have disrupted river flow across the Itawa dambo and Proto-Muniengashi channel. I suggest this likely entailed uplift of the Congo-Zambezi watershed along the Mufilira axis. This tectonic event preceded deepening of the Mweru trough; and it culminated in piracy of the Chambeshi flowing out of Palaeo-Lake Bangweulu, after scission of the Palaeo-Kafila river (Fig. 4.3). To conclude, all the evidence points to the creation of the link between the Chambeshi and Luapula rivers to be the penultimate event in a protracted history of drainage evolution centred in the Katanga Pedicle.



5.8.2 Trans-Katanga Drainage and Palaeo-Lake Bangweulu

A revised model must account for a sequence of connections between the Upper Chambeshi and neighbouring rivers, with their confluences concentrated around the Katanga Pedicle. First, at its largest extent, the Palaeo-Chambeshi flowed into the Kalahari basin, with precursors of the Upper Lualaba, Upper Luongo, and Lufira rivers as its tributaries. Uplift along the axis of the Mufilira syncline fractured the Palaeo-Chambeshi's channel southeast of Bangweulu. The combined evidence reveals how effects of even mild crustal warping, and slight faulting, have been magnified across this flat landscape - with concomitant impacts on drainage.

These events probably changed both the Palaeo-Chambeshi and trans-Katanga drainage systems simultaneously. This reversed the flow to the northwest (formerly southeast) of the Lufira and Kafila rivers, so they now flowed across the Lufira depression into the Kamalondo depression. Third, and finally, the Lower Luapula broke up this trans-Katanga drainage system by river piracy in the vicinity of Kibaya. The Upper Chambeshi was now isolated from the trans-Katanga system, and Palaeo-Lake Bangweulu probably reached its maximum extent thereafter. Flexure along the Mufilira axis may also have created an endoreic drainage centred around the Bangweulu basin. In the penultimate event, quite recently, the Upper Chambeshi became the headwaters of the Luapula feeding Lake Mweru after the Luapula captured the senile channel of the Palaeo-Chambeshi on the southwest edge of the Bangweulu basin (Fig. 4.4). It is unclear how the histories of the Bangweulu basin related to events in Katanga, which saw the Kamalondo and Lufira depressions alternatively isolated and linked. Patterns of dispersals and vicariant speciation (as judged by indicator species, Section 4.11, Appendix 3) suggests that this trans-Katanga drainage probably existed after the Palaeo-Chambeshi had been severed from the Upper Zambezi-Okavango. Nevertheless, plausible explanation for the evolution of endemic fishes and molluscs is most plausibly explained by a significant period of isolation of the Bangweulu-Upper Chambeshi system in its discrete basin.

5.8.3 Links from Western Angola - across the Okavango-Kafue graben - to Bangweulu, Mweru and Katanga

Biogeographical insights derived from this model are interesting in that they revise earlier explanations, notably for fishes and lechwe antelopes. The consensus view is that Zambezian fishes gained access to the Lualaba only after the Upper Chambeshi was captured by the Luapula (Jackson 1962, 2001; Roberts 1975). A revised explanation now has to reconcile with a more complex history of links between key drainage systems in Katanga, which extended south to the Kalahari basin. Key landforms were the Kamalondo and Lufira depressions. This drainage network radiated in a northward arc around

its endoreic hub in the Okavango graben. Thus, the more dispersant of aquatic organisms in Katanga reached watersheds in western Angolan, abutting on Atlantic tributaries, and vice versa. In this region, the Upper Cuanza and Upper Kunene are two landforms of key interest, and this especially applies to their floodplains supporting lechwe antelopes (Chapter 2, Figs 2.1, 2.2 & 4.5). Several possible dispersal routes then existed, which entailed links across the Cubango headwaters, and/or across the Owambo basin (Section 4.10, Fig. 4.10). Based on the reconstructed history of the Etosha basin (Hipondoka 2005), it can be hypothesized that these links between the Kunene and Okavango-Upper Zambezi have influenced aquatic evolution since at least the Pliocene, and have extended into the Pleistocene. In the past, this theatre - one of interlinked wetlands - extended across Katanga and northeast Zambia. Dispersals and vicariance of aquatic biota between these Upper Congo and Upper Zambezi wetlands has entailed a complex history of links between the Palaeo-Chambeshi and Trans-Katanga systems (Figs 4.1-4.4).

5.8.4 Alternative (Greater) Significance of the Chimamba Rapids in Batoka Gorge

One factor cannot escape scrutiny for it points to a niggling doubt in the narrative assembled through this chapter, which must be acknowledged in the nature of the Chimamba rapids; namely why is the ferricrete formation (reflecting reduced if not nil erosion for ~180 Kyr) not reflected in a discernable nick-point in the profile of the Zambezi river below the Victoria Falls? This dissonance in contrasted evidence further highlights the possibility that the Upper Zambezi's erosive power was abetted by perhaps ~30 km³/yr of additional runoff (as hypothesized above, Section 5.4.5). Even should this have really happened, an Early Pleistocene tenure of PLM remains credible - thus reflecting a corresponding break in river flow. This narrative rests on the archaeological evidence around fossil shorelines from desiccated lake sediments, and is also supported by the estimated timing of a statistically significant population expansion in Okavango *Kobus leche*. This peak at 764 Kya is interpreted to reflect exploitation of previously unavailable floodplains, after PLM declined when Zambezi flow ensued through the Batoka gorge (Chapter 6).

5.8.5 Timings of Tectonic Uplift and Flexures

Detailed fieldwork remains to be carried out across northeast Zambia and neighbouring Katanga to establish more precisely how reworking of key landforms related to episodes of tectonics postulated to have acted through the Neogene and Quaternary. Nevertheless, in the absence of such actual dates, one can only invoke reliable constraints established along the Albertine rift. The diastrophic events that buffeted the Malawi and Tanganyika rifts, through the Plio-Pleistocene, are especially pertinent in this respect. Along the Albertine rift, Ebinger (1989) reported Pliocene, and Early and mid-Pleistocene,

lacustrine sediments that today lie at elevations substantially higher than current lake levels. These extend northwards from the southern edges of Lake Tanganyika, but the testimony to their coeval uplift is most spectacular along the Virunga basin, where Pliocene sediments, at 1 450 m asl, tower above Pleistocene facies at 800m (Pouclet 1975). It is noteworthy that uplift of Pleistocene sediments 300m above Lake Tanganyika, correlates with evidence for contemporaneous faulting centred on the Rungwe highlands in the Middle Pleistocene. After corrections for lake level changes (due to erosion and climatic agencies), all this evidence attests to pronounced episodes of uplift. These events punctuated quiescent periods when sediments accumulated and were lithified in these depressions along the EARS.

Resolution of when significant events changed these wetlands, and their connections, is now based on a revised erosion history of the Batoka Gorge (in tandem with the Victoria Falls Formation). It is further correlated with reliable dates of uplifted sediments in the Rungwe formations of the EARS. These events were possibly contemporaneous with those that entailed incipient rifting across the Palaeo-Chambeshi archipelago in repeated episodes since the Pliocene. Reappraisal of what in fact comprises a wealth of published data has been greatly illuminated by availability of high-resolution topographic data. New insights obtained in Chapters 4 & 5 point to the following refinements on published knowledge:

Many of the events, whereby drainage systems have been rearranged, have centred around major basins and graben within south-central Africa. Pertinently to lechwe antelopes (amongst much other biodiversity), these vast depressions have supported immense lakes and floodplains. The concept of an archipelago, introduced in Chapter 2 (and applied in Cotterill 2004, 2005), provides a convenient, heuristic framework in which to study and understand their associated histories across an evolutionary theatre of nearly 3 million km².

At least since the Neogene, the Upper Zambezi, Cuando and Cubango rivers appear to have been significant parts of successive endoreic drainage systems with their depocentres centred in the Okavango graben. So they had direct links with the Chambeshi-Bangweulu drainage (and the proto-Upper Kafue). These links also extended to the proto-Luongo and trans-Katanga systems north to Lake Mweru. Specifically, this involved the Kamalondo, Lufira, and Upper Lualaba drainage systems of Katanga when linked with the Palaeo-Chambeshi system. In the west, abutting the Atlantic margin, this archipelago incorporated close links with the Owambo basin, and also the Upper Kunene and Upper Cuanza systems. The northern limits to

this palaeo-drainage system lay substantially north of the Southern Equatorial divide in the Congo basin.

The archipelago has progressively lost key landforms since the Early Pleistocene. Notable losses on the western plateau include the Upper Cuanza and Upper Kunene rivers, followed by dessication of the Owambo basin. In the north, major headwaters of the Palaeo-Chambeshi were pirated by the Upper Congo, and equally when the Kasai system captured Upper Zambezi headwaters. The Chobe and Upper Zambezi are still becoming firmly established as exorheic rivers to the Indian Ocean. Equally, extant links appear to persist between the Cubango headwaters and both these Atlantic tributaries. Overall, these events of drainage piracy have substantially altered aquatic biodiversity, through a complex history.

Piracy of Upper Zambezi headwater tributary by the Kasai aided southward invasion of the Zambezian region by many fishes, notably *Hydrocyon vittatus* (Section 4.11.7). Since tigerfish did not gain access to the Upper Kafue system; it follows that these Kasai piracy events occurred after scission of the Palaeo-Chambeshi's link with the Upper Zambezi between Mambova and Katimo Mulilo. Archaeological data constrains this event in the Middle Pleistocene, and certainly well after Lake Patrick had formed. It is as interesting that tigerfishes have failed to disperse into the western rivers of the Katanga-Chambeshi region, even though several cichlids have enriched the fauna of the Upper Kunene (Section 4.11.7). These anomalies in the natural history of *Hydrocyon vittatus* constitute further evidence for its relatively recent invasion from the Kasai.

This weight of geological and biotic evidence (Chapter 4, this Chapter) reveals that immense lakes were maintained across the Katanga-Chambeshi region by endoreic drainage systems. Since then the major tributaries of these closed basins have been progressively pirated by exoreic rivers flowing to the Atlantic or Indian Oceans. The largest of these inland lakes, Palaeo-Lakes Kunene and Makgadikgadi appear to have been Pliocene and Early Pleistocene landforms, respectively (Section 4.9 & 5.7).

As a biogeographic barrier, the Palaeo-Chambeshi is invoked to have contained dispersals of terrestrial vertebrates, for periods sufficient to have fostered speciation events. Perhaps, its configuration was established in the Pliocene and persisted until its breakup by early in the Middle Pleistocene (Section 4.13.5).

This scission of the Palaeo-Chambeshi's link to the Okavango graben is hypothesized to approximate the early Middle Pleistocene, perhaps as early as 1 Mya, or more likely ~700Kya, based on estimated ages of the Batoka gorge. Archaeological constraints, combined with less reliable evidence, restricts its break up to relate closely to the tenure of PLM, long before the much smaller PLT existed. This radical change in drainage topologies also occurred before Lake Patrick was established in the late ESA (~500 Kya), as based on evidence synthesized in Scenario II (Section 5.6.4). This drainage rearrangement was one of several that broke up the Palaeo-Chambeshi through a sequence of piracy events (Sections 4.7 & 4.13.5).

The southern margins of the Mweru rift have been an important arena of landscape evolution through the Pleistocene (Figs 4.3 & 4.4). The piracy of the Upper Chambeshi, creating the present source of the Congo, was probably the most recent event in a complex history of landscape evolution, driven by deepening of the Mweru graben. Significant events were centred around, and within, the eastern Katanga Pedicle south of the Mukuku Hook (represented by the sharp capture bend of the extant Luapula river). New evidence suggests the course of the Palaeo-Chambeshi migrated north, to culminate in its penultimate piracy by Luapula headwaters (Section 4.7, Figs 4.4a-e). The timing of scission also occurred before tigerfishes dispersed across the drainage systems of Katanga from downstream in the Congo. Otherwise *Hydrocyon vittatus* would have reached the Upper Kafue. Tigerfishes reached Lake Bangweulu and the Upper Chambeshi through the Luapula, although waterfalls have persistently contain these predators downstream of the Upper Luongo and Kalungwishi rivers.

Preserved channels, which are attributed to where the Palaeo-Chambeshi river flowed southwest, straddle the Mufilira anticline (which coincides with the Southern Equatorial Divide). These abandoned channels are preserved as the Itawa dambo, and represented today by the Kafulafuta and Muniengishi rivers, which today flow in opposite directions. Avulsions of river channels, and a dense network of faults constitute further evidence for a complex history of drainage evolution across the Katanga pedicle, abutting the southwest margin of the Bangweulu basin. Overall, they testify to overwhelming control by Neogene and Quaternary tectonics.

Tectonism expressed around the Mweru graben represents its wider, regional incidence. The Upemba horst and Kundelungu plateau testify to dramatic uplift across Katanga. The rifting activity that deepened the Mweru graben appears to have been contemporaneous with tectonic

events that extended at least as far west as the Kamalondo depression. Its effects included significant uplift of the Kundelungu and Upemba horsts and the Lufira depression. Yet to the southwest, dynamics of drainage evolution around the Okavango-Kafue graben reflect more subtle effects of this tectonic activity. This possibly began in the Pliocene, persisted through the Pleistocene, and likely continues (Section 4.9, 5.6; Figs 4.7a,b, 5.3-5.5). Nevertheless, the history of river impoundment and erosion, preserved around the Batoka Gorge, points to discrete episodes of tectonic activity (Section 5.6, Fig. 5.3).

The Kamalondo depression has formed in an ancient graben inherited from Karoo times. Since the late Pliocene, it has been deepened by tectonism contemporaneous with that which uplifted the Upemba and Kundelungu horsts, and also downwarped the Lufira depression to form Palaeo-Lake Lufira (Section 4.6).

In addition to the Palaeo-Chambeshi *per se*, tectonic-aided deepening of the Mweru Graben disrupted at least two drainage systems with firm links with the Palaeo-Chambeshi. A major vestige of one is represented by the Upper Luongo, intimately linked with the Kalungwishi, and today both rivers maintain the Pambashye Swamps (Section 4.6, Fig. 4.2). The second was the Trans-Katanga drainage that at least linked the Lufira depression with the Bangweulu via the palaeo-Kafila river. Extant signatures of this Trans-Katanga link are represented by the Wiswila and Kafila rivers in Katanga. They flow into the Luapula and Lufira, respectively. Today, the Wiswila exists as a distinctly underfit river in the former channel of the Palaeo-Kafila (Sections 4.6, Fig. 4.3).

These piracy events are suggested to have disrupted the courses of the Proto-Luongo and Trans-Katanga drainages before piracy of the Upper Chambeshi. Disruption of the Palaeo-Kafila entailed its piracy by a headwater of the aggressively eroding Luapula catchment (Sections 4.7).

Archaeological evidence constrains events represented in the Plio-Pleistocene VFF. These provide the most reliable constraints, available, to delimit this postulated disruption of the Palaeo-Chambeshi. They equally reveal insightful aspects of tenures of palaeo-lakes in the Okavango-Kafue graben. On the Kafue Flats (cotemporaneous with the VFF), gravels (OG II) overlie Karoo sediments under younger lacustrine alluvium. They contain Acheulian ESA artefacts coeval with Early Pleistocene deposits in the VFF. These same gravels were

debouched across the Machili Flats. The extent, and incidence, of their deposition testify to considerable inflow by the Palaeo-Chambeshi (and perhaps Palaeo-Kafue) rivers before disruption. Their deposition occurred before the end of the ESA (i.e. earlier than ~ 500 000 years BP) early in the Middle Pleistocene, or earlier in the Early Pleistocene (Sections 5.6, Figs 5.3 & 5.4).

It follows that the alluvium overlying these Palaeo-Chambeshi gravels is attributed to the tenure of Lake Patrick, which inundated the Kafue Flats through the Middle Pleistocene. Lake Patrick had ceased to exist before 300 000 yrs BP (Section 4.9.4, Figs 4.7 & 4.10).

The estimated tenure of Lake Patrick reveals how the modern Kafue river only formed quite late in the Middle Pleistocene. This was when a middle Zambezi tributary captured the lake as its source, and then ultimately pirated the Upper Kafue.

The tenure of Palaeo-Lake Bulozzi appears to have begun around 500 Kya. It appears to have dwindled after the Upper Zambezi was reconnected to the middle Zambezi (approximately ~250 Kya), as represented by later MSA artefacts in YG I of the VFF.

Late Pleistocene sediments in the VVF points to prolonged aggrading by the Upper Zambezi (upstream of Batoka Gorge). This comparatively quiescent period in the Upper Zambezi's history probably began around 300 Kya, and has continued through the Late Pleistocene.

Understanding the interrupted flow regime of the Upper Zambezi, during the Middle Pleistocene, constitutes the critical facet of historical evidence that explicates not just anomalies distributions of certain African mammals, but actual speciation events. Notable examples include peripatry of the Blue Wildebeest complex *Connachaetes taurinus*, and the hartebeests, *Alcelaphus caama* and *A. lichtensteinii* (to be discussed in detail in Chapter 6).

5.9 CONCLUSIONS

5.9.1 Scientific Methods

Polymath and philosopher William Whewell (1794-1866) coined two neologisms - consilience and colligation - to consolidate the explanative power of epistemology. These explicate his epistemic thesis of how palaeontological sciences (pertinently geology) structure data, derived from disparate sources, into synthesized knowledge. Consilient knowledge is invariably constructed of explanations that reveal

unprecedented scope in their explication of properties of the natural world. Such knowledge accrues through a process of discovery, in which a Consilience of Inductions arises from Colligations of Facts (Gould 2002, 2003, Chapter 1). For example, DeMenocal (2004) assembled colligations of geochemical and biochemical patterns from disparate sources (including glacial, marine, aquatic and terrestrial sediments). The resultant, consilient, narrative details how climate has changed across Africa since the mid Neogene. All twenty-two of Darwin's books (Ghiselin 1984), including *Origin of Species* (Gould 2002, 2003) stand as crowning testimony to the ubiquity and power of the hypo-deductive method, whereby consilience can structure discoveries of far reaching scientific relevance. Hypothesis testing of singular historical phenomena is not only challenging but invariably inappropriate. There is only one Earth, and its individuated geological formations and unique species fail to substantiate probability-based statements (of the sort framing knowledge in physics and chemistry) describing historically-derived properties of the natural world, such as "The earth is round ($p < .05$)" (Cohen 1994: 997).

5.9.2 Geomorphological Significance

Beyond their contribution to aid explication of lechwe evolution (developed through Chapters 6-8), the combined evidence assembled in this chapter has several applications. Firstly, these patterns constitute targets for new research. For it is in the very nature of science that advances gained in understanding that little bit more about Earth's history simultaneously reveal new problems to solve. Invariably, we obtain novel resolution, only to discover previously hidden phenomena. These fresh perspectives reorganise established data into previously unrecognized patterns, and so challenge us to readjust our focus on these unforeseen challenges of enquiry. Thus, the data that construct this model of drainage evolution have proposed hypotheses to test, and the sites and organisms to sample. This chapter reveals several anomalies represented in congruent patterns of many aquatic organisms. An example are anomalies represented in the complex distributions of the two predatory fishes - *Hydrocyon vittatus* and *Hepsetus odoe*. Reconstructing the evolutionary histories of these species stands to reveal a great deal about when radical geomorphological events reshaped drainage systems, to influence the biodiversity of High Africa.

Secondly, the data synthesized in Chapters 4 and 5 reveal hitherto unknown historical events. Obviously, precise geochemical dating of alluvial deposits would be a great asset to decipher this complex geomorphological history. There is no substitute for unprecedented fieldwork. And it is in this respect that the chronological significance of the VFF has barely been tapped. Future studies that apply geophysical dating techniques using cosmogenic isotopes (see Von Blanckenburg 2005) should

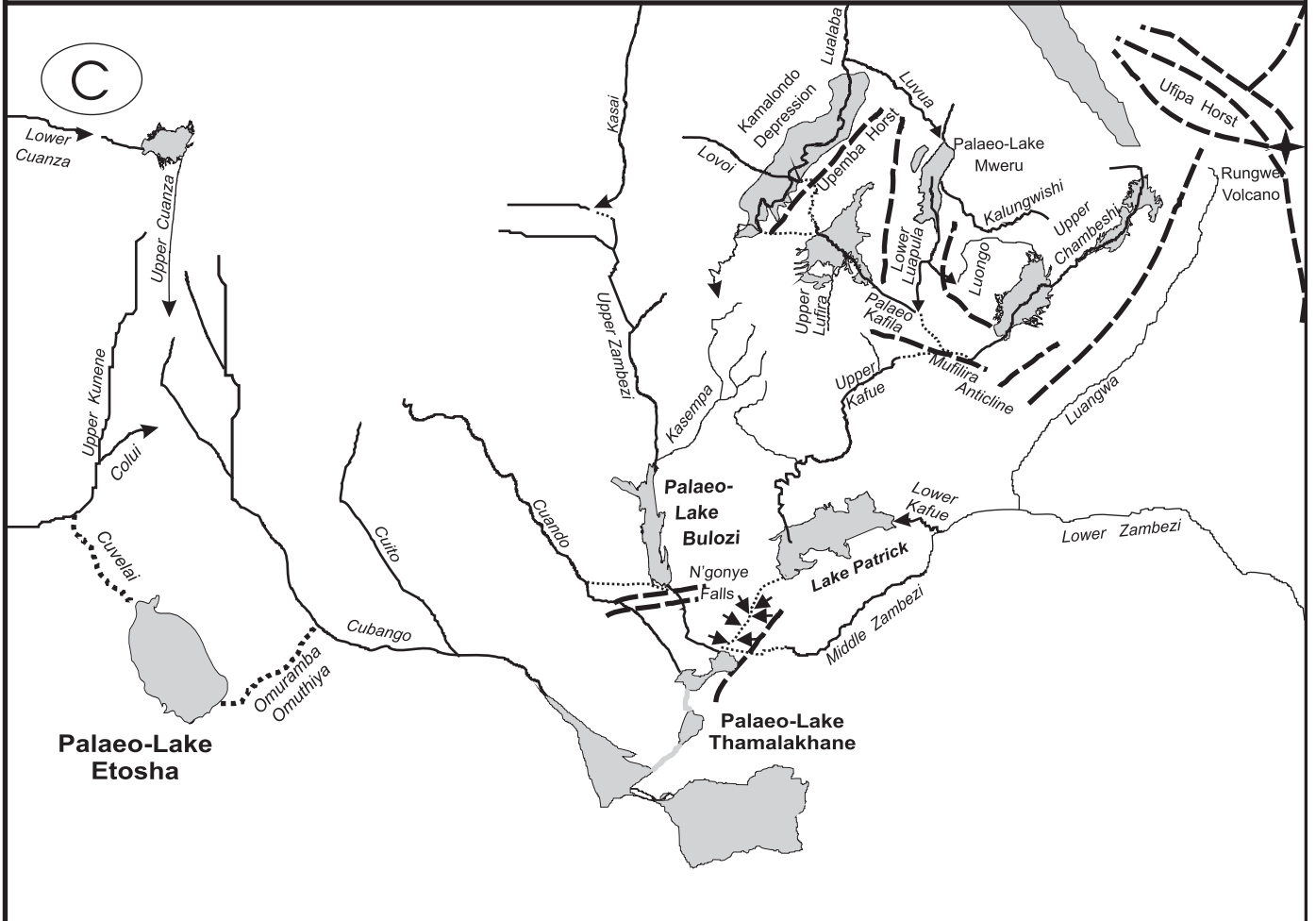
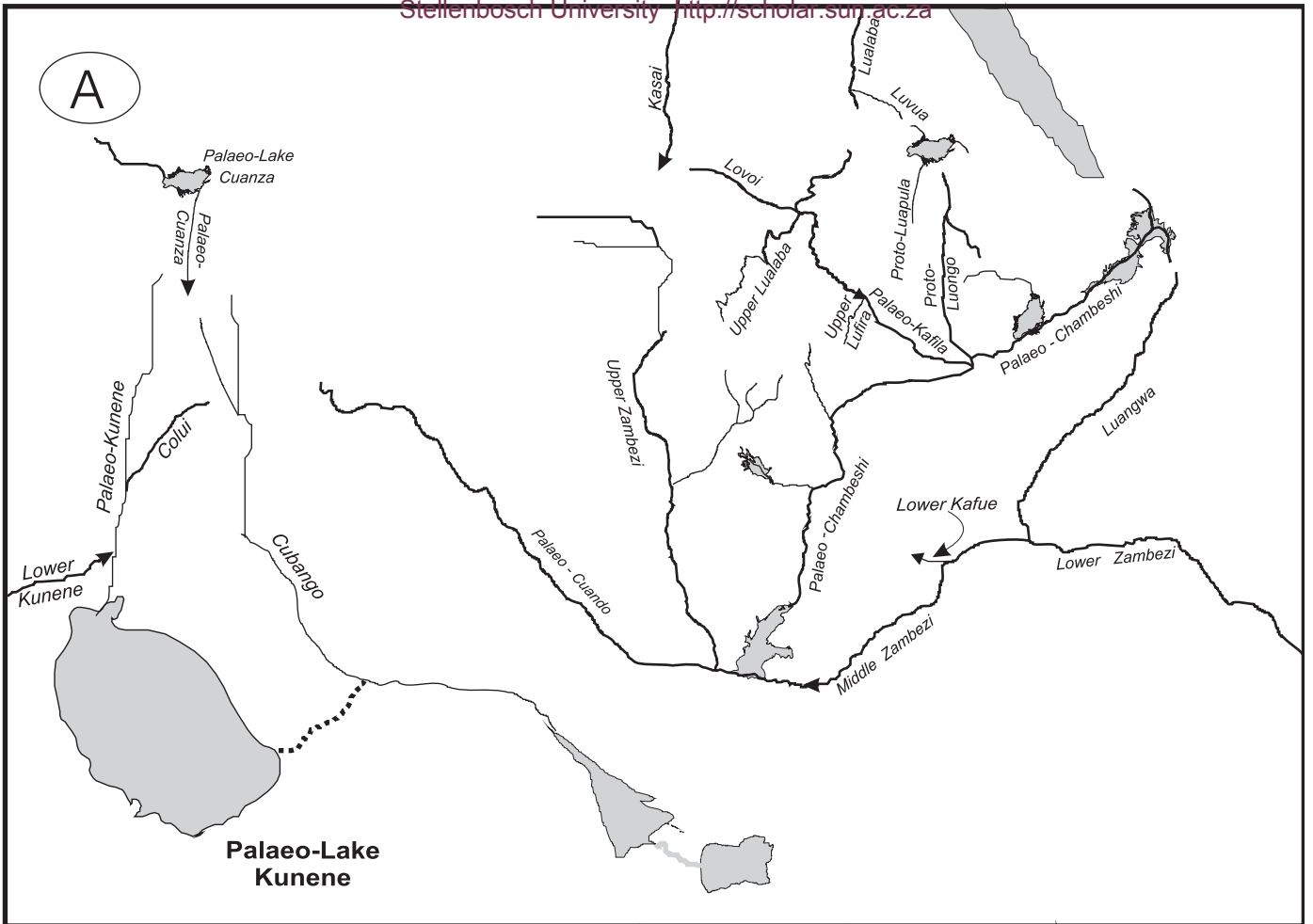
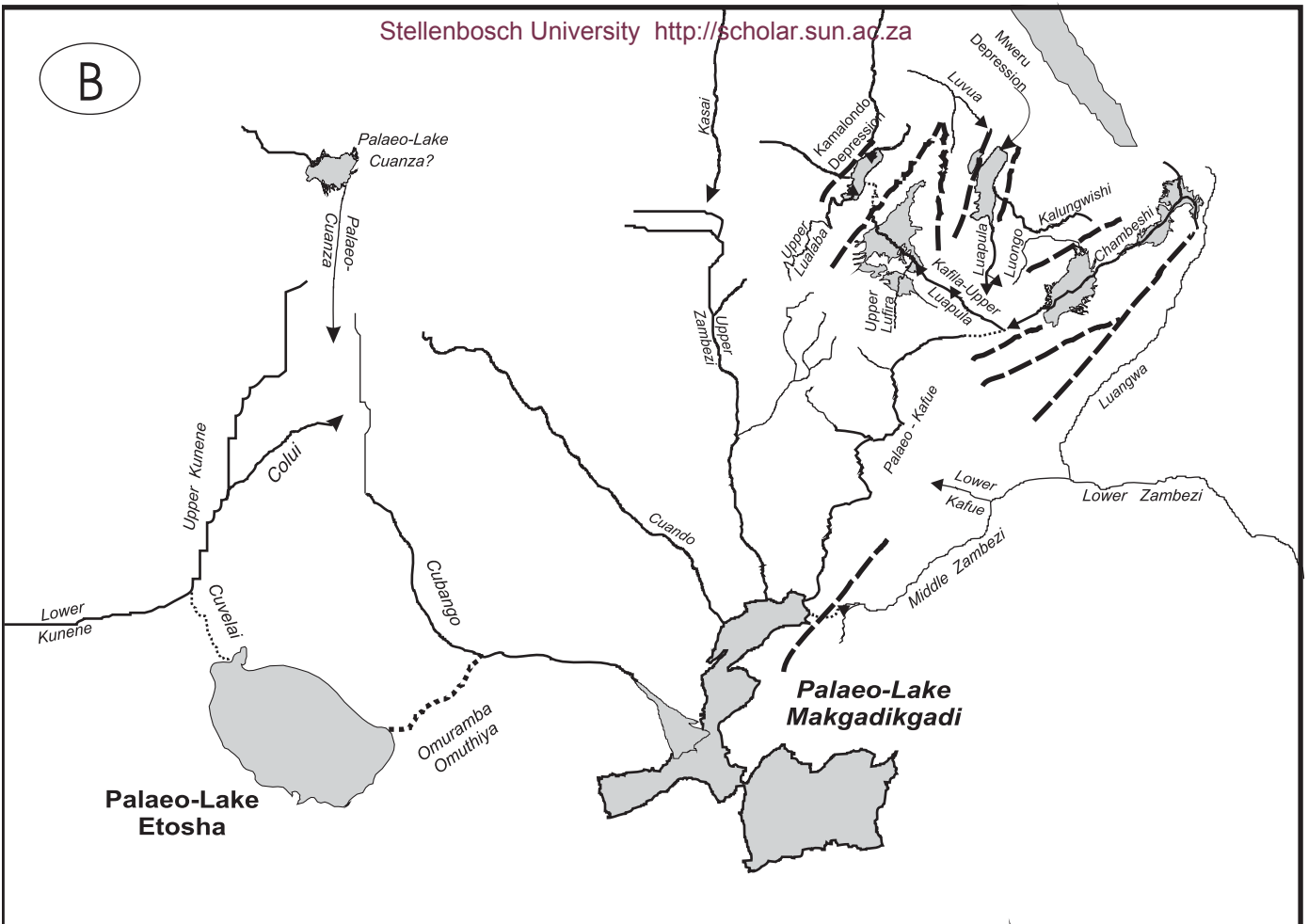


Figure 5.6. [Previous Page] Schematic representation of topologies of drainage systems, across south-central Africa, with respect to their fragmentation since the Miocene. This revises and expands on the models proposed by Moore & Larkin (2001) and Cotterill (2004). The focus is on past configurations of rivers, including connections of Katanga's wetlands with the Palaeo-Chambeshi. Broad broken lines denote zones of uplift and/or faulting. Grey shaded areas represent wetlands existing at that time. Dotted lines indicate abandoned river channels. Palaeo-climatic control over the repeated existence, and expansions, of the Mega-Kalahari sandsea (Fig. 5.7) would have interacted with these dynamics of landscape evolution to further control hydrological patterns and processes.

a). **Late Pliocene.** The original configuration - established in the Miocene and persisting into the late Pliocene and Early Pleistocene - of drainage across the south-central African plateau. The Palaeo-Chambeshi was at its greatest extent, as the longest tributary then connected to the Zambezi, which has established its modern topology in the late Pliocene. The Palaeo-Kafila is a major western tributary connected across the Lufira depression, and connects the Kamalondo graben in the Trans-Katanga drainage system. Palaeo-Lake Kunene is at its maximum extent just prior to piracy of the Upper Kunene by an eroding Atlantic tributary. The Zambezi erodes the eastern Batoka Gorge from the late Pliocene into the Early Pleistocene.

c). **Middle Pleistocene.** The Upper Zambezi became reconnected to the mid-Zambezi in the Middle Pleistocene (738 - 597 Kyr), to cause contraction of Palaeo-Lake Makgadikgadi; where after the Upper Zambezi incises a significant extent of the western Batoka Gorge. The Lower Lufira river becomes reconnected to the Kamalondo depression, incising the Lufira Gorge across the Upemba horst; where, previously, the large, shallow Palaeo-Lake Lufira has persisted in an isolated endoreic drainage system. The link between the Upper Kafue and Palaeo-Chambeshi rivers was broken permanently at, or soon after, this event; when uplift across the Mufilira Anticline, southeast of the Bangweulu basin, contains the headwaters of the Palaeo-Chambeshi to create Palaeo-Lake Bangweulu. Headwaters of the Lower Luapula behead the Palaeo-Kafila, to initiate isolation of the Lufira drainage from the Bangweulu depression and its Upper Chambeshi tributary. To the southwest, the Machili flats desiccate. Impoundment of the Upper Zambezi at both Mambova and Sioma Falls is associated with the tenures of Palaeo-Lake Bulozhi and Thamalakhane. These persist late into the Middle Pleistocene. The isolated Upper Kafue river is now the principal endoreic tributary of Lake Patrick, covering the Kafue Flats. Several species of mammals disperse across the dry Zambezi valley, which is covered by Kalahari Sands I. The Colui, an Upper Kunene tributary, is eroding northeast toward a Cubango tributary; while southward eroding headwaters of the Upper Cuanza are establishing a connection to the Cubango river. The Kasai captures headwater tributaries after scission of the Palaeo-Chambeshi. Faulting focused around the Ufipa plateau is constrained by repeated eruptions of the Rungwe volcano at 520 and 420 Kya.

B



D

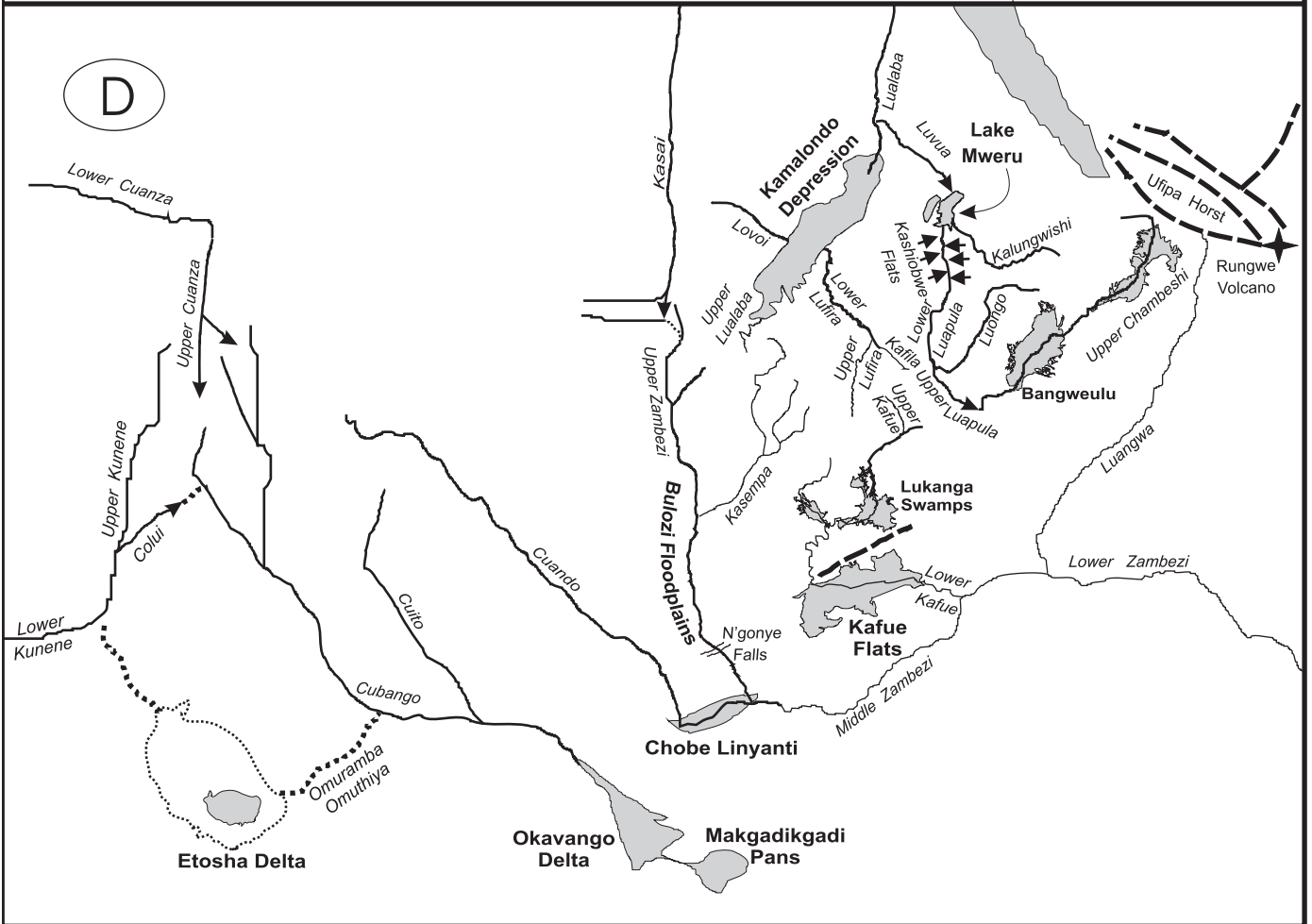


Figure 5.6 cont. [Previous Page]

b). **Early Pleistocene.** Widespread tectonic activity in the early Pleistocene deepens the Lufira depression, and the Kamalondo and Mweru graben; with simultaneous uplift of the Kundelungu and Upemba horsts. The latter's uplift impounds the Lower Lufira to enhance Palaeo-Lake Lufira, with intermittent disruption of the Trans-Katanga drainage system. Palaeo-Lake Makgadikgadi (PLM) reaches its maximum extent after the Zambezi is impounded by faulting across the Mambova and Katombora rapids. A vast endoreic drainage system maintains PLM, and includes the Palaeo-Chambeshi, which aggrades ESA artefacts in gravels that are covered subsequently by alluvial clays.

d). **Early in the Late Pleistocene.** The penultimate events of Quaternary drainage evolution have nearly played out. It appears this extant configuration of drainage has only existed since the late Pleistocene. The Zambezi has reestablished its modern topology, and has been grading Younger Gravels (YGI) across its channel since the middle of the Middle Stone Age. The Lower Luapula has finally captured the Upper Chambeshi to form the modern topology of the Upper Chambeshi - Luapula - Mweru system (Zambian Upper Congo system). The Lualaba has also graded its bed to the south - to link the Kamalondo depression with the Congo system. Capture by the Luvua drained Palaeo-Lake Mweru, to create the Kashiobwe Flats. The Upper Kafue is firmly established as a major north bank tributary of the Zambezi, which has attained its modern configuration. Palaeo-Lake Lufira has drained after further down-cutting of the Lower Lufira - through its deep gorge - flowing across the Upemba Horst into the Kamalondo depression. The precursor of the Kafue Flats is established, as a north bank tributary of the mid-Zambezi begins to capture Lake Patrick, and thus the Upper Kafue as its headwaters. The seasonally flooded Kafue Flats form in the Late Pleistocene, governed by the annual flow regime of the Kafue river, which is now a major north bank tributary of the Middle Zambezi river. Actively eroding headwaters of the Lower Luapula back-cut southwards, and so widen the Mweru depression.

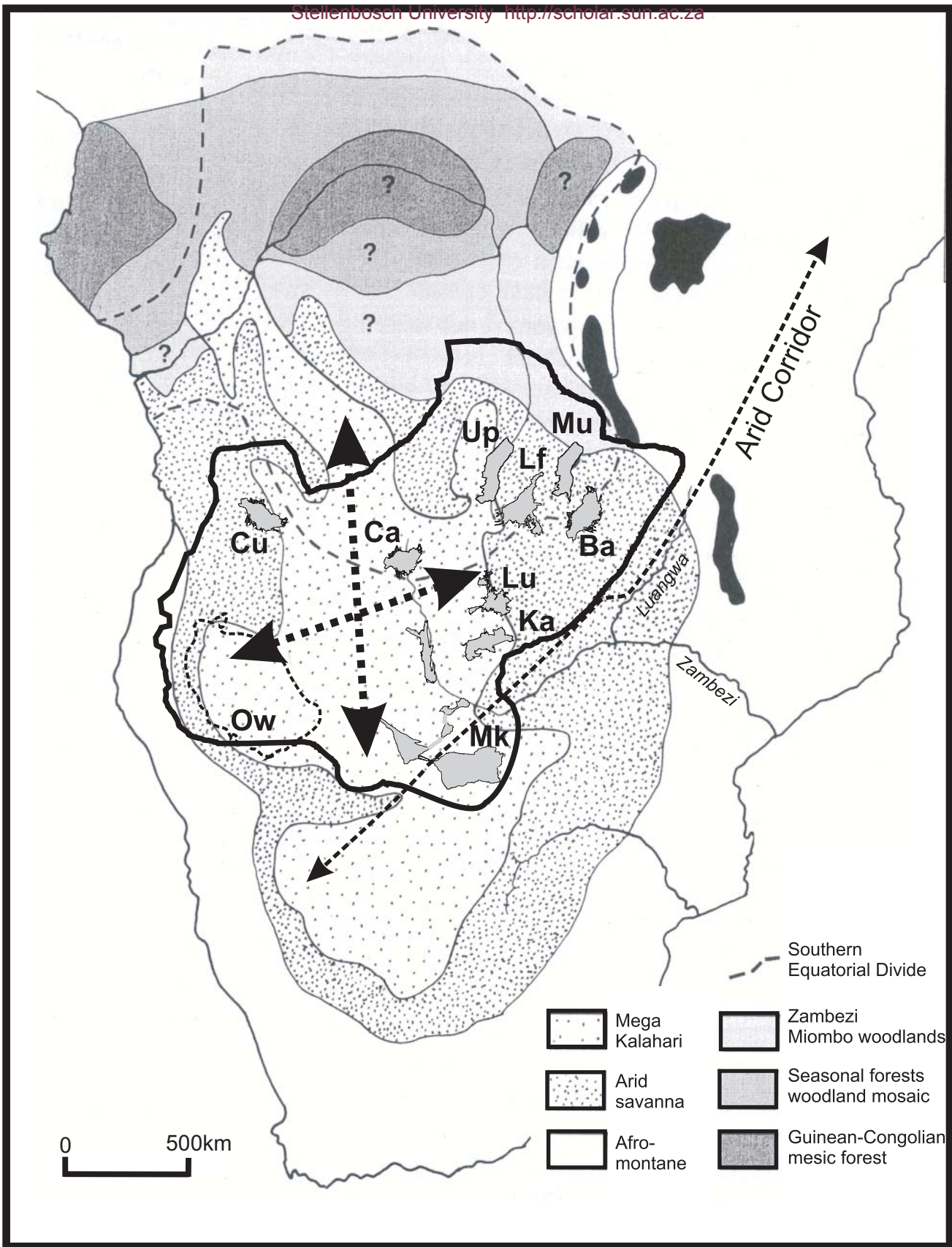


Figure 5.7. A representative narrative of palaeo-environmental evolution must accommodate all prominent events through the Neogene and Quaternary, especially those driven by vicissitudes of palaeo-climates. The approximate extent of the Mega-Kalahari sand-sea is compared to that of the Katanga-Chambeshi region (solid line) which encompasses principal depocentres of the wetland archipelago. The shaded biomes represent the hypothesized extents of major vegetation assemblages, at Glacial Maxima, with xeric adapted habitats relatively widespread under arid palaeo-climates (hypothesized to have corresponded to MIS 16, 12, 8, 4 and 2, Fig. 5.3). The dotted arrows represent the north-south axis of expansion and contraction of the sand-sea, which paralleled expansions of Guinean-Congolian forests. The hypothesized axis of the “Arid Corridor” of Plio-Pleistocene Africa is illustrated. The Arid biomes of northeast and southwest Africa were intermittently linked during at least two periods in the Early and Middle Pleistocene (see Fig. 5.3). Annotated facsimile of Barham (2000), modified after Thomas & Shaw (1991). Abbreviations follow Fig. 2.2.

constrain ages of landforms in the VFF with unprecedented precision. This will allow rigorous testing of the hypotheses and reconstructions developed in this chapter.

Nevertheless, it is in their consilient combination, that this combined review (Chapters 4 & 5) reveal how tectonics has been the first-order causative agent, which has reworked drainage topologies across the Palaeo-Chambeshi archipelago - across over 2.5 million km² of the south-central African plateau (Chapter 8). Clearly, drainage evolution centred around the Bangweulu, Kamalondo and Lufira depressions (and latterly Mweru) has been very complex. The quintessential results of this, and the previous, chapter are more precise timings obtained as to when important Quaternary landforms existed in the Katanga-Chambeshi region. In the following chapter, this history of the wetland archipelago proves critical to understand major events in the evolutionary history of lechwe antelopes.

5.9.3 Evolution of Biodiversity

Providing reciprocal illumination of evolutionary events, patterns of vicariant speciation are married with those of landscape evolution. Overall, data combined from a scattered literature reveals a significant endemism in aquatic biodiversity across the Katanga-Chambeshi region. Congruent patterns point to persistence of particular landforms through disturbances. Their individuality has been maintained, even though topologies of wetlands have been distinctly dynamic, involving radical re-configurations of drainage systems. It is most significant that particular aquatic biota have been confined within these wetlands, which they have tracked through space and time. These rivers, lakes, swamps or floodplains constitute islands within the larger archipelago. Overall, this evidence substantiates a narrative of drainage evolution across the south-central African plateau, where diversification of aquatic and terrestrial taxa reveals strong controls from geological events.

Neotectonic activity along the southwest extension of the African Rift system is invoked as driving this landscape and biotic evolution. This synthesis of geological and biotic knowledge explicates common evolutionary patterns across a wetland archipelago since the late Neogene. Not least, this new model revises long established interpretations of the biogeography and geophysical history of south-central Africa.

The dynamics associated with the individuation of new landforms, from antecedents, appears to have been equally important. Disparities in the time spans over which these wetlands formed would have greatly facilitated persistence of intermittent ecological conditions, of great significance to biological processes: especially dispersals of aquatic biota and thus gene flow. The significance of such inductive lags to biogeographical narratives was introduced in Chapter 1. River piracy events - exemplified by

the VFF and Batoka Gorge - can indeed take hundreds of thousands of years to mature in new topologies from their antecedent rivers. The two capture-elbows of the Kasai River piracy of Upper Zambezi testifies to the magnitude of geological scale (compared to demographic processes) at which these landforms individuated. Bell-Cross (1982) justifiably emphasized how profoundly this event mixed two major fish faunas. As we shall see with lechwes, and other vertebrates, the consequences for certain other species seem to have been as profound. This allowed ample time for major exchanges of fish faunas, and other aquatic organisms, as such rivers slowly individuated. Parallel situations applied to the creation of vast, residual swamps as palaeo-lakes dessicated. In what can be recognized as the critical consequences of palaeo-drainage dynamics, within the Katanga-Chambeshi region, each eclipse of a palaeo-lake within an endoreic basin seems to have progressed as a comparatively protracted event. Although direct evidence for this hypothesis needs to be tested (against fluvial and lacustrine facies), it appears that Lake Patrick dwindled slowly, which was a pertinent event for lechwes in the Kafue graben. Overall, the dessication of Palaeo-Lakes Bulozzi, Makgadikgadi and Patrick likely ensued over many thousands of years as new drainage topologies came to be. Thus, a movie of palaeo-dynamics of the entities, depicted schematically in Fig. 5.6, would render blurred movements as lakes slowly formed and vanished, while channels switched as slowly.

This overview of the complex history of geomorphological evolution has highlighted many uncertainties, in both relative and absolute timings of important events. These challenges present research opportunities begging chronological refinements. These targets includes geological strata, archaeological formations, and extend to complexes of recently individuated species. Such resolved dates will reveal when topologies of drainage systems changed, and establish when vast palaeo-lakes existed during the Quaternary.

Nevertheless, new insights and refinements as to where and when geomorphological events occurred, provides a framework to interpret the evolution of lechwe antelopes. Amongst a diverse aquatic biota, lechwe antelopes can be expected to have occurred widely through the Palaeo-Chambeshi, as they did through floodplains of the modern Upper Zambezi, Cuando and Okavango rivers until extirpations in the 20th century (Chapter 2).

A testable hypothesis is that lineage divergence between these lechwes represents dichopatric speciation (*sensu* Cracraft 1984). The most obvious mechanism is vicariance of wetland habitats, which influenced many other organisms. I invoked break up of the Palaeo-Chambeshi drainage system (Plio-Pleistocene, since 5 Mya BP) to explain vicariant speciation of lechwes (Cotterill, 2003c, 2005):

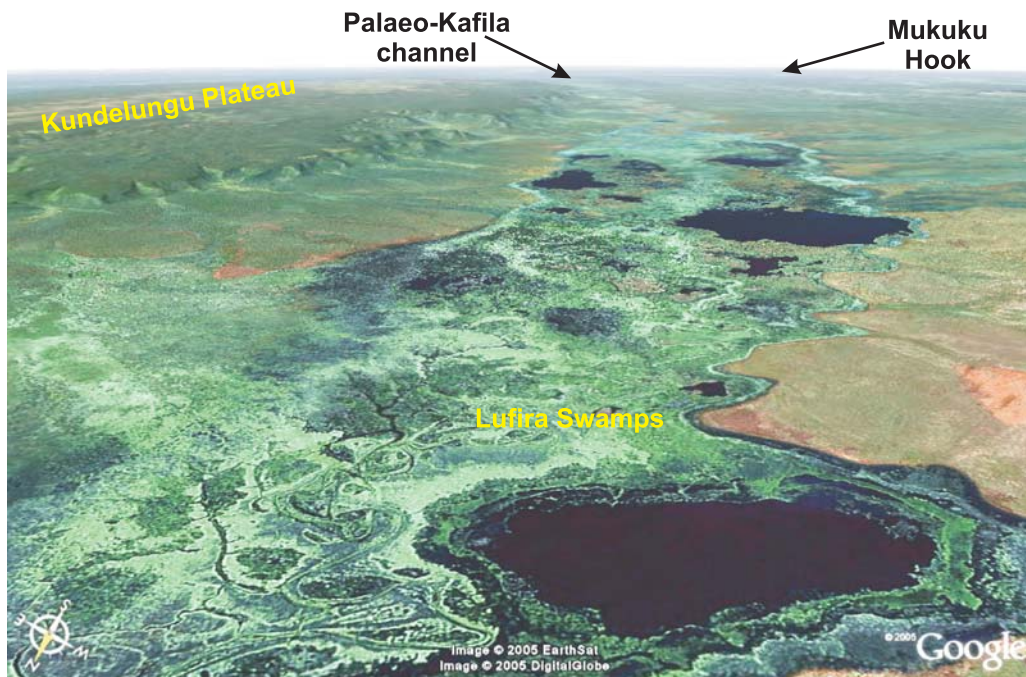
isolated today in the Upper Zambezi-Okavango (*K. leche s.s.*); Kafue Flats (*K. kafuensis*); Bangweulu (*K. smithemani*), Upemba Swamps (*K. anseli*) and Luongo-Kalungwishi (*K. robertsi*) in their respective wetland islands. The synthesis through Chapters 4 and 5 have overhauled what can now be seen to be a simplistic explanation. A more intricate understanding of key events reveals their evolution has entailed a complex interplay among events linked across neighbouring drainage systems. This is especially true of the Bangweulu basin and Kafue Flats.

The primary aim of the phylogeographic component of this study is to reconstruct the evolutionary history represented in the extant lineages comprising the *K. leche* complex. Fortuitously, key insights derived about the evolutionary history of lechwe populations and lineages reciprocally illuminate challenging puzzles of landscape evolution. It follows that some of these answers could be obtained from statistical interrogations of phylogeographic patterns (Chapter 6).

“Insignificant in height, it is true; but when one stands on the brink of the lower cataract and sees the whole volume of the great Zambezi converging into a single pass only 50 to 60 feet in width, shuddering, and then plunging for 20 feet in a massive curve that seems in its impact visibly to tear the grim basaltic rocks asunder, one learns better than from the feathery spray-fans of the Victoria Falls what force there is in the river, and one wonders no longer at the profundity of the gorge!”

Description by G. W. Lamplugh (1908: 150-151) of the Chimamba Rapids delimiting the western and eastern sections of the Batoka Gorge.

CHAPTER 6



[Top] View southeast across the Lufira depression and Katanga Pedicle toward the Bangweulu basin. The Kundelungu Plateau lies to the north. The Mukuku Hook and Palaeo-Kafila channel are arrowed.

[Bottom] Katanga, southeast Congo basin. View north along the Kamalondo graben, downstream along the Upper Lualaba River. The floodplains of the Upemba Swamps and Lakes are the habitat of the recently described Upemba Lechwe, *Kobus anselii*.

Aspects of Plio-Pleistocene evolution of these landforms are discussed in Chapter 4.
Photographs: GoogleEarth

CHAPTER 6 PHYLOGEOGRAPHY OF THE *KOBUS LECHE* COMPLEX

"One of the important insights we have gained from coalescent theory is that the same population history may generate very different gene trees if repeated and that very different historical scenarios may sometimes generate gene trees that are surprisingly similar. The connection between population history and gene tree is complex, and inferences regarding population history and demography can only proceed by careful consideration of the processes that generated gene trees." R. Nielsen (2006: 209)

6.1 INTRODUCTION

6.1.1 The Scope of this Chapter

The preceding chapters described, in detail, a complex history of landscape evolution, in which wetland habitats changed radically across south-central Africa. The model of Plio-Pleistocene landscape evolution (summarized at the end of Chapter 5) constitutes the framework to examine how populations of extant organisms relate to dynamics of landscape evolution. Chapter 2 concluded that the recent distribution of lechwe antelopes suggests profound control by peculiar conditions of the landscape. It is reasonable to hypothesize that evolution of these floodplain habitats may have altered lechwe populations. The science of phylogeography presents rich opportunities to quantify how these large mammals have responded to changes in their habitats, in concert with influences of Pleistocene palaeo-climates. Mutations accumulated in the genomes of study organisms can be revealed by sequencing selected genetic markers. Subject to representative sampling of related populations, significant insights can be obtained about how a population has responded to ecological disturbances.

This chapter describes, analyses and applies findings represented in 208 mtDNA sequences of the control region hyper-variable 1 (CRHV1) marker for all the individuals sampled within the *K. leche* complex. The overall phylogeographic structure exhibited in these populations is discussed in the context of the wetland archipelago in which lechwe antelopes have evolved. Where sequence data permit, the evolutionary histories of the principal populations are quantified and compared. These analyses reveal interesting facets of the evolutionary histories of each population, within limits of sample sizes and resolution of sequenced markers. Comparisons of four principal populations reveal both similarities and important differences in their shared histories of genetic diversity. These findings are discussed in the context of the geological history of the Katanga-Chambeshi region presented in Chapters 4 and 5.

With respect to the geographic isolation of extant lechwe antelopes, no less than eight principal island floodplains can be singled out in the Katanga-Chambeshi region (Figs 2.1). I have concentrated on

elucidating the history of lechwe populations, where sufficient sampling of genetic diversity permitted. Thus, five principal populations were distinguished *a priori* for phylogeographic analyses, based on criteria of their geographical isolation and established taxonomic distinctiveness. As reviewed in Chapter 2 (their distributions are mapped in Fig 2.1). These comprise Upemba (*anselli*), kafuensis (Kafue), Red (*leche*), Roberts' (*robertsi*) and Black (*smithemani*). In addition, the status and history of geographically isolated demes within these taxa were investigated where material data permitted (namely population on the Busanga and Luapula Flats currently classified as *K. l. leche* by Ansell 1978). This design of the study also structures the taxonomic analyses in Chapter 7. Unfortunately, lack of specimens meant lechwe populations in the Cuanza and Owambo basins (western Angola and northern Namibia) could not be evaluated. Nevertheless, tissues from museum specimens enabled an unprecedented coverage of wetlands that are today difficult, if not impossible to sample. This is principally because they are logistically inaccessible, or more tragically because their populations of lechwes became extinct during the past century.

Historical demographic changes that have affected a population can be preserved as signatures, which contribute to its genetic structure. Aspects of this evolutionary history can be quantified as phylogeographic patterns in the currency of genetic mutations; where a suite of statistical methods can quantify aspects of lineages' histories in currencies variation of alleles and/or haplotypes, and accumulated variation of sampled sequence data (Hein *et al.* 2005). The resolution of these data is contingent on several inter-dependent factors: especially the relative evolutionary rate of genetic markers; sample size; and notably, the demographic changes of the population (Avice 2000a, 2004). Radical reductions in population size can expunge archived signals from a population's evolutionary history (Harpending *et al.* 1998, Schneider & Excoffier 1999). As successive populations fluctuate in size, changes in levels of genetic diversity occur because haplotypes/alleles carrying unique mutations are either lost or preserved in the gene pool as a function of the size of the breeding population. Where the pairwise distribution of sequence diversity sampled in a population is presented graphically (mismatch distributions), these dynamics among individuals manifest in the waves of a fluctuating profile that generally characterise long-term stability. Conversely, a smoother (less ragged), unimodal profile denotes a relatively recent, and major, change in the demographic profile of a population (Rogers & Harpending 1992, Harpending 1994).

The burgeoning growth of phylogeographic studies has applied these principles of historical exploration to elucidate phylogeographic histories of many different species. Perhaps the best known

example, with respect to both detail and publicity, has quantified the genetic structure of *Homo sapiens* with increasingly improved resolution (Awise 2000a, 2004; Templeton 2002; Garrigan & Hammer 2006). These improvements have included more thorough sampling of extant human populations, thereby quantifying a greater breadth of historical genetic diversity. Where these studies interface closely with medicine and evolutionary anthropology, they have profound impacts by improving knowledge of our species' evolutionary heritage (Venter *et al.* 2003). Inaugural studies centered on the phylogeography of mtDNA markers, especially CRHV1, to demonstrate support for a singular origin and expansion of humans from within Africa. The latest synthesis of data using both nuclear and mtDNA markers from a vast number of extant human samples reveals a more complex history wherein subtle historical signals, preserved as mutations, point to ancient assimilation of archaic human populations into our modern lineage (Eswaran *et al.* 2005).

6.1.2 Recent Phylogeographic Studies of the Bovidae and other Large Mammals

Important phylogeographic studies have quantified evolutionary histories of selected Bovidae species, notably in Africa and Asia. More thorough studies have sampled domesticated livestock and their closest evolutionary relatives. Examples include several studies of *Bos taurus* and *B. indicus* (e.g. Mannen *et al.* 1998; Hanotte *et al.* 2000, 2002), *Bubulus* (Kierstein *et al.* 2004); wild and domestic Ovis (Tserenbataa *et al.* 2004) and Caprini (Luikart *et al.* 2001; Joshi *et al.* 2004). Phylogeographic studies of domesticated bovids have benefitted from large sample sizes and revealed complex patterns of hybridization between lineages as well as long range gene flow. Each domesticated species exhibits its own natural history (Diamond 2002; Bruford *et al.* 2003; Zeder *et al.* 2006). Latterly, understanding of the genetic structure and evolution of the Bovidae has benefitted from genome sequencing projects targeting *Bos taurus* and *Ovis*, which are among the model organisms of Cetartiodactyla targeted for genomic studies (Murphy *et al.* 2004).

Phylogeographic studies have targeted several of the wild bovids, including Buffalo, *Syncerus caffer* (Van Hooft *et al.* 2000, 2002) and more distantly related taxa. Species complexes studied within an African context include hartebeests (Arctander *et al.* 1999; Flagstad *et al.* 2001), Kudus, *Tragelaphus strepsiceros*, *T. imberbis* and *T. chora* (Nersting & Arctander 2001) and the Impalas, *Aepyceros melampus* and *A. petersi* (Nersting & Arctander 2001; Lorenzen & Siegismund 2004). These have been complemented by continental-scale studies of Warthog, *Phacochoerus africanus* (Muwanika *et al.* 2003) and Hippopotamus, *Hippopotamus amphibius* (Okello *et al.* 2005). The phylogeography of hippotragine antelopes has received close scrutiny, beginning with an inaugural study by Matthee &

Robinson (1999b) of both roan, *Hippotragus equinus*, and sable, *H. niger* complexes. The status of the *H. equinus* complex has been further detailed by Alpers *et al.* (2004). Pitra *et al.* (2002) employed patterns in inheritance of mtDNA to reveal an hitherto unsuspected pattern of introgression among sable antelopes. An exceptionally high degree of divergence among east and southern African populations in the *H. niger* complex was an equally surprising finding. Most recently, the status of the Giant sable, *H. varians* has been characterized with respect to its demographic history and phylogeography of the *H. niger* complex (Pitra *et al.* 2006). Last, but not least, deep mtDNA divergence was discovered in a phylogeographic study of the Kobs, *Kobus kob* complex by Birungi & Arctander (2000). This study preceded a more complete phylogeny obtained of the Reduncini, that included lechwes (Birungi & Arctander 2001; Chapters 2 & 7). Pertinent aspects of these phylogeographic studies, which illuminate interesting facets of the evolutionary history of south-central Africa, are discussed in this chapter.

6.1.4 Phylogeography and Landscape Evolution

Given the habitat speciality of lechwe antelope (Chapter 2), it is hypothesised that previous phylogeographic studies on aquatic organisms in Africa can be used to describe patterns of biotic evolution in wetlands to further understanding of the history of these landscapes. Indeed, a burgeoning contribution to the phylogeographic literature comprises genetic studies of many aquatic organisms, especially fishes and molluscs, which relate patterns of biotic evolution to geological history. The extreme stenotopy of these study organisms makes them ideal surrogates to examine how aquatic biodiversity has been influenced by geological dynamics. Such studies are potentially highly informative, where as they reveal how geomorphological dynamics account for speciation events in aquatic taxa. As semi-aquatic mammals, lechwes are obviously not so closely dependent on aquatic landscapes, but their dependency on water-meadows (Chapter 2) can be construed as tight habitat fidelity. A central goal of this chapter is employ phylogeographic analyses to test how tightly lechwe diversification has been controlled by discernable events in palaeo-drainage summarized in the Geomorphic dataset and suggested by the Biogeographic dataset, respectively (Chapters 4 & 5). Carstens *et al.* (2004, 2005) employed coalescent-based estimates of divergence of indicator taxa in this way to review the evolutionary history of the Pacific Northwest forest ecosystem.

Hrbek *et al.* (2004) revealed how the evolution of two genera of cyprinid fishes reflects strong control by Pliocene tectonism that rearranged drainage topology across the Anatolia region of Turkey. Mateos (2005) related divergence in three lineages of poeciliid fishes to Plio-Pleistocene vicariance across the

Trans-Mexican Volcanic Belt. Sturmbauer *et al* (2001) demonstrated that the explosive radiations in the flocks of African cichlid fishes occurred very recently (~11 000 yr BP) in Lakes Malawi and Victoria in association with pronounced fluctuations in water levels. Rate of evolution of mtDNA CR in these cichlids was calibrated against the geological history of Lake Malawi (Delvaux 1995) to constrain these estimates (Sturmbauer *et al* 2001). The geologically recent molecular divergences revealed between Nearctic gastropod molluscs were applied to establish which drainage model, among several competitors, most credibly explained the geobiotic evolution of the Snake and Columbia rivers, in relation to the Oregon lakes and Humboldt River (Hershler & Liu 2004). A recent phylogeographic study of an assemblage of North American salamanders (Kozak *et al* 2006) revealed drainage history to exerted strong control over diversification of extant populations. Furthermore, these genetic data proved valuable in confirming key aspects of geological history entailed in rearrangements in topologies of drainage systems.

Clearly, the geological history of drainage basins is a fertile arena against which phylogeographic patterns can be tested with respect to origins of genetic structure (Carstens *et al.* 2004). This section has highlighted only certain recent studies, which demonstrate how phylogeography can unravel facets of evolutionary history. Such studies can reveal hitherto unsuspected genetic relationships and historical events. A remarkable example is the long distance dispersal by the ancestor of a haplochromine cichlid fish lineage, through the Nile drainage system, from equatorial Africa to the Levant. This was calculated as occurring in the late Pliocene, 2.5 to 3.3 Myr BP (Werner & Mokady 2004). A somewhat surprising result revealed that genetic divergences among Amazonian small mammals exhibit strong control by Neogene tectonism as compared to river barriers within the Amazon Basin (Patton & Da Silva 2005). Most recently, Burrige *et al.* (2006) employed phylogeographic studies of fish species to test for genetic signatures of known river capture event.

Finally, phylogeographic methods have the potential to unravel patterns of speciation across archipelagos. This is indeed demonstrated by an updated study of a genus of freshwater fishes, *Nothonotus*, where robust phylogeny and molecular divergence estimates revealed that 69% of speciation events are not explained by simple vicariance models or dispersal from adjacent regions (Near & Keck 2005), and resulted in a revision of the classic study by Mayden (1988). The revised study invoked island biogeography theory, specifically neutral theory (Hubbell 1995, 2001, 2005), to quantify rates and incidence of speciation across an archipelago of isolated habitats (Near & Keck 2005). Deciphering patterns of speciation across archipelagos forms a principal challenge in modern

evolutionary biology (Coyne & Orr 2004). The two most intensively studied cases involve *Drosophila* on the Hawaiian Islands (Coyne & Orr 2004), where over 50% of Hawaiian fruit flies have originated through peripatric speciation events (DeSalle 1995), and Darwin's finches on the Galápagos Archipelago. Peripatric speciation has predominated among birds on islands (Coyne & Price 2000). Furthermore, the overall incidence of speciation in Darwin's finches exhibits a striking correspondence to the availability of islands that were extant at a given time (Grant & Grant 1996). The fragmented distribution of lechwe antelope suggests they provide an ideal candidate taxon to investigate patterns of speciation in an African Archipelago setting.

To return to the main objective of this study, the data compiled in this chapter will be used to test whether the geographically isolated populations of lechwe (of which four have been sampled adequately) represent a single, or more, evolutionarily distinct taxon. Furthermore, these sequence data are interrogated with statistical techniques to examine whether distinct signatures of past demographic and evolutionary events reflect influences of known events in landscape evolution. The findings will be discussed in the context of the treatment of species categories (Chapter 3) and lechwe evolutionary history in the context of landscape evolution. Here the narrative of palaeo-drainage dynamics (incorporating the Geomorphic and Biogeographic datasets, Chapters 4 & 5) is brought to bear on these taxonomic findings.

6.1.5 The Relative Accuracy and Precision of Phylogeographic Estimates

Inferences of reconstructed biogeographical patterns hinge on interpretations of chance events. Within reason, phylogeographic studies are challenged to consider and quantify the extent of probable errors in estimated phylogeographic patterns (Knowles & Maddison 2002; Templeton 2004). This especially applies to estimates of Quaternary diversification events (Arbogast *et al.* 2002; Carstens *et al.* 2005). Coalescent-based methodologies appear to be superior in such studies, because confidence limits can be quantified around estimations of variables. This is another reason why coalescent methods are superior to *a priori* methods, pertinently Nested Clade Analysis (NCA) that require that clades be delimited first. This treatment can obscure important signals in phylogeographic datasets and reduce the accuracy of historical reconstructions. Besides avoiding *a priori* structuring of populations, coalescent-based methods incorporate a measure of precision as their credibility intervals bracket the estimated parameters, accounting for coalescent stochasticity (Knowles 2004; Kizirian *et al.* 2004; Pearse & Crandall 2004). They can be compared to estimated ages of landforms and geomorphological events. Pertinently, these include estimates in Chapter 4 based on published

geochemical dates, and other evidence: pertinently erosion rates of the Zambezi river gauged against archaeological evidence (Chapter 5).

6.2 METHODS

6.2.1 Samples and DNA Extraction

Sampling structure of this study targeted the five populations of the *K. leche* complex distinguished from the literature review on criteria of taxonomic distinctiveness and geographical segregation (Chapter 2, Section 6.1.1, Fig. 2.1). A total of 208 complete CRHVI sequences were obtained for analyses from the combined tissue samples. Museum specimens accounted for a total of 89 of the 208 individuals sequenced (Table 6.2, Appendices 1 & 2, Figs 6.2a & 6.2b). Total representations of each taxon are: *anselli* (26); *kafuensis* (54); *leche* (67); *robertsi* (3); and *smithemani* (60) individuals. Pieces of salted skin were collected from legally hunted safari trophies (n=121). Tissue samples from 108 museum specimens were obtained from four museum collections. These included the Field Museum of Natural History (FMNH), Chicago, Musée Royale d'Afrique Centrale (MRAC), Tervuren, Belgium, the Natural History Museum of Zimbabwe, Bulawayo (NMZB), and The Natural History Museum (BMNH), London, UK. Museum specimens provided otherwise unattainable data for important populations - including two specimens of the extirpated taxon, *K. robertsi*, as well as 35 *K. anseli*. Complete details of these specimens are listed in Appendix 1, which identifies which of the 89 museum specimens are included in the analysis of CRHV1 variation in this Chapter. Only full sequences of this mtDNA were included.

Two different protocols were applied to extract DNA from salted skin and museum tissues. Fresh skin was extracted using Phenol:Chloroform (Amos & Hoelzel 1991) and it was found that the protocol based on 1% Chelex resin in doubly-distilled H₂O (Singer-Sam *et al.* 1989; Walsh *et al.* 1991) gave good yields for samples of fresh tissue. Small pieces of skin (~10mm³) were rinsed and soaked in doubly-distilled H₂O, and then digested at 55°C with commercial Proteinase-K (10 mg/ml). Extracted DNA was resuspended in Tris-EDTA (pH 8) and stored at 4°C during laboratory procedures and at -20°C for longer term. The commercial Qiagen DNAEasy Extraction Kit and Qiagen DNA Micro Kit were employed to extract small pieces of skull tissue from museum specimens. A 2-5 mm³ piece of tissue obtained from skulls was washed twice (using vortexing ~ 2 minutes) by making use of 100% ethanol followed by a final wash in 70% ethanol. The sample was then soaked for 24 - 48 hrs in doubly-distilled H₂O until softened, and then removed from the water and transferred to a clean 1.5 ml eppendorf tube. It was then digested with the propriety extraction buffers in the Qiagen DNAEasy kit.

The same extraction protocol was repeated with the DNA MicroKit on museum samples that had shown poor results with the DNAEasy Kit.

Where insufficient external tissue was available from the skull of a museum specimen, an individual tooth was loaned from the museum collection. This protocol broadly follows that of Rohland *et al.* (2004) with modifications. The tooth was represented by either a lower incisor, or an upper or lower premolar. All teeth were maintained separately in sealed polythene bags and tubes. Great care was exercised to clean and extract each sample in isolation in a DNA free area. To remove external contamination, each tooth was rinsed twice in 100% ethanol, followed by doubly-distilled H₂O, with repeated vortexing in a sterile 10 cm³ sampling tube. The washed tooth was then transferred to the extraction buffer in a new, sterile 10 cm³ tube sealed with Paraplast film. Soft tissue adhering to the surface of the tooth was digested at 37°C in an enclosed waterbath for 2-5 days. The extraction buffer followed the protocol based on guanidium thiocyanate (GuSCN) recommended by Rohland *et al.* (2004). GuSCN is a chaotropic agent that breaks down proteins. This extraction buffer comprised: 5 M GuSCN, 50mM Tris, pH 8.0, 25 mM NaCl, 1.3% Triton X-100, and 20 mM EDTA. Although listed in the original formula PTB (N-phenacylthiazolium bromide) could not be obtained, and was excluded from the solution. PTB breaks cross-strands in proteins (Vasan *et al.* 1996), and was considered critical in a study by Poinar *et al.* (1998) where samples of sloth dung were digested to obtain ancient DNA. Although the contribution of PTB could obviously not be tested in this study, its absence did not appear to severely influence the practical performance of this buffer in extracting DNA from museum specimens.

When digestion was complete, one or more 1 cm³ aliquots of the extraction buffer (in which the tooth had been digested) was then processed through the DNAEasy Extraction Kit to clean and extract the DNA, as described above. Extracted DNA products were visualized by ethidium bromide (EtBr) on a 1% agarose gel under ultraviolet light. DNA in some samples of very low yield was quantified directly with a digital Nanodrop spectrophotometer.

6.2.3 Primers and PCR Protocols

A 600 bp region of the Hypervariable portion of the 5' end of the mtDNA Control Region (HVCR) was targeted for PCR (Fig. 6.1). Sequences of all primers employed are listed in Table 6.1. Initial sequencing of lechwe DNA used the universal primer pairs of BatC and BatE developed for Chiroptera (Wilkinson & Chapman 1991), and the forward primer N777 (Hoelzel *et al.* 1991). From

these sequences additional lechwe specific primers were designed. The increased database of sequences revealed previously unknown variable sites, so the first set of lechwe-specific HVCR internal primers were modified (to take into account all potential nucleotide changes) in an attempt to maximize amplification of museum specimens (Fig 6.1). Microsatellites (as for example used by Alpers *et al.* 2004) were not attempted due to the difficulties encountered in amplifying nuclear markers in museum specimens (Section 7.2.5).

PCR was performed in 30 µl reaction volumes containing ~10 - 50 ng of target DNA, 1 µM of each primer, 0.2 mM dNTPs, 1 X Reaction Buffer, 2.5 mM MgCl₂, and 1 Unit of Super-Therm Taq Polymerase (JMR Holdings, UK). The basic protocol for fresh samples of lechwe DNA used an ABI 2700 thermocycler for 35 cycles of: 94°C denaturation step (40 s), annealing step 49°C (45 s), and an extension step (60 s) at 72°C. The initiation and termination of each PCR used a 94°C denaturing step (5 minutes) and a 7 minute extension step (post-cycling) at 72°C. Amplified PCR products were electrophoresed on a 1% agarose gel and visualized with EtBr under ultraviolet light. The product band was excised with a scalpel and cleaned using the Promega Wizard SV Gel and PCR Clean-up System. Purified PCR products were cycle-sequenced using ABI BigDye Terminator chemistry following the recommendation of the manufacturer. Fragments were analysed on an ABI 3100 genetic analyser.

PCR of the DNA samples of museum samples was initially attempted as above, but the majority of extractions did not amplify. This is to be expected as DNA from historical samples is invariably degraded, and the PCR may be inhibited by other biochemicals. So a 'Primerless-PCR' protocol, following Stemmer (1994) and applied by Weber *et al.* (2000, 2004), was employed for these samples. This method aims to reconstruct the degraded template whereby the PCR protocol uses 20-50 ng of target DNA in a PCR cocktail to which no primers are added. PCR entailed 45 cycles of 94°C denaturation step (40 s), annealing step 50°C (45 s), and an extension step at 72°C (60 s). Initiation and termination of each PCR reaction used a 94°C denaturing step (5 minutes) and a 7 minute extension step (post-cycling) at 72°C. PCR reactions were performed on an ABI 2700 thermocycler. The resultant primerless-PCR product was then amplified in a standard PCR reaction using lechwe-specific primers (Table 6.1). For the majority of museum samples, PCR was performed on a Hybaid Thermal Cycler. Reaction conditions were the same as above, albeit scaled up to 50 : 1 reaction volumes. A cold annealing temperature PCR protocol improved yields from museum DNA. This entailed 5 - 8 cycles of

Table 6.1. Details of the primer sequences used to amplify the mtDNA control region of the *Kobus leche* complex.

Primer	Sequence
Bat C ¹	5' - TGAATTGGAGGACAACCAGT - 3'
N777 ²	5' - TACTGTTGGTCTTGTAACC - 3'
L1	5' - CTATCAATATAGTTCCACAATCACC - 3'
L1a	5' - TACCAACCTCCCTAAGACTC - 3'
L2	5' - TCGTCACCCGCCATTACAG - 3'
L2n	5' - CyCGTCAyCCGCCATTACAG - 3'
L3	5' - CCTTGCATATAAGCCAGTAC - 3'
H1	5' - CAAGTrCAAGGTCGGTATTG - 3'
H2n	5' - GCATATnTAGTAAATATATAGTGTG - 3'
H2	5' - GTGTTTCATTATGTGGTGGTTATG - 3'
H3	5' - GAGAATGGATTTGACTTAAATGTGC - 3'
H3n	5' - GATTTGACTTAAATGTGCyATG - 3'
Bat E ¹	5' - CCTGAAGTAGGAACCAGATG - 3'

¹Wilkinson & Chapman (1991); ²Hoelzel *et al.* (1991)

Table 6.2. Details of collection dates for 108 museum specimens of the *Kobus leche* complex sequenced in this study. Complete details of provenance and accession numbers are listed in Appendix 1. Complete sequences were obtained for 89/108 specimens, and these were analyzed in this study.

Collection date	Number of samples
1905 – 1914	5
1915 – 1926	12
1927 – 1939	3
1940 – 1949	25
1950 – 1959	24
1960 - 1969	35
1970 - 2003	4

a 94°C denaturation step (40 s), an annealing step 45°C (30 s), with an extension step at 72°C (60 s); and this was followed by 30 - 35 cycles of: 94°C denaturation step (40 s), annealing step 49°C (40-60 s), and an extension step at 72°C (60 s). The overall initiation and termination of each PCR also used a 94°C denaturing step (5 minutes) and a 7 minute extension step (post-cycling) at 72°C. The oldest specimens sequenced in this study (including all three *K. robertsi*) were collected in the early 1900s

(preserved in BMNH, UK). The oldest specimens of *K. anseli* were collected before 1926 with the majority collected between 1946-1948. The majority of museum specimens from Zimbabwe were collected in the 1950s and 1960s (Table 6.2).

Chromatograms of DNA sequences were edited in Chromas 2.3 (Technelysium Pvt Ltd www.technelysium.com.au) to correct any anomalous and/or conflicting calls of nucleotide bases. Final amplification comprised 561 bp of control region sequence (208 individuals). After the ends were trimmed 547 bp, these sequences were aligned in BioEdit Version 7.0.5.2 (Hall, 1999), with additional alignment by eye.

The invaluable contribution of museum specimens in preserving taphonomic evidence (*sensu* Cotterill 2002a) places a profound precedent on establishing their authenticity. Hofreiter *et al.* (2001) listed criteria that establish the authenticity of ancient DNA amplified from sub-fossil material many hundreds of years old. In the case of museum specimens, sampled in this study, fresher bovid material provided the greatest risk of contamination. The following criteria and precautions were applied in the laboratory:

1. All extractions of museum tissues were carried out in a flow hood where no fresh tissue was ever used for DNA extraction. The work surface was swabbed with bleach between individual extractions. The instruments used during extraction were washed twice in 100% ethanol, and when possible sterilized in a gas flame between processing of each sample. To remove external contamination, extraction protocols also entailed repeated washing of museum tissue in 100% ethanol.
2. Negative controls were incorporated into both extractions and all PCRs, including the Primerless-PCRs.
3. The majority of sequences obtained from museum specimens constitute unique haplotypes. This reduces significantly the likelihood of cross-contamination between samples.
4. Extractions and PCR were repeated on representative museum samples to verify correct sequences had been obtained for key individuals. The latter were selected where a sequence corresponded to a known haplotype, and also in the case of selected specimens of *K. anseli*.

All three museum specimens of *K. robertsi* were independently repeated to verify results of sequences. In total, these repeats comprised: *anselli* (13); *kafuensis* (3); *leche* (5); *robertsi* (3); and *smithemani* (10).

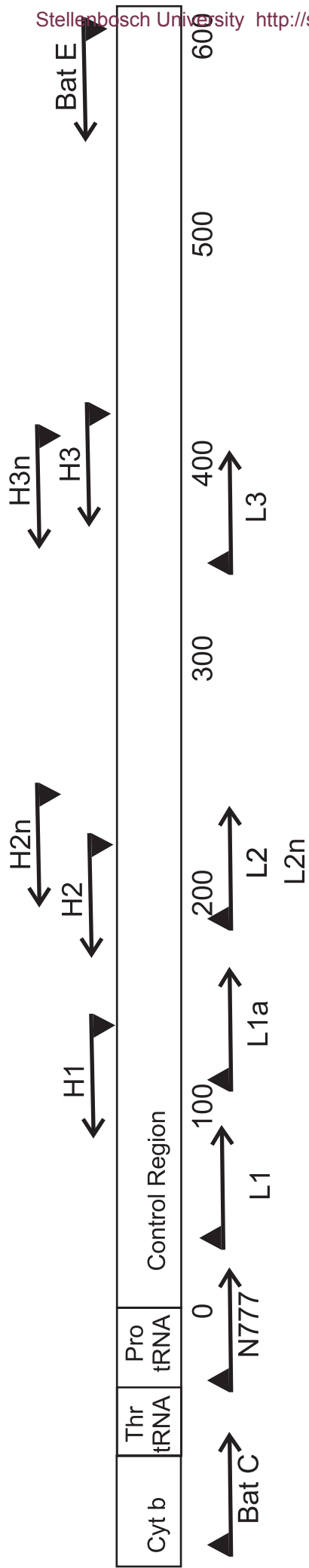


Figure 6.1. Schema of the oligonucleotide primers used in this study to amplify HV1 of the mtDNA control region (CR) of the Kobus leche complex. See Table 6.1 for details of each primer.

6.2.5 Statistical analysis of DNA sequence data: Nucleotide Diversity, Models of DNA substitution, and Calculation of Genetic Networks

A multiple sequence alignment analysis was carried out in CLUSTALW Version 1.4 (Thompson *et al.* 1997) and the number and frequency of unique haplotypes present in the complete dataset of mtDNA CR sequences (561 bases) was identified using COLLAPSE Version 1.2 (Posada 1999). Standard genetic diversity estimates and descriptive statistics of mutation frequencies, including Transition/Transversion ratios, were calculated over all sequences in ARLEQUIN Version 2.001 (Schneider *et al.* 2000).

To evaluate the optimum model of DNA substitution within the data set, haplotypes were analysed using Modeltest Version 3.06 (Posada & Crandall 1998) to determine the best-fit model of molecular evolution. AIC criteria selected the TVM+I+G with shape parameter of the gamma distribution = 0.3418. The proportion of invariable sites was estimated at 0.48. Calculated base frequencies are reminiscent of the commonly documented bias in mammalian mtDNA, and in *K. lechwe s.l* comprised: A= 0.3289; C = 0.2502; G = 0.1423; T = 0.2789.

6.2.6 Genetic Structure, Phylogeography and Demographic History of Populations

Global exact tests of differentiation (Raymond & Rousset 1995), based on haplotype frequencies within the four lechwe populations, were performed in ARLEQUIN 2.001. To compare genetic diversity within, and among, the four populations of lechwe antelopes an analysis of molecular variance (AMOVA; Excoffier *et al.* 1992) was estimated in ARLEQUIN 2.001 using Kimura 2-parameter (Kimura 1980) corrected distances.

The statistical theories and algorithms to compare and test phylogeographic patterns continue to evolve (Templeton 2002). This is especially true of methods to construct networks from genetic sequence data. Until very recently, there has been no firm consensus as to a superior method to depict historical relationships among relatively closely related genotypes (Cassens *et al.* 2003). Huson & Bryant (2006) reanalysed the dataset first compared by Cassens *et al.* (2003), and concluded that a split-decomposition algorithm provides the most accurate representation of historical relationships among genotypes. Nevertheless, a neighbour-net algorithm may be superior to resolve complex networks of larger datasets, such as those generated in comprehensively sampled phylogeographic studies (Bryant & Moulton 2003; Huson & Bryant 2006). A number of approaches were therefore employed to investigate relationships among CRHV1 haplotypes. Genealogies were inferred from the complete

sequence assembly using the neighbour-net and neighbour-joining network approaches in SplitsTree Versions 4.2 and 4.3 (Huson & Bryant 2006). Networks allow the inference of ancestral versus derived relationships among haplotypes based on the position and prevalence of a haplotype within a network, and the number of lineages that connect to it (Castelloe & Templeton 1994).

The demographic histories of the lechwe populations were investigated using a number of approaches. Mismatch analysis of substitutional differences between pairs of haplotypes in each population was calculated in ARLEQUIN 2.001. Populations that have been stable for long periods are expected to show a multimodal or 'ragged' distribution of pairwise differences whereas those that have undergone recent rapid expansions are expected to demonstrate a unimodal distribution (Rogers & Harpending 1992). ARLEQUIN 2.001 was used to test the fit of the observed mismatch distributions to Roger's (1995) model of sudden population expansion using Harpending's (1994) Raggedness Index (*Hrag*) and the sum of the squared deviations (*SSD*) between the observed and expected distributions.

Deviations from neutral predictions expected for a constant-sized population (Fu 1997, Tajima 1989) can also be used to detect demographic traces of past population growth; ARLEQUIN 2.001 was used to calculate Tajima's *D* statistic and Fu's F_S test of selective neutrality to investigate signs of departure from mutation-drift equilibrium in the four lechwe populations. Tajima's *D* tests for deviations from neutrality by assessing whether the number of polymorphic sites in a data set is correlated with the average number of nucleotide differences, whilst Fu's F_S specifically tests for demographic change and has been shown to be one of the best statistics for this in comparisons of statistical power (Ramos-Onsins & Rozas 2002). Fu's F_S is based on the probability of observing a random neutral sample with a number of haplotypes similar or larger than the observed value (Fu 1997), such that an excess of low-frequency haplotypes as compared to that expected under neutrality results in strongly negative F_S values. Significance levels for both measures were generated by comparing the test statistic against a distribution generated from 10000 random samples under the hypothesis of selective neutrality and population equilibrium.

A time scale for the demographic expansion events was estimated by computing *tau* (J), the moment estimator of time to expansion, along with the substitution parameter *theta* (\mathcal{Z}) before and after the expansions ($\mathcal{Z}_0 = 2 \cdot N_0$ and $\mathcal{Z}_1 = 2 \cdot N_1$, respectively); *tau* is calculated from the relationship $J = 2 \cdot t$, where \cdot = mutation rate, t = time since expansion in generations, and N is the effective population size. Approximate confidence intervals around the parameter estimates were generated by parametric

bootstrapping with 1000 pseudo-replicates in ARLEQUIN 2.001 (Schneider *et al.* 2000). Generation time was applied from published studies of lechwe populations (Nefdt & Thirgood 1997; detailed in Chapter 2). A mutation rate of 13% was applied as estimated for the bovine CRHV1 by Mannen *et al.* (1998).

6.2.7 Estimations of Gene Flow and Timing of Genetic and Lineage Divergence

Compared to traditional F_{ST} based methods, coalescent-based methods provide more confidence in estimates of gene flow between populations. The latter also confer the powerful ability to discern ancestral polymorphism from recurrent gene flow simultaneously from sets of aligned sequences in pairwise comparisons of populations (Nielsen & Wakeley 2001; Pearse & Crandall 2004; Bowie *et al.* 2006). The software program MDIV applies the Bayesian sampling coalescent-based method of Nielsen & Wakeley (2001) to estimate four parameters simultaneously, based on an explicitly non-equilibrium approach. These comprise migration rate (an index of gene flow, $M = 2N_{ef}m$), time to most recent common ancestor ($TRMCA = t \cdot \mu$), and time of population divergence ($T = t/N_{ef}$), and the theta statistic, a measure of genetic diversity ($\theta = 2N_{ef}\mu$), where N_{ef} is the effective population size, t is the generation time, and μ is the per-locus mutation rate (Nielsen & Wakeley 2001). MDIV calculates standardized scalar estimates of M , T and $TMCA$, which are multiplied by θ to account for differences in effective population size. This enables direct comparisons of estimated parameters (Griswold & Baker 2002; Bulgin *et al.* 2003; Bowie *et al.* 2006). Values were converted to years before present using an estimated generation time of 2 years, and an instantaneous mutation rate for CRHV1 of 1.244×10^{-4} , calculated from that of 13% as applied above (Section 6.2.6). Ninety five percent credibility intervals were calculated to bracket estimates derived from the mode of the posterior probability in plots of M , T and θ

All simulations were carried out, via remote internet access, on multiprocessor clusters at the University of Cornell's Computational Biology Service Unit, which hosts their Web Computing Resources Microsoft High-Performance Computing Institute (<http://cbsuapps.tc.cornell.edu/>). Computer resources permitting, each pairwise comparison was replicated four times for all taxa, to determine whether estimates of the posterior probability had converged to a stationary distribution. These independent runs of 8 - 16 million iterations of MDIV used priors set at $M_{max} = 10$ and $T_{max} = 5$, of which the first 10% was discarded as burn-in. A finite sites (HKY) model of molecular evolution (Hasegawa *et al.* 1985) was used in all analyses. It proved demanding for calculations for θ to achieve stationarity in certain pairwise comparisons with relatively large numbers of sequences for each population. Although

extended to 21 and 25 million iterations (with single computing times of ~2 weeks), only maximum estimates of Z were obtained for more challenging comparisons (*anselli* vs. *leche*; *anselli* vs. *smithemani*; and *leche* vs. *smithemani*), where no upper credibility interval could be calculated for these estimates of Z . Nonetheless, complete estimates of M and T (with credibility bounds) were replicated fully in all comparisons.

6.3 RESULTS

6.3.1 Molecular Diversity of Control Region and Haplotype Frequencies

The total of 208 individuals of the *K. leche* complex, sequenced for CRHV1, represent 141 unique haplotypes (in addition to the outgroup, a single specimen of Nile lechwe *K. megaceros*, see Appendix 3 for alignment). The 89 museum specimens represent 73 haplotypes i.e. more than half the total genetic diversity discovered in this study (Table 6.2, Appendices 1 & 2, Figs 6.2a & 6.2b). A total of 59 polymorphic sites were identified within the 547 bp aligned segment, with the respective genetic variation apportioned among four of the five populations detailed in Table 6.3. *Kobus robertsi* was not included due to the small sample (3). Mean uncorrected sequence divergence among all pairs of haplotypes was 2.9% (0.4 – 6.1%); haplotype diversity (H_d) was high for all four lechwe populations (range 0.89 to 0.99), whilst nucleotide diversity (D) in *anselli*, *leche* and *smithemani* was close to/or more than double that observed in *kafuensis* (Table 6.3). A single indel was identified that comprised a poly G sequence of at least 10 bp. This character was present in only 2 *anselli* (Ka 2 and Ka3), 1 *leche* (K120) and 28 *smithemani* haplotypes, in which it characterized 43/60 (72%) of all *smithemani* individuals sequenced. The single base pair insertion/deletion was confirmed by sequencing both directions.

6.3.2 Verification of Sequences of Museum Specimens

The large contribution of DNA sequences from museum specimens to this study provided a significant contribution to the total dataset, not least the entire samples of *K. anselli* and *K. robertsi*. The three sequences of *K. robertsi* provide the only tangible evidence of the phylogeographic affinities for what has become an extinct taxon (Table 6.2). Equally, the majority of historical specimens obtained for *K. leche* represent localities from where lechwe have been extirpated (Chapter 2, Appendix 1).

Table 6.3. Genetic variation of 208 sequences of the mtDNA Control Region (HV1 547 bp) of the *Kobus leche* complex.

Genetic Variable	<i>anselli</i>	<i>kafuensis</i>	<i>leche</i>	<i>smithemani</i>
Total Sequences	26	54	67	60
Total Haplotypes	24	29	44	44
Polymorphic Sites	48	43	59	59
Transitions	40	39	53	52
Transversions	9	5	6	7
Indels (no. of samples)	1 (n=2)	0	1(n=1)	1(n=43)
Genetic Diversity H_d	$0.99 \pm \text{S.E. } 0.015$	0.89 ± 0.036	0.97 ± 0.009	0.98 ± 0.008
Nucleotide Diversity B	0.026 ± 0.013	0.009 ± 0.005	0.016 ± 0.008	0.023 ± 0.018

Table 6.4a. Analysis of Molecular Variance (AMOVA) for the four principal populations of the *Kobus leche* complex, calculated from 547 bp of CRHV1 mtDNA for 141 haplotypes representing 206 individuals.

Source of Variation	degrees of freedom	Sum of squares	Variance Components	Percentage of Variation
Among populations	1	315.55	4.89	45.48
Within populations	125	733	5.86	54.52
Total	126	1048.55	10.76	
Fixation Index	$F_{st} = 0.4548$ ($p < 0.05$)			

Table 6.4b. Comparisons of pair-wise Analysis of Molecular Variance (AMOVA) for the four principal populations of the *Kobus leche* complex, calculated from 141 haplotypes representing 206 individuals. Italicized top-right portion of table lists among taxa variance, with corresponding Fst and its confidence value below.

	<i>kafuensis</i>	<i>leche</i>	<i>smithemani</i>
<i>anselli</i>	16.00	23.41	34.65
	Fst = 0.16	Fst = 0.23	Fst = 0.34
<i>kafuensis</i>	p < 0.0001 -	p < 0.0001 28.82	p < 0.0001 56.30
		Fst = 0.28	Fst = 0.56
<i>leche</i>		p < 0.0001 -	p < 0.0001 45.48
			Fst = 0.45
			p < 0.0001

6.3.3 Population structure

Haplotype frequency distributions were found to differ significantly between all pairwise comparisons of lechwe taxa (Pairwise Exact test; all values $p < 0.001$); the overall global exact test of differentiation was therefore highly significant ($p < 0.0001$). AMOVA indicated significant structuring of genetic diversity among the four lechwe taxa, where 45.5% ($p < 0.01$) of the total genetic variance could be explained by differences among the lechwe groups (Table 6.4a). Furthermore, all pairwise comparisons between lechwe populations were significant. Pairwise AMOVA comparisons are detailed in Table 6.4b, where results reveal the largest degree of differentiation in comparisons between *smithemani* and *kafuensis* ($F_{st} = 0.56$) and *smithemani* and *leche* ($F_{st} = 0.45$) respectively.

6.3.4 Phylogeographic Patterns

Despite the disjunct geographic distribution of the four lechwe taxa analysed, mtDNA haplotypes did not segregate into monophyletic groups. The presence of shared haplotypes among the populations obviating the collapse of links among the large numbers of haplotypes

into a network such that clusters are linked by multiple routes. And whilst Huson & Bryant (2006) conclude that split-decomposition networks yield the ultimate resolution (depicting all possible links among mutational steps), such a network is challenging to depict, let alone interpret, when many genotypes make up the data set. Following Bryant & Moulton (2003) the neighbour-net (NN) network effectively illustrates the degree of complexity among lechwe haplotypes (Fig. 6.2a). Given the high number of reticulations, this network is difficult to interpret and visualized. The neighbour-joining (NJ) network provided a more visual friendly depiction of the complexity among the large numbers of haplotypes obtained in this study (Figs 6.2b & 6.3).

In both the NN and NJ network, presented as trees (Figs 6.2), the mtDNA diversity of lechwe antelopes exhibits a partial partitioning into five dominant groupings. One comprises primarily *smithemani* haplotypes (green), which nearly all segregate distinctly within the network. The second group is dominated by *kafuensis* (turquoise), but includes four representative haplotypes of *anselli* (light blue) and *leche* (red; including Busanga Red lechwe) respectively, and a single *smithemani* (Ks16). One haplotype (Kk100) occurs at a high frequency in the sample of *kafuensis* (32% of all *kafuensis* individuals). Following methodology proposed by Crandall *et al.* (1994) this central haplotype is probably ancestral. The nucleotide diversity of this *kafuensis* clade is significantly enhanced by 4 *anselli* haplotypes, two of which have long branches (Ka26 and Ka31), likewise four haplotypes of the Busanga *leche* (Bu7 and Bu11-13) are also present. The third clade is dominated by 37 *leche* haplotypes (66% of samples) with its remaining structure contributed by 8 *anselli*, 3 *kafuensis*, the 3 *robertsi*, and 5 *smithemani* haplotypes. It is noteworthy how these *kafuensis*, *leche* and *smithemani* relate to the overall distribution of the genetic diversity of the 24 *anselli* and three *robertsi* haplotypes. Tellingly, haplotype Ka10 (depicted as a blue circle) lies near the nexus of the NJ tree. Moreover, the mtDNA diversity of *anselli* is scattered across the network. Considering the sample size is under half that of the other three populations (excluding *robertsi*), *anselli* haplotypes are shared among all clusters, and are generally characterized by long branch lengths. Furthermore, two clusters that form a discrete branch near the centre of this *leche* cluster are dominated by *anselli* haplotypes (Fig. 6.2b). Relationships between and among the four, better sampled taxa, depicted separately in Fig 6.3, are standardized in comparison against *K. megaceros*. The longer branch lengths of *anselli* stand out, especially compared against *kafuensis* and *leche*, and each network also

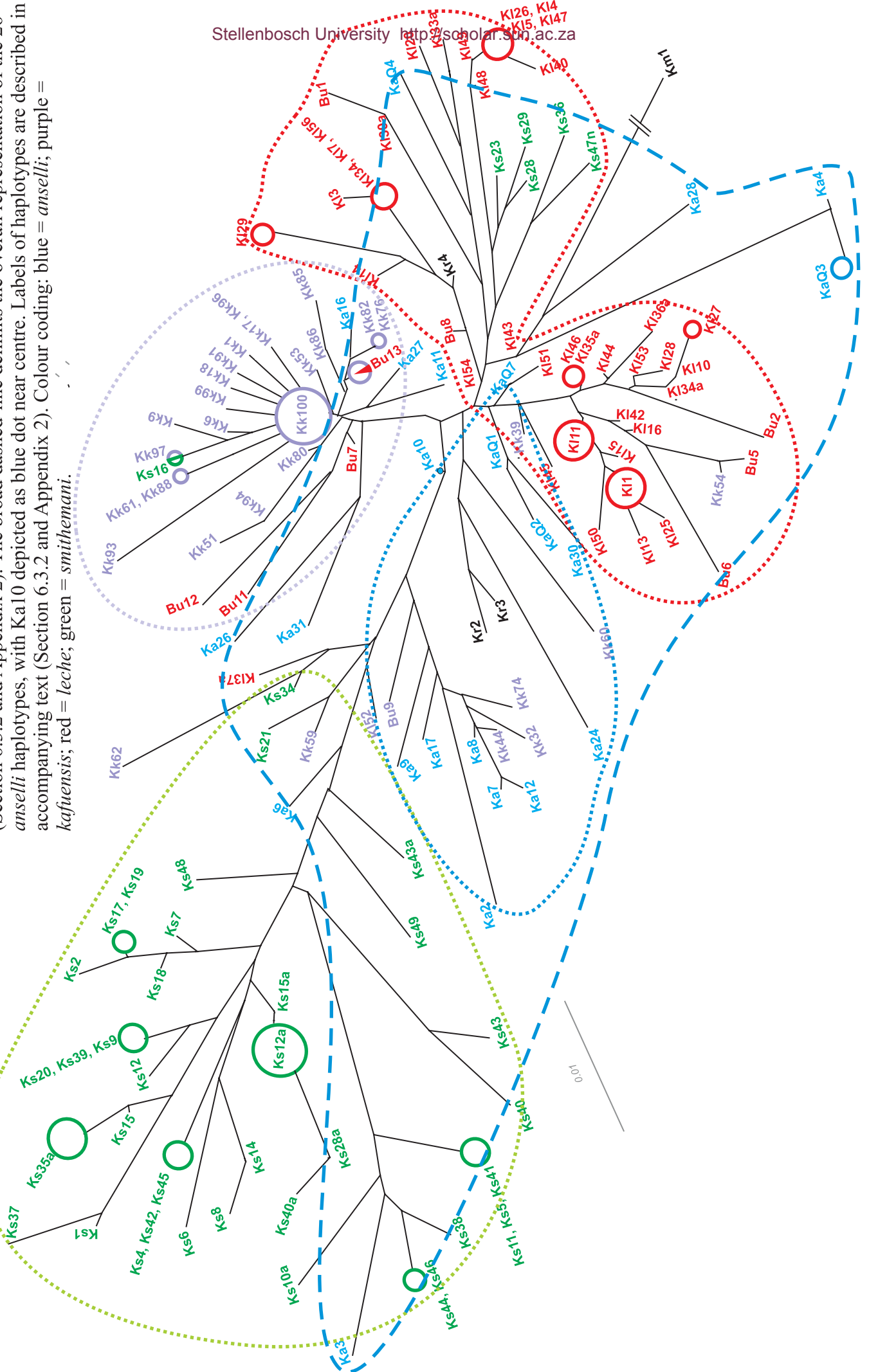
points to ancestral polymorphisms.

All three *robertsi* haplotypes are positioned close to the base of the *leche* cluster, but the small sample renders it difficult to draw unequivocal conclusions as to the status of this taxon. In addition, this cluster of haplotypes includes four *anselli*, one *kafuensis*, eight *leche*, and five *smithemani*. One *robertsi* haplotype groups with *leche* in a discrete lineage (Fig. 6.2b). It appears that incomplete lineage sorting characterises the recognized taxa of extant lechwes, even though they each exist as a geographically isolated population. It is thus possible that ancestral polymorphisms also contribute to the overall structure of the network (Figs 6.2 & 6.3). Two hypotheses could account for these patterns – firstly, the retention of haplotypes after isolation and secondly, low levels of female-mediated gene flow among the lechwe taxa. In light of understanding of landscape evolution, and thus palaeo-dynamics of lechwe habitats, it is more likely to be the former; and testing of these hypotheses with MDIV analyses confirms this (Section 6.3.5). Nonetheless, as argued by Whitlock & McCauley (1999), patterns of gene flow cannot be interpreted from estimates of F_{ST} as it does not quantify migration rate nor effective population size (see MDIV results below).

6.3.4 Demographic Histories

With the exception of *K. robertsi* (insufficient sample size) the observed pairwise mismatch distributions for all four lechwe taxa reveal evidence for major expansions in their demographic histories (Fig 6.4 a-d). All four populations did not deviate significantly from a unimodal distribution of an expanding population (Harpending 1994). Harpending's raggedness index and the sum of the squared deviations (detailed in Fig. 6.4) between the observed and simulated mismatch were consistent with Roger's (1995) expansion model. While the mismatch distribution of *K. smithemani* did not deviate significantly from model expectations, the fit is weaker than that observed in the other three taxa; the distribution suggests that *K. smithemani* may have undergone two expansion events in its recent history.

Figure 6.2b. A representative neighbour-joining (NJ) tree of 140 haplotypes, of CRHV1 sequences, exhibited across the *Kobus leche* complex. Labels of haplotypes are described in accompanying text (Section 6.3.2 and Appendix 2). The broad dashed-line delimits the overall representation of the 26 *anselli* haplotypes, with Ka10 depicted as blue dot near centre. Labels of haplotypes are described in accompanying text (Section 6.3.2 and Appendix 2). Colour coding: blue = *anselli*; purple = *kafuensis*; red = *leche*; green = *smithemani*.



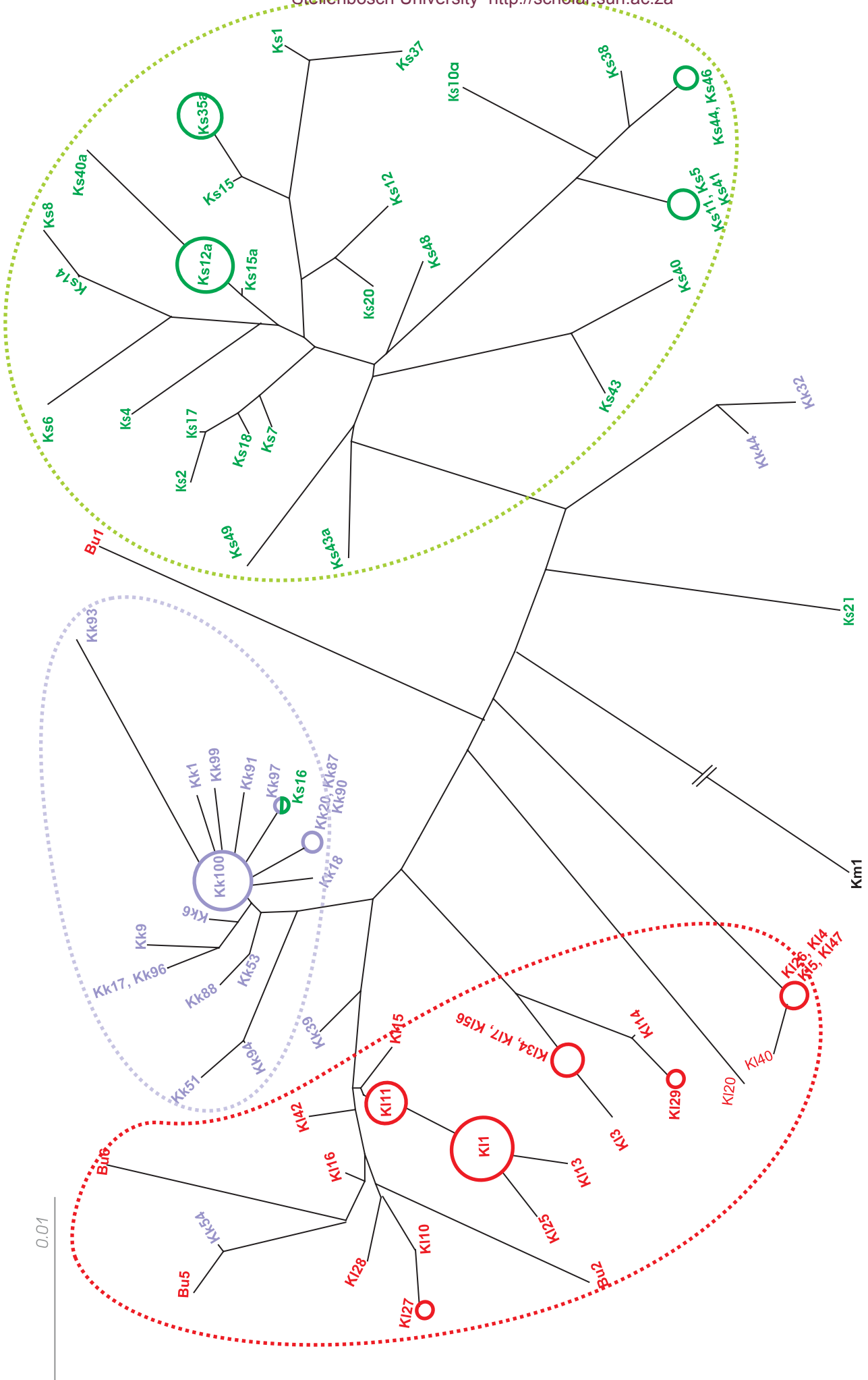


Figure 6.2c. A neighbour-joining (NJ) network of 68 haplotypes representing CRHV1 sequences for the *Kobus lechwe* complex. This reconstruction of phylogeographic structure is based solely on fresh tissue samples (skin snips). Colour convention follows Figs 6.2a-b.

When analysed using only haplotypes that grouped into *smithemani* cluster (in the NJ network, Fig 6.2a) a stronger unimodal pattern is recovered (Fig. 6.4f). Significantly, negative Fu's F_s values further support a pattern of past demographic change for each of the four lechwe taxa (detailed in Fig. 6.4). The respective *tau*-value for each taxon was employed to estimate expansion times within 95% confidence limits. Clearly, *kafuensis* has undergone the most recent of these population expansions. In currency of generation timing, this is over an order of magnitude lower than those exhibited in any other population (Table 6.5). This is consistent with the star-shaped pattern revealed in the network analysis (Figs 6.2 & 6.3) and the low level of nucleotide diversity observed in the control region data (approximately half that of *anselli*, *leche* and *smithemani*, Table 6.3). This pattern is further supported by the peak towards the left side of the mismatch distribution and, which together with highly significant Fu's F_s and Tajima's D values, confirm that a large demographic change occurred in the recent history of this population (Fig. 6.4b). The moment estimator of time to expansion, calculated from the J -value, estimated this event occurred ~36 000 generations ago. Based on a generation time of two years (Nefdt 1996), this expansion event dates ~72 000 yr BP. It is important to note that whilst it is not possible to accurately establish whether this event represents an expansion after a founder event, or either expansion of an ancestral population already resident on the Kafue Flats. It is noteworthy how the change in theta suggests that, after the expansion, the effective population size of *K. kafuensis* increased by approximately one thousand times ($Z_0 = 3.15$; 95% CI = 0.00-9.24; $Z_1 = 853.75$; 95% CI = 13.2—6103.75).

It is clear that extant populations of *anselli*, *leche* and *smithemani* preserve evidence of ancient expansion events. This is especially evident in *smithemani*, where the wide 95% confidence intervals loosely constrain this event within 1 123 - 66 Kya. The mismatch distribution points to two discrete expansions, one of which is much more recent, and is evident in the structure of the *smithemani* clade, particularly when the pairwise distribution is recalculated solely for the *smithemani* cluster determined from the NJ tree (Fig. 6.4e). Here, comparisons of the two mismatch distributions point to an earlier expansion in the

It is clear that extant populations of *anselli*, *leche* and *smithemani* preserve evidence of ancient expansion events. This is especially evident in *smithemani*, where the wide 95% confidence intervals loosely constrain this event within 1 123 - 66 Kya. The mismatch

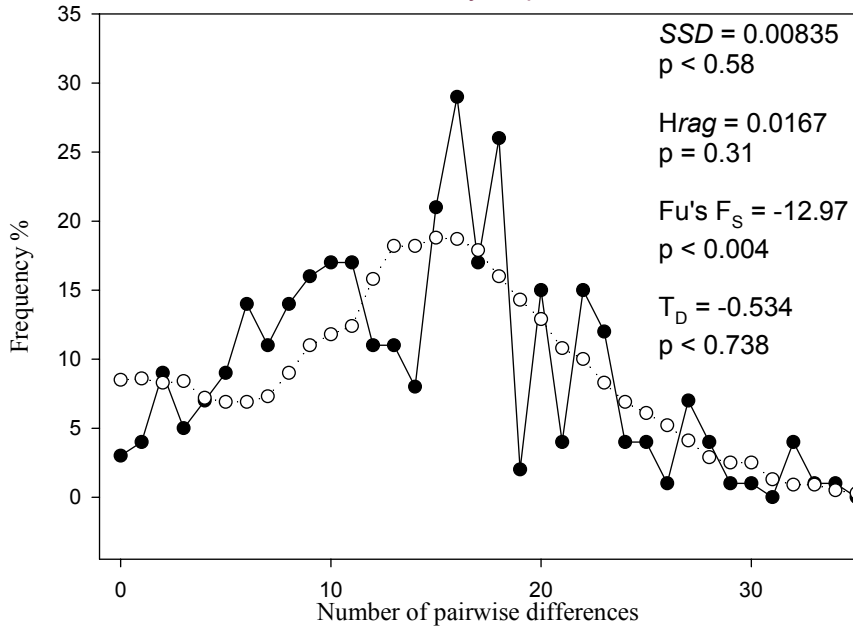
Table 6.5. The estimated time since expansion (thousands of years BP) for each population of lechwe antelopes, as calculated from CRHV sequences using the J -value, from the equation $J = 2t$, where generation time, $t = 2$. The respective J -value and t is listed under each time estimate (bold font).

Population(s)	Lower 95% CI	Mean (Kya)	Upper 95% CI
<i>K. ansellii</i>	400 $J = 7.211; t = 200\ 000$	722 $J = 13.0; t = 361\ 000$	1 547 $J = 27.843; t = 773\ 000$
<i>K. kafuensis</i>	35 $J = 0.633; t = 18\ 000$	72 $J = 1.3; t = 36\ 000$	239 $J = 4.306; t = 120\ 000$
<i>K. leche</i> (All)	384 $J = 6.907; t = 192\ 000$	732 $J = 13.174; t = 366\ 000$	1 079 $J = 19.428; t = 452\ 000$
<i>K. leche</i> (Okavango)	314 $J = 5.657; t = 157\ 000$	764 $J = 8.182; t = 382\ 000$	1 115 $J = 20.715; t = 575\ 000$
<i>K. smithemani</i> (All)	66 $J = 1.196; t = 33\ 000$	212 $J = 3.816; t = 106\ 000$	1 123 $J = 20.208; t = 561\ 000$
<i>K. smithemani</i> Clade	156 $J = 2.81; t = 78\ 000$	358 $J = 6.441; t = 179\ 000$	1 034 $J = 18.614; t = 517\ 000$

distribution points to two discrete expansions, one of which is much more recent, and is evident in the structure of the *smithemani* clade, particularly when the pairwise distribution is recalculated solely for the *smithemani* cluster determined from the NJ tree (Fig. 6.4e). Here, comparisons of the two mismatch distributions point to an earlier expansion in the *smithemani* population. This older expansion is also suggested by the presence of five *smithemani* haplotypes clustered within the *leche* clade, as well as the clustering of the Ks16 haplotype in the *kafuensis* clade (Fig. 6.2b). A bimodal mismatch profile is also exhibited in *K. leche*, notably in a dataset of only Okavango specimens (Table 6.5; Fig. 6.4c-d), which suggests that two discrete expansions occurred.

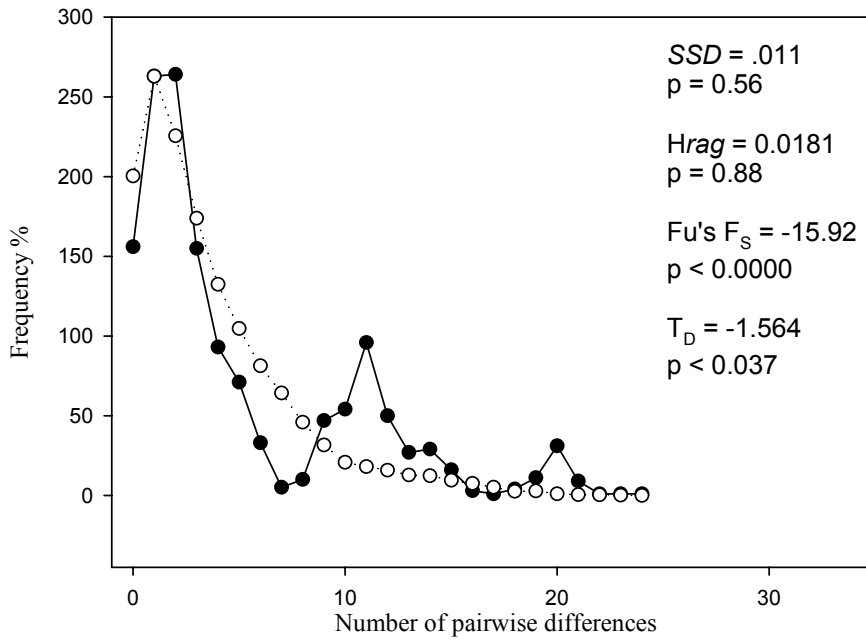
Figure 6.4. (following two pages). Mismatch distributions for taxa (see Table 6.5 for details) within the *Kobus leche* complex, showing observed (solid line) pairwise differences and expected (dotted line) distributions under Roger's (1995) demographic expansion model. a) *K. ansellii*; b) *K. kafuensis*; c) *K. leche*; d) *K. leche* (Okavango only); e) *K. smithemani* and f) *K. smithemani* cluster only. Test statistics are reported on each graph.

a)



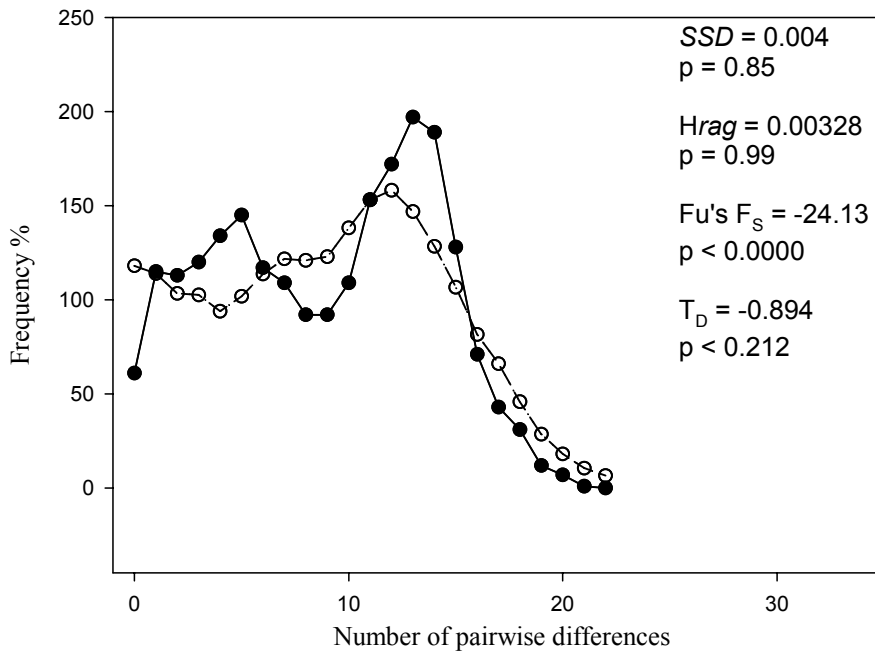
anselli

b)



kafuensis

c)



All leche

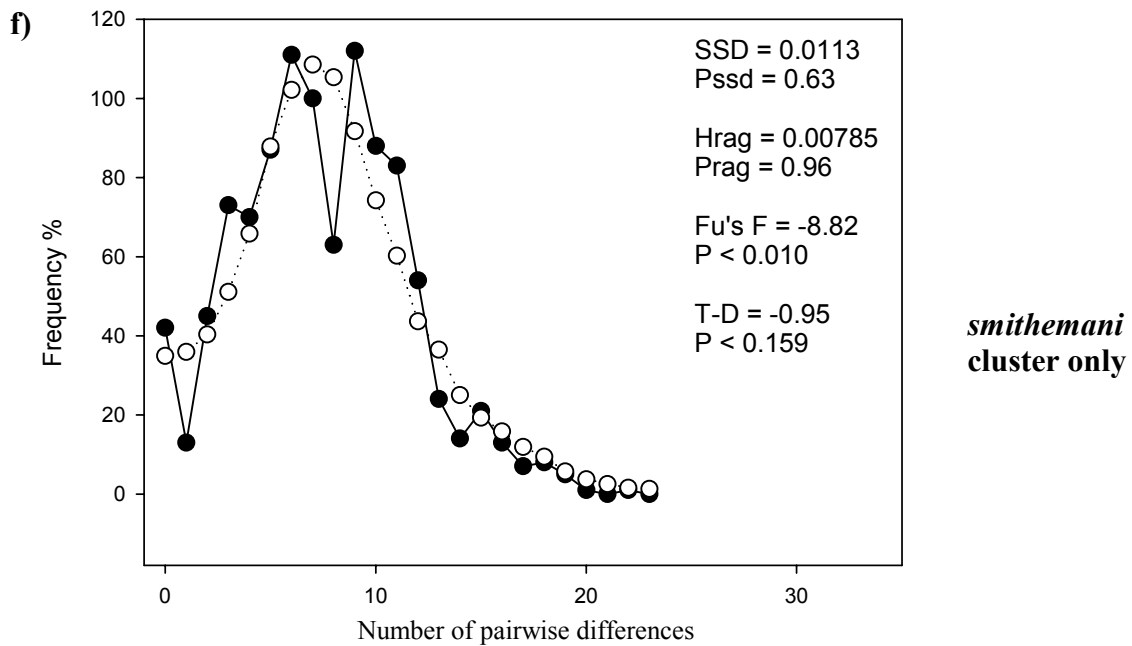
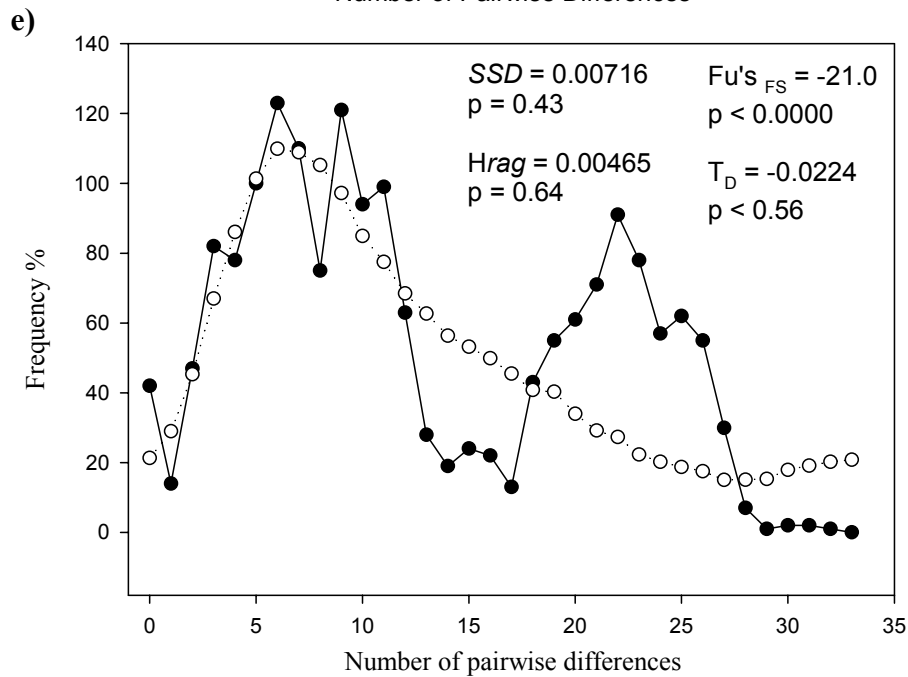
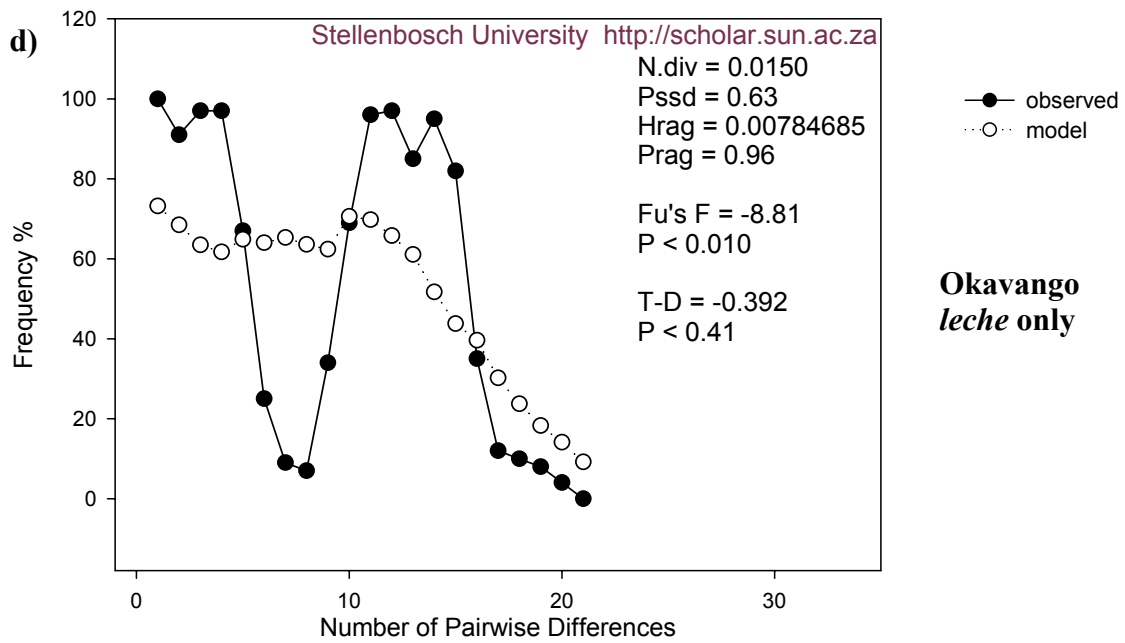


Table 6.6. Pairwise comparisons, calculated using MDIV, of four lineages (samples sizes in parentheses) of the *Kobus leche* complex summarizing estimates of \mathcal{L} , Gene Flow (M), Divergence Time (T) and Time to Most Recent Common Ancestor (TMRCA) from mtDNA CRHV1 sequence data. Estimates are calculated on a generation time = 2, and mutation rate = 1.244×10^{-4} . Where resolved, scaled 95% confidence intervals for each pairwise estimate of divergence time are estimated from the posterior distributions and given in round parentheses. The 95% confidence intervals for T was converted to years BP [in square parentheses]. NR = Not Resolved.

	<i>kafuensis</i> (n = 49)	<i>leche</i> (n = 63)	<i>smithemani</i> (n = 53)
<i>anselli</i> (n = 26)	$\mathcal{L} = 26.94$ (17 - 38) $N_{ef} = 108280$ $M = 4.6 \times 10^{-6}$ (1.0) (0.2 - 4.1) $T = 106836$ [0.25] (0.15 - 1.1) [54662 - 733119] TMRCA = 386772	$\mathcal{L} = 37.3$ (24 - NR) $N_{ef} = 149920$ $M = 2.6 \times 10^{-6}$ (0.78) (0.3 - 2.6) $T = 269801$ [0.28] (0.2 - 0.9) [38585 - NR] TMRCA = 410356	$\mathcal{L} = 39.9$ (26 - NR) $N_{ef} = 160370$ $M = 1.2 \times 10^{-6}$ (0.4) (0 - 2.8) $T = 166784$ [0.26] (0.2 - 0.8) [41801 - NR] TMRCA = 463118
<i>kafuensis</i> (n=49)		$\mathcal{L} = 29$ (18 - 34) $N_{ef} = 116560$ $M = 6.8 \times 10^{-6}$ (1.6) (0 - 4.3) $T = 129466$ [0.28] (0.2 - 0.9) [57878 - 655949] TMRCA = 347728	$\mathcal{L} = 22.9$ (14.5 - 37) $N_{ef} = 92042$ $M = 3.1 \times 10^{-6}$ (0.58) (0.27 - 1.9) $T = 191280$ [0.52] (0.2 - 1.3) [46624 - 773312] TMRCA = 383028
<i>leche</i> (n=63)			$\mathcal{L} = 33.4$ (24 - NR) $N_{ef} = 134244$ $M = 1.4 \times 10^{-6}$ (0.4) (0 - 1.8) $T = 214792$ [0.40] (0.2 - 0.9) [38585 - NR] TMRCA = 417724

Figure 6.5a-c. (following two pages) Bayesian probability plots of representative estimations using the coalescent-based model in MDIV for the taxa compared above (Table 6.6). Theta ($\mathcal{L} = 2N_{ef}$), migration ($M = 2N_{ef}m$), and time of population divergence ($T = t/N_{ef}$). Time to most recent common ancestor ($TMRCA = t$) in each case is also listed. a) *anselli-kafuensis*; b) *anselli-leche*; c) *anselli-smithemani*; d) *leche-smithemani*; e) *kafuensis-leche*; f) *kafuensis-smithemani*.

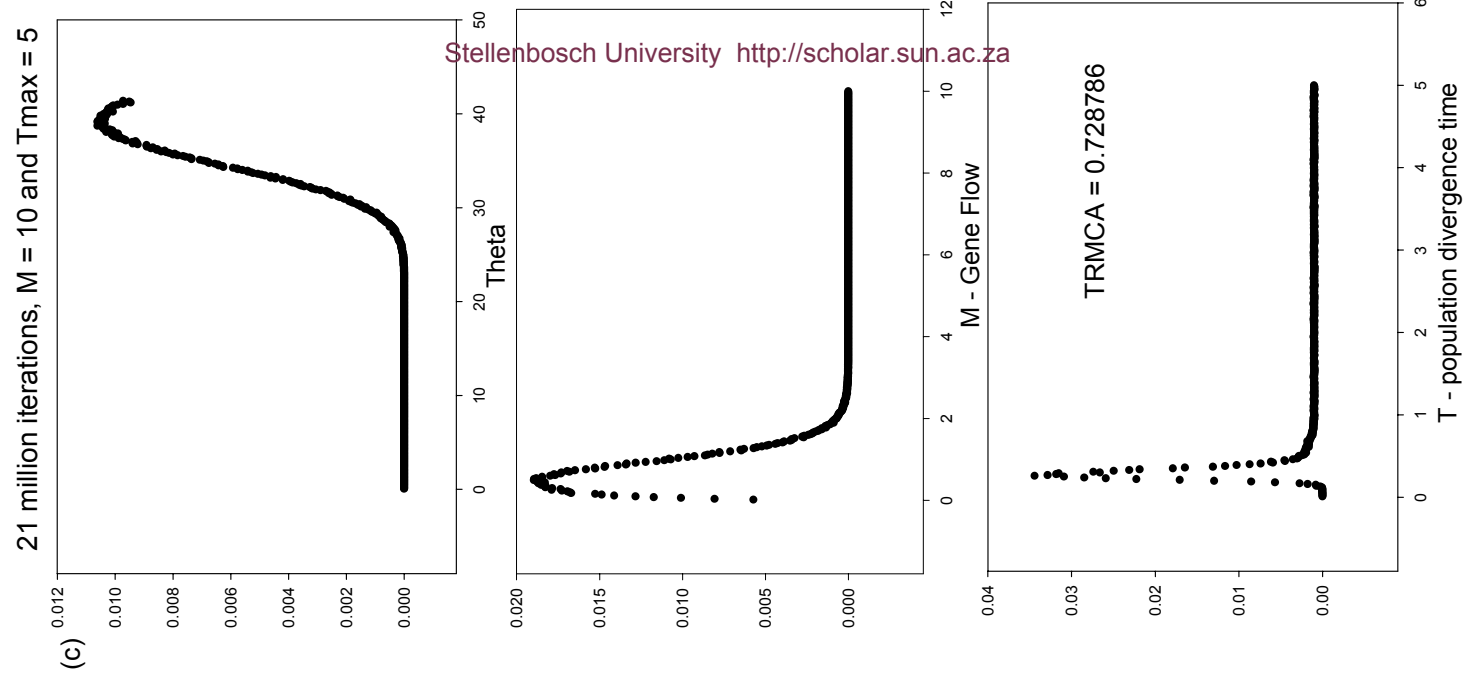
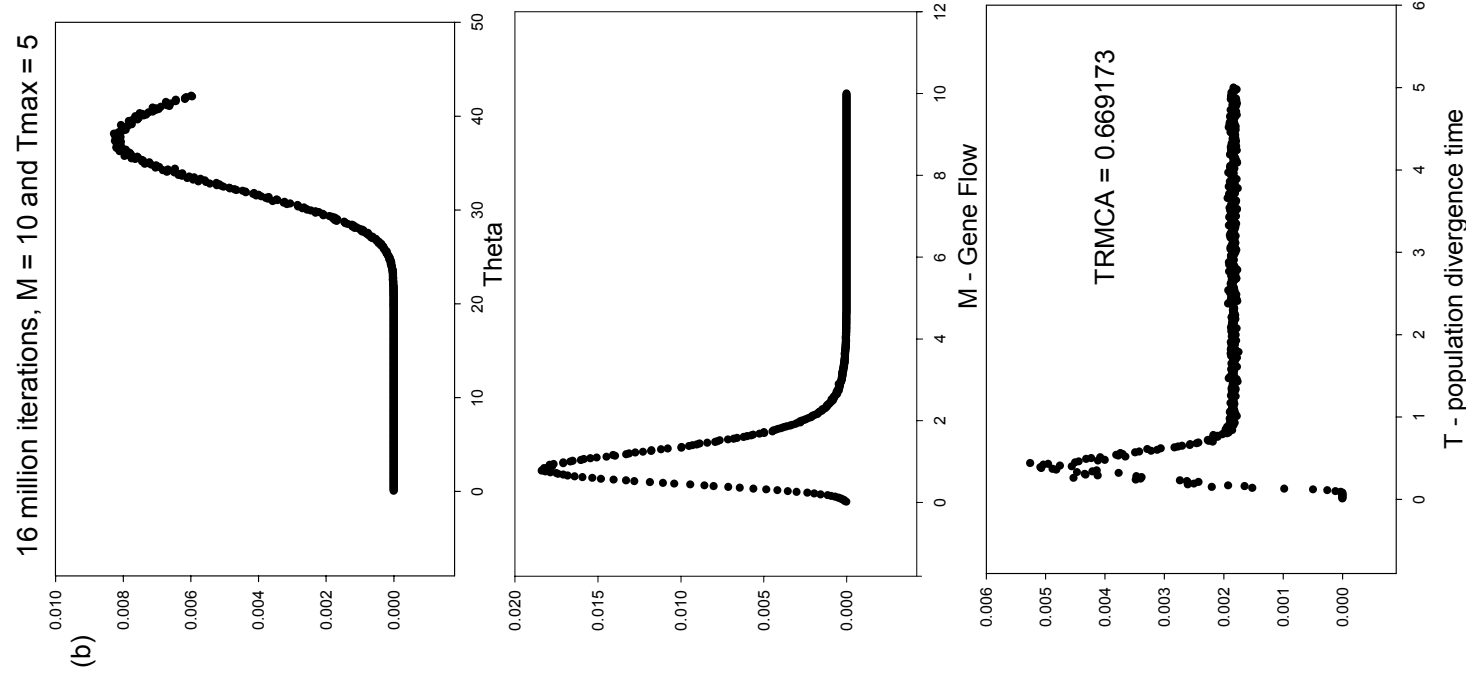
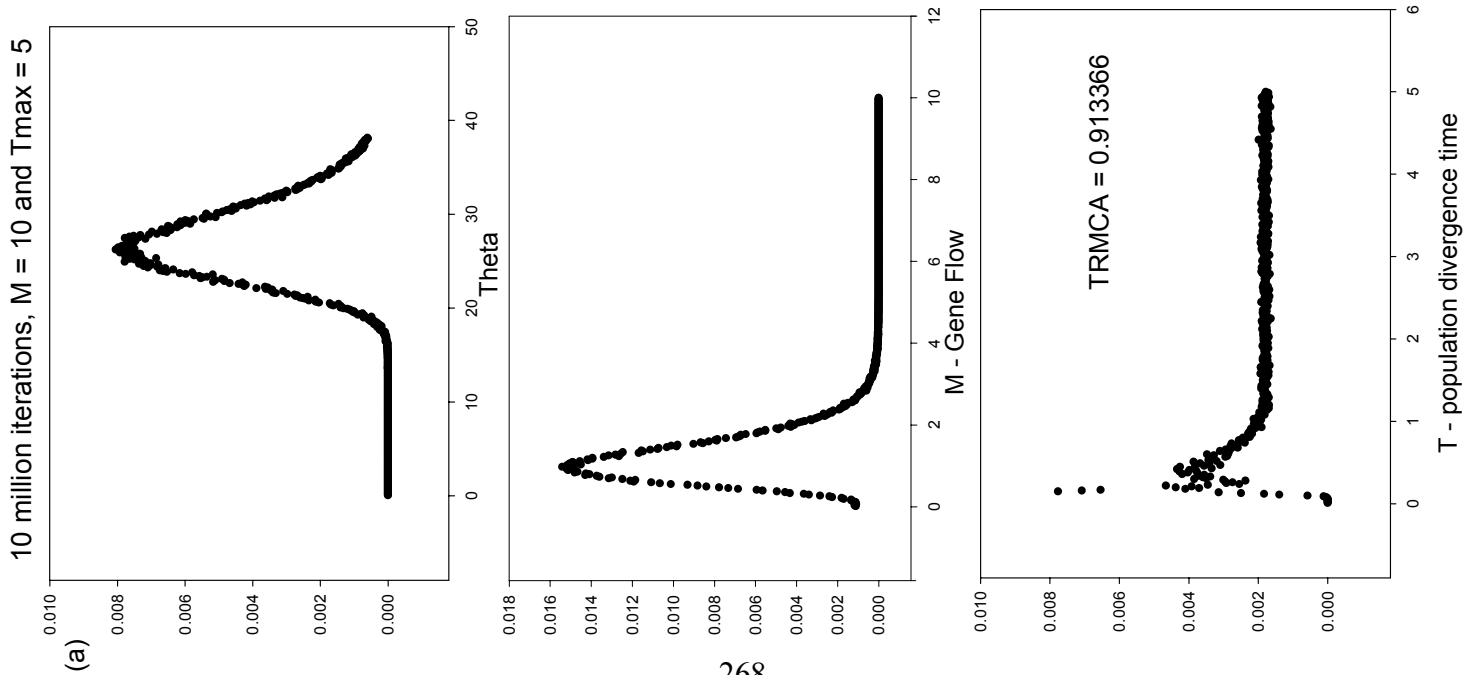
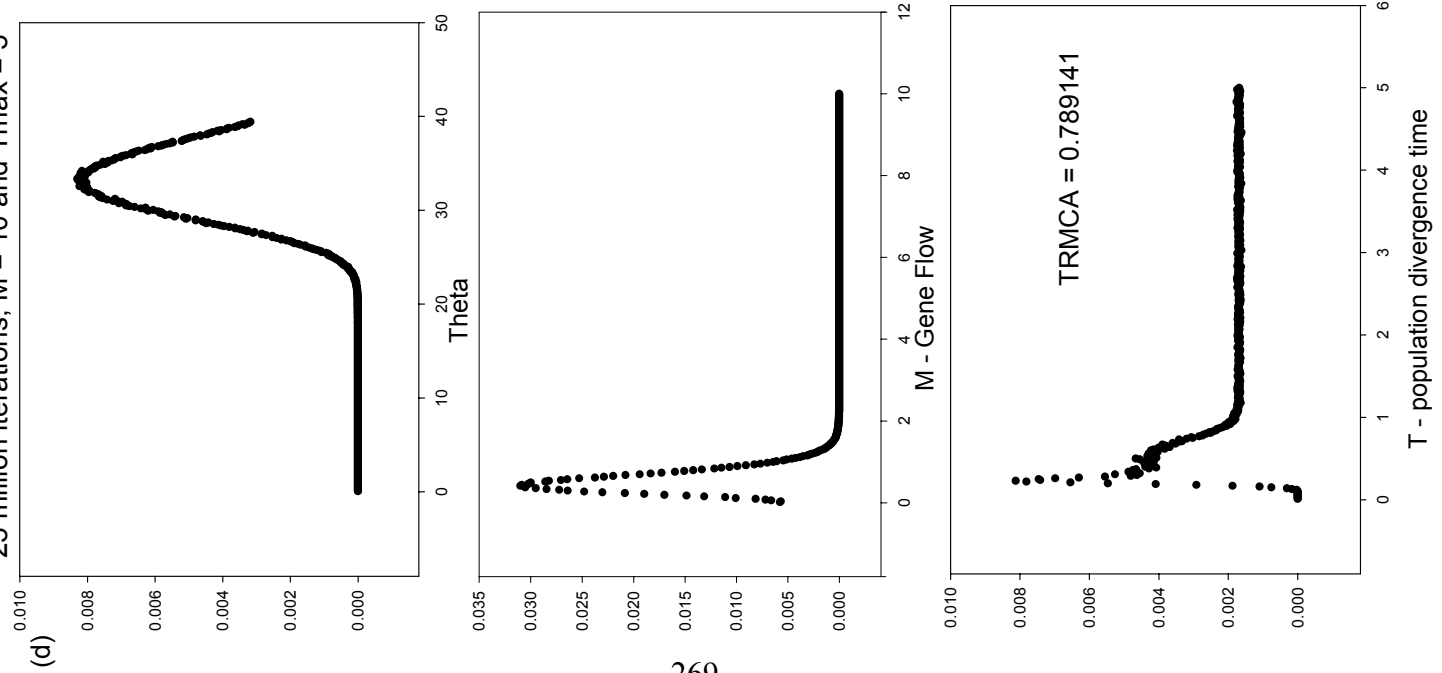
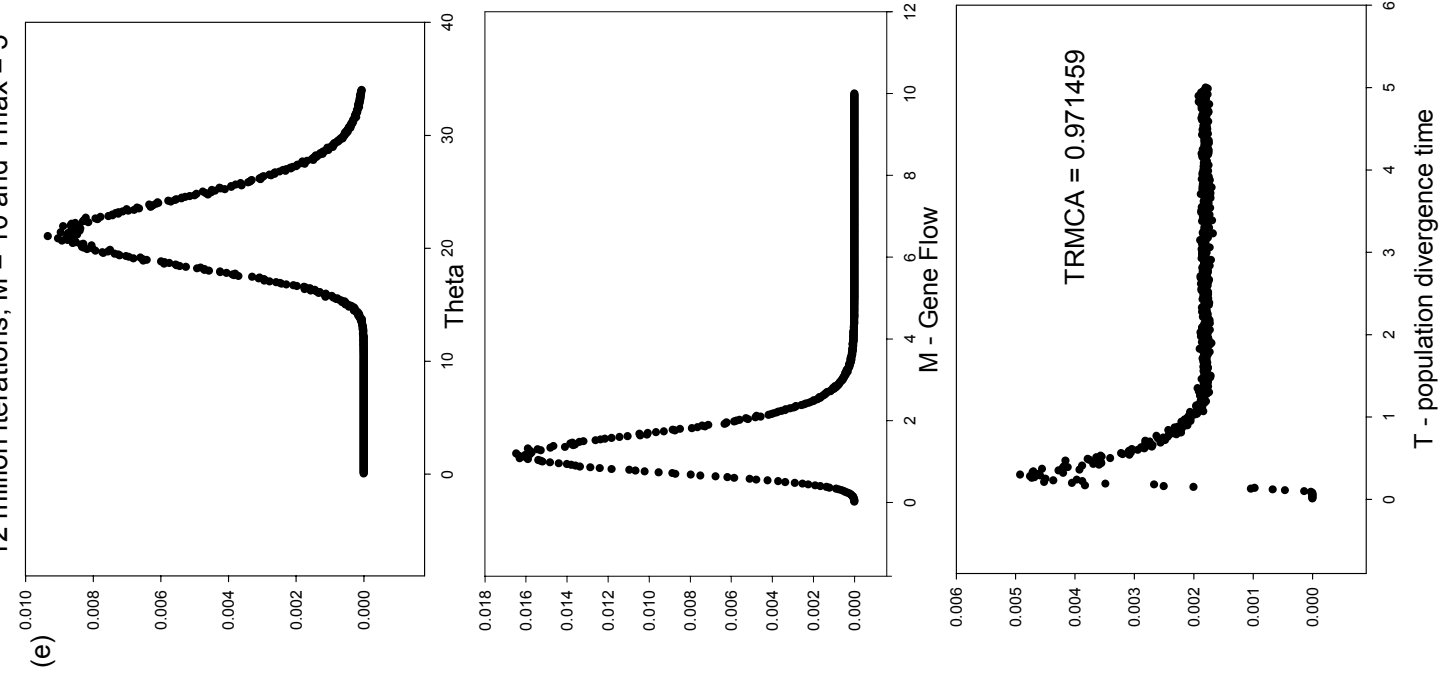


Figure 6.5. cont.

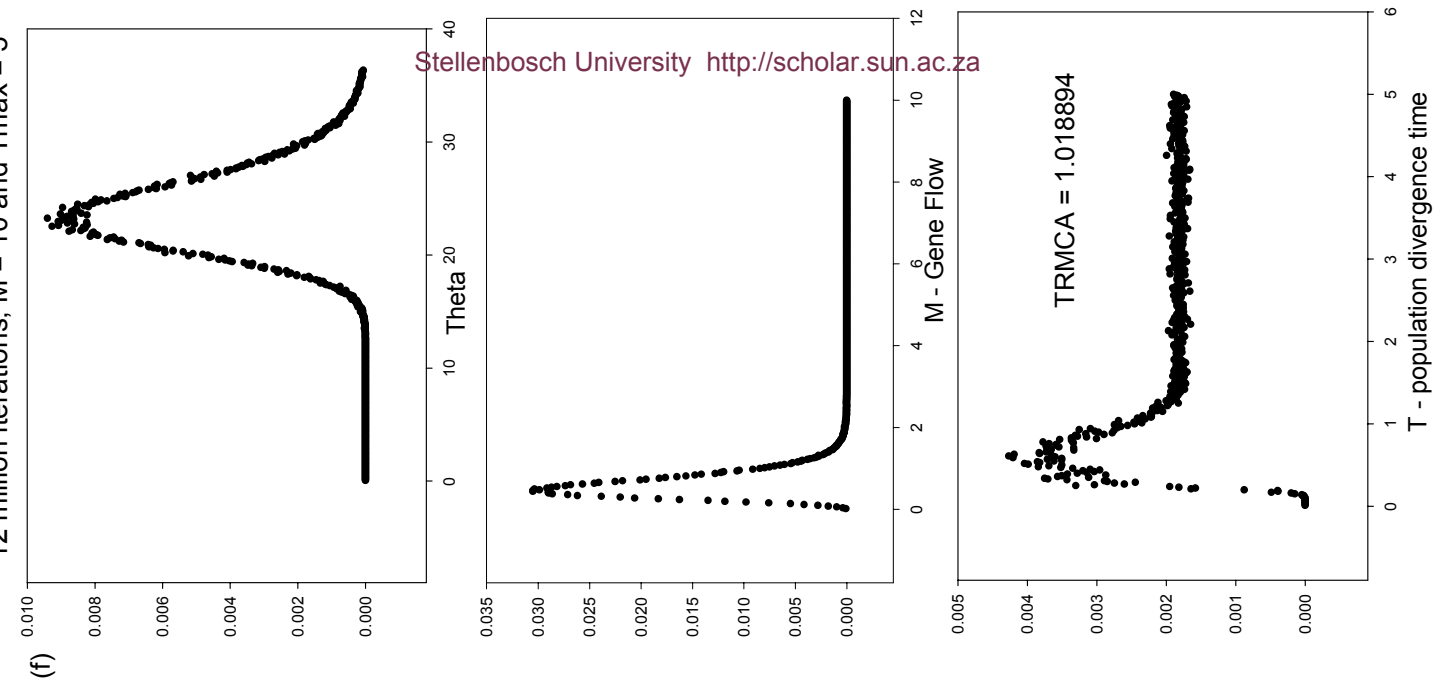
25 million iterations, $M = 10$ and $T_{max} = 5$



12 million iterations, $M = 10$ and $T_{max} = 5$



12 million iterations, $M = 10$ and $T_{max} = 5$



6.3.5 Gene Flow and Timings of Population Divergence

The MDIV results are summarized in Table 6.6 and Fig. 6.5. As based on literature searches, this appears to be the first application of this methodology in a phylogeographic study of mammals, certainly for African bovids. Estimated gene flow (migration rate, M) is close to zero in all six pairwise comparisons. The overall signal revealed in all four principal populations compared is that ancestral polymorphisms account for mixed haplotypes across lineages (Table 6.6). Despite long runs (20-25, and even 55 million iterations), the upper bound on Theta was unresolved in pairwise comparisons between *K. smithemani*, *K. anselli* and *K. leche* (Figs 6.5b-d). Nonetheless, principal estimates for Theta, M , T and $TMRC A$ were obtained in all comparisons.

6.4 DISCUSSION

More encompassing interpretations of lechwe phylogeography are challenged to relate these new findings to published knowledge, and especially to palaeo-environmental determinants. The evolution of several taxa of African mammals, through the Pleistocene, turns out to provide valuable context to frame the reconstruction as to how the *K. leche* complex has evolved. Alongside reconstructed palaeo-environments, evolutionary histories of other indicator taxa (including terrestrial mammals) provide additional threads to strengthen the overall narrative.

6.4.1 Case Studies in Other African Bovidae

This section summarizes published phylogeographic studies of selected African bovids, with respect to the evolutionary theatre of the Katanga-Chambeshi region, for which aspects of geomorphological and palaeo-climatic history has been reviewed (Chapters 4 & 5). Evolutionary processes reflected in the demographic histories of African large mammals establish a framework of documented patterns against which the Pleistocene evolution of lechwe antelopes can be contrasted and elucidated within the context of landscape evolution presented in Chapters 4 & 5.

6.4.1.1 Alcelaphine Antelopes

Flagstad *et al.* (2001) demonstrated the primary divergence of hartebeests (*Alcelaphus buselaphus* complex) into northern and southern clades. Their calculated mtDNA divergence time of 495 ± 85 Kya and 389 ± 41 Kya might well represent two, consecutive events that

corresponded to MIS 14 and 12, respectively, with acute glacial conditions (Chapter 5, Fig. 5.3). Xeric habitats would have expanded at the expense of contracting miombo woodlands (Barham 2000; Chapter 5). Patterns in these phylogeographic data concur with primary control by vicissitudes of Pleistocene climates (Flagstad *et al.* 2001). These would have affected mesic miombo and arid savanna in fundamentally different ways, with concomitant effects on the *lichtensteini* and *buselaphus* lineages, respectively. This study however did not take into account that Middle Pleistocene diastrophism focused in the Rukwe-Rungwe region. The latter is potentially a critical factor to explain primary divergence among African hartebeest, as invoked between the *Damaliscus korrigum* and *D. lunatus* clades (Cotterill 2003a; also see Ebinger 1989; Ebinger *et al.* 1993; Delvaux *et al.* 1992, Delvaux 1995 Chapters 4 & 5)

The mtDNA structure of the southern hartebeest lineage described by Flagstad *et al.* (2001) reveals that *A. caama* was seeded from *A. lichtensteini* in the north. Based on its historical distribution (Smithers 1983), the data suggests *A. lichtensteini* expanded its range south of the Lower Zambezi river across the Mozambique coastal plain and up adjacent river valleys. So it appears these antelopes reached drier miombo savanna in central Zimbabwe via a circuitous route through southeast Africa. Divergence between the Southwest Arid endemic *A. caama* from the miombo endemic *A. lichtensteinii* was estimated at 212 ± 24 Kya (Flagstad *et al.* 2001). This estimate for vicariance between the *A. caama* and *A. lichtensteinii* lineages exhibits an interesting congruence with a critical event in the evolution of Upper Zambezi valley. This is based on two sets of evidence. Firstly, the respective ranges of these taxa are divided either side of this landform. Secondly, dispersal of these antelopes southwards correlates with the second impoundment of palaeo-lakes Bulozzi and Thamalakane. As dated by a molecular clock, their divergence correlates, tellingly, with the Batoka Unconformity. Thus, the divergence ensued between these hartebeests after this dispersal when the Upper and Middle Zambezi became reconnected. But the estimated divergence time, from CRHV1 data, underestimates the age of this geomorphological event - as delimited by the archaeological record (Sections 5.7 & 5.8.4, Fig 5.3).

There are several other species of southern African mammals whose extant populations extend north of the Upper Zambezi across the Choma highlands as far as the Kafue Flats. Blue wildebeest, *Connachaetes taurinus* is one, and unfortunately the only suitable species

complex whose phylogeography has been studied. Further phylogeographic studies need to focus on this interesting situation, and especially target mammal taxa that exhibit anomalous distributions, contained west of the Upper Zambezi (see Table 6.7). It especially pertains to vicariant populations of *C. taurinus* in central Zambia, which are not only isolated east of the Upper Zambezi, but further divided northwest and south of the palaeo-Chambeshi axis (Ansell 1978; Cotterill 2003c). Divergence between CRHV1 haplotypes of *C. taurinus*, restricted to the Kafue Flats (admittedly a small sample), is most plausibly explained by geomorphological control reflected in Middle Pleistocene evolution of the Upper and Middle Zambezi rivers (Chapter 5).

The Luangwa valley endemic, *C. cooksoni*, is closely related to the Kafue population. Contrary to hartebeests, wildebeests dispersed northwards, as inferred from the longer branches of southern lineages compared to less divergent mtDNA lineages in east Africa (Arctander *et al.* 1999). Larger samples are required to date these phylogeographic events, but the northward dispersal of wildebeests into east Africa probably coincided with the southward dispersal of hartebeests into southwest Africa. Overall, these patterns raise interesting questions about habitat selection, especially as to why *A. caama* evolved into an arid specialist, as against *A. lichtensteini* confined to mesic savanna. The obvious answer is that the ancestor was a specialized grazer in seasonal savannas, while invasion of mesic miombo dry forest entailed derived specialization in *lichtensteini*. The dispersal corridor between east and southern Africa appears to extended across the Rukwa-Rungwe region, as suggested for *Damaliscus* by Cotterill (2003a,c). Nevertheless, some of these large mammals, pertinently wildebeest, may also have dispersed east, across the Shire valley, and north into southern Tanzania (Arctander *et al.* 1999).

6.4.1.2 Hippotragine Antelopes

Studies of sable antelopes, *Hippotragus niger* complex of south-central Africa reveal interesting biogeographical patterns. Here, the vicariant distribution and taxonomic status of the Giant Sable, *H. variani*, a localized endemic in central Angola can be singled out with respect to palaeo-environmental dynamics across this part of the Katanga-Chambeshi region. The status of this taxon has formed a subject of some controversy (Walker 2002), the details of which lie beyond the scope of this study. Nevertheless, multivariate comparisons of the skull morphology of 32 museum specimens of *variani* reveals its distinctiveness from all

other taxa, including *H. kirkii* of western Zambia and Katanga (Cotterill *unpubl. data*). This supports the original suggestion of Blaine (1922) as to the taxonomic distinctiveness of *variani*. Following on Matthee & Robinson (1999b) and Pitra *et al.* (2002), Pitra *et al.* (2006) demonstrated that *variani* forms a distinct clade as based on distinctiveness of mtDNA CRHV1 haplotypes (499 bp). Furthermore, distributional records of these sought after trophy species (Schouteden 1946; Ansell 1978; Crawford-Cabral & Veríssimo 2005; Cotterill *unpubl. data*) appear to be representative. The record of *H. variani*, mapped by Schouteden (1947: 371) to Sandoa (9.41°S, 22.56°E) represents the correctly identified voucher RMAC 11521. Nevertheless, its anomalous occurrence in west Katanga might well constitute a false locality, perhaps of a thin disguised trophy poached in Angola. These distributional data reveal how southern Sable (*H. niger s.s*) are confined between the Cuito and Cuando rivers in southeast Angola (south of 14°S) while *H. kirkii* is confined east of the Kasai and Upper Zambezi rivers. It is especially pertinent to recognize that *H. kirkii* is separated from *H. niger*, where the Zambezi River flows across the Okavango graben to the Gwembe trough. This is interpreted as a distributional break congruent with alcelaphines.

As based on the argument for the supremacy of the ESC as the universal species concept (Chapter 3), these three lines of evidence clearly reveal *H. variani* as an endemic species in central Angola. Its isolation in miombo woodland, north of the Southern Equatorial Divide, is especially interesting, because it lies within a zone (termed a geobiotic congruity - see Section 8.6) of active geomorphological evolution, where the Upper Cuanza river has expanded its catchment southward through drainage capture (Chapter 4, Figs 4.5 & 4.6). It is currently impossible to reconstruct how geomorphological evolution across the Cubango-Cuanza headwaters interacted with Pleistocene palaeo-climates to possibly influence the evolution of *Hippotragus*. Nevertheless, the estimated divergence date of *H. variani* at ~200 Kya (Pitra *et al.* 2006, based on Mannen *et al.* 1998) approximates the boundary between the Middle and Late Pleistocene (Fig. 5.3). One can speculate that vicariance of Giant sable more likely corresponded to MIS 8, with contraction of miombo woodlands into northwest Angola, and concomitant expansion of the Mega-Kalahari (Chapter 5).

6.4.1.3 Phylogeography of Elephants and Pleistocene Expansions of Guinean-Congolian Forests across the Katanga-Chambeshi region

Roca *et al.* (2005) discovered that mtDNA haplotypes representing Forest elephants, *Loxodonta cyclotis* form a prominent signal in extant Savanna elephants, *L. africana*, across northern Botswana and Zimbabwe. Subject to comprehensive genotyping of elephant populations across south-central Africa, especially Zambia and Angola, this interesting anomaly is most plausibly explained to represent a mesic period when moist forests extended hundreds of kilometres south of their present limit in the Congo basin. Thus, the range of *L. cyclotis* expanded concomitantly during this mesic period and has since contracted, but mtDNA signatures of their dispersal persist in *L. africana*. Detailed analysis of elephant phylogeography in terms of Pleistocene forest history awaits deserving study and discussion, beyond the realm of this study. Nevertheless, aspects of palaeo-environments discussed in Chapter 5, with respect to the tenures of PLM, and stratigraphy of the Victoria Falls Formation, turn out to pertain to the wetland archipelago of the Katanga-Chambeshi region.

Roca *et al.* (2005) further invoked the existence of the PLM stage, in the Okavango graben, as possibly forcing regional climate with locally higher precipitation. Thomas & Shaw (1991) hypothesized that Palaeo-Lake Makgadikgadi would indeed have maintained a moister climate across a swathe of south-central Africa, which probably extended northwards from the Okavango graben. Such a persistence of PLM can be invoked to have maintained a southward expansion of the Inter-Tropical Convergence Zone by drawing the Congo Air Boundary southwards. The persistence of significantly higher rainfall across a region (which today averages 500 - 700 mm/ annum) has major implications for palaeo-environmental, and palaeo-hydrological regimes across the southern African interior (McFarlane & Segadika 2001; Table 4.2) not just the Katanga-Chambeshi region.

A large literature has discussed dynamics of forests and savanna biomes across the African plateau, today dominated by grasslands and savannas (Barham 2000, 2001). Pleistocene expansions of forest have frequently been invoked to explain discontinuous ranges in forest birds, especially isolated between western Angola and northern Zambia (Moreau 1966; Benson & Irwin 1965a-c), and also other fauna with Guineo-Congolian affinities today localized around the headwaters of the Upper Zambezi (Ansell 1978; Cotterill 2002, 2006). The latter are confined to narrow strips of gallery forests that anastomose through the

southern Congo basin across northeast Angola and northern Zambia. These patches of forest are under strong edaphic control along drainage lines, and have long been believed to represent residual outliers of southward forest expansions (White 1983; Cotterill 2002b-c). The evergreen Mavunda forests on Kalahari sands in northwest Zambia and eastern Angola probably also represent remnants of moister, regional conditions. The endemic tree, *Cryptocephalum pseudotaxus*, dominates the tall canopy of mavunda above the dense, floristically diverse understorey. These *Cryptocephalum* persist successfully on Kalahari Sands (where mavunda is confined) because high soil moisture buffers seasonal aridity (Benson & Irwin 1965c; Cottrell & Loveridge 1966; White 1983). Elephants have been extirpated from nearly all these forests; yet, interesting questions relate to whether isolates of *L. cyclotis* persisted in mavunda long after savannas expanded.

It is especially informative that mtDNA haplotypes (ND5) of *L. cyclotis* were revealed in *L. africanus* from Mashatu (SE Botswana) nor Etosha (Owambo basin of N Namibia), but are confined only to the populations in northeast Botswana and NW Zimbabwe (Roca *et al.* 2005). Similar results were obtained with a complementary sample of mtDNA sequences of the entire Cyt b and the complete CR (Debruyne 2005). This phylogeographic anomaly is best explained by an expansion of moist, evergreen forests in an interglacial, when warm, wet conditions can be expected to have approximated that prevailing across northern Angola and south-central DRC today. Persistence of these conditions might have been reinforced if this Early Pleistocene interglacial coincided with a maximum extent of Palaeo-Lake Makgadikgadi (PLM). The latter's tenure appears to have ended before the Middle Pleistocene ~970 - 783 Kya (Section 5.7, Fig. 5.3). Yet high similarity between these haplotypes (many with identical sequences) between *L. cyclotis* in the Congo basin and these southern African *L. africana* can be explained as a range expansion of forest elephants relatively recently in the Pleistocene. This suggests that mesic conditions, supporting suitable *L. cyclotis* habitat, may have reflected partial influence by the late Middle Pleistocene configuration of Lake Patrick, and palaeo-lakes Bulozzi and Thamalakhane. Their combined area (totaling ~ 50 000 km²) could have maintained a locally mesic palaeo-climate, particularly earlier in MIS 7 - an interglacial. Climatic forcing by such palaeo-lakes was much less likely to have occurred since MIS 7, after both the Kafue and Zambezi rivers established their modern topologies (Chapter 5, Fig. 5.3). Elephants are successful dispersers, even across water bodies as wide as that of the artificial Lake Kariba, so their movements are

not at all contained by rivers approximating the width of today's Zambezi. Thus, this hypothesis of forest expansion most plausibly explains this interesting facet of the evolutionary history of Africa's two elephant species.

6.4.1.4 Examples of Dispersals and Speciation in Other Mammals

Phylogeographic divergences between southwest and northeast representatives of savanna bovids is also represented in Kudus of the *T. strepsiceros* complex (Nersting & Arctander 2001) and Impala, *Aepyceros melampus* and *A. petersi*, where the latter is restricted to the Owambo basin (Fig. 4.11). Vicariance of *A. petersi* probably reflects control by vicissitudes of Pleistocene palaeo-climates (Lorenzen & Siegismund 2004), but could equally reflect dispersal westwards into the Owambo basin (Fig. 4.1) from the Cubango valley, appropriately through the headwaters of the Omuramba-Omuthiya from the Namungundo, a Cubango tributary (Section 4.11, Fig. 4.11b). Historically, *A. melampus* occurred upstream along the Cubango valley to around its confluence with the Colui River, which Moore & Larkin (2001) invoked as a dispersal route for aquatic organisms between the Cubango and Kunene systems. Impalas may have dispersed along either or both these routes across the Owambo basin. Distributional data (Smithers 1983, corrected for Angola by Crawford-Cabral & Veríssimo 2005), reveals that the isolated range of *A. petersi* exhibits close congruence with Damara dikdik, *Madoqua damarensis* and Angolan giraffe, *Giraffa camelopardalis angolensis*.

The phylogeography of molerats (Bathyergidae: *Cryptomys s.l.*) awaits further, detailed study to pay deserving justice to the fine-scaled vicariance across west and north Zambia revealed in their patterns of cytogenetic evolution (Van Daele *et al.* 2004) and regional patterns revealed by initial phylogeographic studies (Faulkes *et al.* 2004; Ingram *et al.* 2004). On going research in Zambia (P. Van Daele *pers. comm.*) and Angola, Botswana, southern Congo, Mozambique and Zimbabwe aims to resolve many tantalizing questions as to when and where molerats have speciated with respect to Plio-Pleistocene palaeo-environments (Faulkes & Cotterill *in prep.*).

In significant aspects, this combined evidence refines when and where expansions of arid palaeo-environments established an Arid Corridor across the Katanga-Chambeshi region. The deeper divergences revealed in the arid-adapted Ground squirrels, *Xerus princeps* complex,

by (Herron *et al.* 2005) demonstrates this Arid Corridor has likely existed in discrete periods through the Plio-Pleistocene. The reappraised phylogeography of alcelaphine antelopes would then represent the most recent of these events, when a pulse of peripatric speciation events occurred (toward the end of the Middle Pleistocene) controlled by geomorphological events across the Okavango-Kafue graben. Further northeast, centred around the Ufipa Plateau (between the Malawi and Tanganyika rifts) repeated episodes of volcanism and diastrophism also controlled mammalian dispersals (Grubb *et al.* 1999; Cotterill 2003c; Chapter 4). Now, the combined patterns in phylogeographic case studies (see above) and palaeo-environments (Chapters 4 & 5) desiccation of the Upper Zambezi valley facilitated dispersals of large terrestrial mammals around 400 - 250 Kya, and possibly earlier in the Early Pleistocene. Geodynamics of this landform also appears to have influenced the *K. leche* complex, but in distinctly different ways. This possibility is one of several palaeo-environmental controls that deserve consideration, toward deciphering the evolutionary history of lechwe antelopes.

6.4.2 Phylogeography of the *Kobus leche* Complex

6.4.2.1 Explanation of Overall Patterns

Compared to the case studies, discussed above, the phylogeographic patterns amongst the four extant populations of lechwe antelopes differ in important respects. Besides the more localized study area, and the consequent more detailed geographical focus compared to the near continent-wide context of previous studies of bovids, habitat requirements of lechwe antelopes (Chapter 2) differ fundamentally from those terrestrial antelopes whose phylogeography has been studied (notably alcelaphines and hippotragines). The latter all inhabit savanna landscapes (Smithers 1983; Du Toit 2003). The aquatic environment is one difference that sets lechwes apart. Clearly, factors to be considered include controls by landscape evolution, where patches of wetland have been radically rearranged across the Katanga-Chambeshi archipelago - driven by Pleistocene palaeo-environments.

6.4.2.2 Demographic Histories of Populations

The accumulation of a preponderance of recent mutations in *K. kafuensis* reflects this population's expansion, estimated by J-values at ~73 Kya, but perhaps as recently as 35 Kya (Table 6.5, Fig. 6.4b). Zheng *et al.* (2003) argued such patterns of pairwise mutations invariably represent the composite result of recent and ancient dynamics within the

Table 6.7. Species of mammals whose extant ranges extend northeast of the Okavango graben, or are confined southwest of the Zambezi River. This congruence in their distributions all point to containment (upstream of Victoria Falls) by the Upper Zambezi river during the Pleistocene. Through this critical period (estimated 400 - 200 Kya) flow of the Upper Zambezi was contained in Palaeo-Lake Bulozzi (Chapter 5). Phylogeographic patterns of *Alcelaphus* and *Connochaetes* (Arctander *et al.* 1999; Flagstad *et al.* 2001) constitute case studies of how savanna biota dispersed between southwest and east Africa when arid palaeo-environmental conditions prevailed and the Upper Zambezi valley dried out between downstream of the Bulozzi floodplain (Chapter 5).

Species	Comments	Data sources
<i>Proteles cristatus</i> Sparrman 1783	arid corridor indicator: northern-most distribution in Zambia is confined south of both the Kafue and Machili Flats	Smithers 1971; Ansell 1978
<i>Giraffae camelopardalis infumata</i> Noack 1908	considered distinct from <i>G. c. angolensis</i> Lydekker 1901, with its range centred around Owambo basin. <i>G. camelopardalis</i> is absent from the middle Zambezi valley	Crawford-Cabral & Verissimo 2005
<i>Connochaetes taurinus</i> cf <i>taurinus</i> (Burchell 1823) <i>Raphicerus campestris steinhardtii</i> (Zukowsky 1924)	both these populations of Blue wildebeest and Stenbok are arid corridor indicators. Confined south and west of the Upper Zambezi river, and <i>C. taurinus</i> is absent from the middle Zambezi valley.	Smithers 1971; Ansell 1978
<i>Connochaetes t.</i> cf “ <i>kafuensis</i> ” <i>Raphicerus c.</i> cf <i>kelleni</i> (Jentink 1900)	both representatives of Blue wildebeest and Stenbok are confined to central Zambia between the Upper Zambezi and Upper Kafue rivers, where this population of the <i>C. taurinus</i> complex appears to be evolutionary distinct, but has not been described. It is obviously distinct from <i>C. cooksoni</i> , endemic to the Luangwa valley	
<i>Ourebia ourebi</i> cf. <i>hastata</i> (Peters 1852)	northeast Zambia, but relationship between separate Luangwa and Upper Chambeshi populations is unclear.	Ansell 1978
<i>Ourebia ourebi</i> cf. <i>rutila</i> Blaine 1922	formerly widespread in eastern Angola, and northeast Botswana and Kazuma depression, NW Zimbabwe	Smithers 1971; Cotterill 2003c,d, Crawford-Cabral & Verissimo 2005
<i>Lepus capensis</i> Linnaeus 1758	Morphologically distinct populations of <i>L. capensis</i> and <i>L. saxatilis</i> are confined southwest and northeast of the Upper Zambezi river, respectively. This nomenclature is subject to taxonomic revision of the overall diversity of the <i>L. capensis</i> species complex.	Smithers 1971; Ansell 1978
<i>Lepus saxatilis</i> Cuvier 1823		

population. This is evident in the wide range of J-values, especially for *K. anseli* and *K. smithemani* (Table 6.5), which would place the initial divergence in the Early Pleistocene, if not earlier. So, this expansion of lechwes across the Kafue Flats would then place its initiation in the Middle Pleistocene (given the upper 95% interval of 240 Kya). Such timing is indeed contained within speculative margins, but it does nonetheless concur with a significant feature in the Pleistocene history of the wetland. Moreover, this recent expansion of *K. kafuensis* is reflected by the Mismatch distributions when compared to the other three lineages. The causative event that plausibly could have resulted in a range expansion is when the Kafue river attained its modern topology (Section 5.8.4, Fig. 5.6). In other words, the Kafue lechwe population expanded as the Kafue Flats became established as a floodplain of ~ 20 000 km² through the Late Pleistocene, after Lake Patrick was drained by the Lower Kafue. It appears unlikely that this expansion coincided with glacial maxima (pertinently MIS 4 at 71 - 57 Kya), because the population existed throughout interglacial conditions that prevailed in either MIS 5 or 7: either 130 - 71 or 242 - 186 Kya, respectively (Section 4.9.4, Fig. 5.3).

6.4.2.3 Admixture or Incomplete Lineage Sorting (Ancestral Polymorphisms)?

The shared haplotypes among lechwes likely reflects the combined consequences of ancestral polymorphisms through incomplete lineage sorting, although rare admixture events could have contributed to the heterogeneity of haplotype composition in the principal clusters. Complete lineage sorting requires the extinction of all, but one, gene lineage within respective lineages (Avise & Wollenberg 1997; Avise 2004). Nevertheless, such high levels of stochastic extinction of genetic diversity within sundered lineages removes valuable phylogeographic signal from populations (Dolman & Moritz 2006). Low levels of female gene flow could possibly explain the 5 *smithemani* specimens that are nested within the *leche* grouping. A more likely explanation, however, is that these represent ancestral haplotypes, which suggests dispersal of the latter northwards into the Luapula system. This inference is based on the nesting of the 2 Luapula *leche* haplotypes (K136a and K154) in the *leche* clade.

MDIV analyses (Table 6.6) support low levels of gene flow (approaching zero) between all four lineages since initial divergence of the gene tree. An analogous use of MDIV by Bowie & Fjeldså (2005) similarly demonstrated that gene flow had effectively ceased between two allopatric populations of Afrotropical forest partridges, *Xenoperdix*, which had diverged recently in Pleistocene. This coalescent-based method provides two complementary insights into the history of lineage divergence. *TMRCAs* estimates a likelihood of when sundering of the gene tree initiated, while *M* and *T* are likelihood estimates of when each population attained its respective independent structure (Nielsen & Wakeley 2001; Griswold & Baker 2002).

As calculated by the deeper range of *J*-values, expansions within the *anselli*, *leche* and *smithemani* lineages followed on comparatively ancient founder events (relatively early in the Pleistocene, perhaps more than 1 Mya in the case of *anselli*). These ancient events contrast against that revealed in *kafuensis*. It is, nevertheless, difficult to discern whether the wide confidence intervals around estimated expansion times reflect the preservation of ancestral genetic diversity, and thus not deeper divergence of these lineages (Tables 6.5 & 6.6). Perhaps, vicariance of previously contiguous wetlands - pertinently the Palaeo-Chambeshi River - was a relatively protracted event compared against the finer scaled dynamics exhibited by demographic processes. Thus, these regions of river piracy (especially across the Katanga Pedicle) could have functioned as porous barriers to gene flow, perhaps for tens of thousands of years and longer.

With one exception (*K. kafuensis*), persistence of large effective population sizes (*N_{ef}*) more likely explains how estimated population expansions pre-date estimates of *TMRCAs* and *T* (Table 6.6). Following initial expansions, all the south-central African lechwes have existed at relatively large effective population sizes (*N_{ef}*), so these signatures have persisted in these lineages even after they diverged in the late Middle Pleistocene. Ancestral haplotypes have been preserved after vicariance parsed them among relatively large populations following more recent speciation events. This persistence of ancestral polymorphisms in these lechwe is supported by the occurrence of relatively deep mutations in *K. anselli* and *K. smithemani*, especially (Figs 6.2 & 6.3). It further follows that gene flow was insignificant among these principal demes in the metapopulation after respective expansions, but prior to ensuring vicariance. Thereafter, demographic conditions - namely large *N_{ef}* - preserved ancestral

haplotypes in the CRHV1 gene tree in all daughter lineages, and this outweighed the effects of genetic drift. Whitlock & McCauley (1999) calculated that a population whose N_{ef} 10 000 would only reach genetic equilibrium after ~100 000 generations. As suggested by MDIV, only *K. kafuensis* has a N_{ef} under ~100 000, with lineage divergence initiated ~200 000 generations BP (Table 6.6). Moreover, the latter population likely began from a small founding population (Section 6.3.4), any such ancestral state is masked in this analyses, because MDIV calculated only an average of N_{ef} in the pairwise comparisons. This is seen in how all comparisons of the three taxa against *kafuensis* estimated a consistently lower N_{ef} . The logical solution is to employ IM (Isolation and Migration) software developed by Hey & Nielsen (2004), which estimates independent values of Theta (and thus N_{ef}) for each lineage, as well as resolving direction of gene flow. Use of this computationally intensive analysis was not available, but is planned to explore these data more fully.

6.4.2.4 Controls of Palaeo-Environments on Evolution of the *Kobus leche* complex

To further investigate whether phylogeographic structure of the *K. leche* complex reflects a predominance of gene flow versus ancestral polymorphisms, is to reconstruct Quaternary palaeo-environments through time (building on the model obtained in Chapters 4 & 5). This would aim to model the extent of palaeo-habitat available to lechwe antelopes through the Pleistocene. Such an endeavour would be framed by the dynamics of drainage evolution assembled through Chapters 4 & 5, coupled with palaeo-climates and thus palaeo-hydrological dynamics. The objective is to quantify the extent of floodplains where lechwe populations could have persisted, and also routes of dispersal. Such a project lies in future. Nevertheless, I focus this discussion within two time frames - the Early and Middle Pleistocene, respectively, which are relatively well supported by the combined geological and biogeographical evidence (Chapters 4 & 5). I further base this reconstruction on the premise - derived from ecological studies of extant lechwes (Chapter 2) - that maximum levels of palaeo-lakes (notably in the Okavango-Kafue and Barotse basins) would have created sub-optimal conditions for lechwes. These would contrast against optimal conditions available on vast floodplains, with similar hydrological regimes to those around the Bangweulu, Kafue, Kashiobwe and Kamalondo depressions today. As described in Chapter 2, all four of these wetlands are characterized by pronounced seasonal fluctuations in water levels. These floods recharge the water meadows with nutrients, and equally invigorate the herbaceous layer with

nutrients at a time when high impacts of herbivory are reduced. It follows that such landscapes comprise the optimal matrix habitat where lechwes could persist as source populations (following principles of the matrix of landscape patches discussed in Chapter 2).

Time Frame I: Early Pleistocene

It is interesting that the estimated population expansion of Okavango Red lechwes, *K. leche*, (Table 6.5) relates directly to the end of the tenure estimated for Palaeo-Lake Makgadikgadi (PLM) in the Early Pleistocene. The estimated timing of this event is derived from the reconstructed erosion history of Batoka gorge, and archaeological preserved on fossil lake beds and in the VFF (Chapter 5). This estimated population expansion at $1115 > 764 < 314$ Kya preserved in CRHV1 sequence variation is interpreted to represent an ancient expansion of lechwes across the floodplains that formed across northeast Botswana following on the desiccation of PLM.

An equally ancient expansion event is preserved in *K. anelli*, but unfortunately the tenure of lacustrine stages in Pleistocene Katanga awaits delimitation. This more ancient expansion of Upemba lechwes at $1547 > 722 < 400$ Kya is distinctly older than its geographically closest population, that of Black lechwes in the Bangweulu - Upper Chambeshi system ($1034 > 358 < 156$ Kya). The topology of haplotypes across the NJ network reveals that ancestral, divergent haplotypes predominate in *K. anelli*.

This insight into the phylogeographic history of *K. anelli*, isolated in the Upemba Swamps of the Kamalondo graben is especially interesting. The drainage model points to this wetland having been isolated for the longest. This inference is based on the geomorphological history of the Kamalondo depression, which was isolated for a significant period in the Pleistocene as were the Lower Luapula-Mweru, Lufira and Upper Lualaba drainage systems. The high endemism of fishes also sets the Kamalondo depression apart from all other drainage basins (Chapter 4). Several interpretations follow from this observation. One has to do with the direction of gene flow in lechwe evolution, and also the relative timing of events when lechwes have alternatively been able to disperse across these landforms, and also became geographically isolated. In the absence of additional genetic markers, the primary direction of dispersal cannot be reconstructed. Estimations using the coalescent-based software IM

(Isolation and Migration), which estimates direction of gene flow (Hey *et al.* 2004; Pavlova *et al.* 2005), could possibly quantify whether initial colonization was from Katanga southwards toward the Okavango-Kafue graben or vice versa. IM performs better with multilocus evidence (as demonstrated in estimations of speciation events in chimpanzees, Won & Hey 2005), which sets difficult practical challenges for future studies of these lechwe, as the nuclear markers sampled exhibit minimal variation (Chapter 7). While Alpers *et al.* (2004) employed microsatellites successfully, they are very difficult to amplify in museum specimens (as experienced in sequencing nDNA markers, Section 7.2.5). Nevertheless, available evidence from extant populations (available to sampling) points to Upemba lechwes seeding all other extant lineages (Table 6.5, Figs 6.2 & 6.3). An additional caveat of this conclusion is that lechwes have persistently occupied the Kamalondo depression.

Time Frame II: Middle Pleistocene

The vicariance between *K. smithemani* and *K. anselli*, most likely followed on scission of the Palaeo-Chambeshi drainage system in the Middle Pleistocene. Nonetheless, the high diversity of haplotypes preserved in the entire sample of *K. smithemani*, and their distribution across the NJ-network, also signifies vestiges of an older expansion event, given that 5 *smithemani* haplotypes cluster in the *leche* clade. Moreover, subject to the vagaries of small sample size, the three haplotypes of *K. robertsi* also cluster in this portion of the network (Fig. 6.2b). These are interpreted to represent retention of ancestral haplotypes from an older expansion event that have persisted after the sundering of lineages into the clusters formed in the gene tree (estimated $TMRC A = \sim 463$ Kya, Table 6.6).

Kobus kafuensis appears to have been seeded from a population represented today as *K. leche*. Combined evidence reveals this was the most recent speciation event that elevated diversity of the *K. leche* complex. Pairwise MDIV comparisons estimated a consistently younger divergence of the *kafuensis* lineage from all its sister taxa. $TMRC A$ approximates 387 and 383 Kya against *anselli* and *smithemani*, respectively. Given the more plausible geographical scenario that *kafuensis* was founded from *leche*, the $TMRC A$ of 348 Kya, for initiation of divergence, is a more credible estimate (Table 6.5). It also concurs with Ur-Series dates on which Simms (2000) concluded that Lake Patrick had ceased to exist by ~ 300 Kya. Structuring of the genetic uniqueness of *kafuensis* with respect to *leche* then occurred

over ~ 200 000 yrs, which concurs with a recent population expansion across the Kafue Flats; although this estimate is bracketed within broader credibility margins (Table 6.5). This peripatric origin of *K. kafuensis* contrasts against the other three taxa, which all exhibit significantly greater genetic diversity (Table 6.3) and slightly larger effective population sizes (Table 6.5). Compared against lechwes, there is a distinct discordance between the phylogeographic of cichlid fishes, of the *Pseudocranilabrus philander* complex, genotyped in the Upper Kafue and Zambezi systems (Katongo *et al.* 2005, Section 4.12). Although samples sizes are small, *P. philander* scarcely differ across the two rivers systems, which contrasts to the genetic distinctiveness of *K. kafuensis* reflecting the unique evolutionary history of the lineage since initial divergence after draining of Lake Patrick. Nonetheless, the overall phylogeographic history of the *P. philander* complex concords with the *K. leche* complex in a shared origin in wetlands today represented by the Bangweulu-Upper Chambeshi region. More representative geographic and locally representative samples are still required, nonetheless, to fully understand the evolutionary history of these cichlids.

Haplotypes from central and northeast Zambia comprise an important contribution to the overall genetic diversity of *K. leche s.s.*, beyond testifying to the make up of the likely progenitor of *K. kafuensis*. Notable examples include sequences from museum specimens from extinct populations on the Kasempa River (flowing into the Barotse floodplain) and the Minginga-Luswishi Confluence (Upper Kafue headwaters). The mtDNA diversity of the Busanga Red lechwes needs to be singled out as noteworthy to both evolutionary history and conservation importance (Figs 2.1, 6.2 & 6.3). Overall, this inference is subject to inadequacies of small sample size ($n = 13$), these Busanga individuals represent a surprisingly high diversity of mtDNA haplotypes, also shown by the long branch lengths (ten haplotypes labeled Bu1 through to Bu13, Figs 6.2 & 6.3). Busanga Red lechwe are represented in all haplotype clusters, with the exception of the *smithemani* cluster. The hypothesis follows that *K. kafuensis* was seeded by a southbound dispersal from wetlands in the Upper Kafue system. The three *kafuensis* haplotypes, in the *anselli* cluster, are most likely ancestral polymorphisms, shared with the Busanga Red lechwes, and pertinently *anselli*. This pattern is further surprising when one acknowledges that this population of Red lechwe in central Zambia recovered recently from a very small population, estimated at less than 100 individuals in 1947 (Howard & Chabela 1987; Chapter 2).

A colonization of the Kafue graben, from the north, possibly paralleled establishment of the *K. leche* complex across the wetlands of Angola. The logical route for these dispersals was through the Okavango graben. This explanation accounts for close similarity of haplotypes at Grootfontein on the Cubango river in Namibia (K156, BM 35.9.1.350), and especially Gabangwe in western Angola (K146, RMAC 18924), which at 13°50'S 16°18'E is ~900 km upstream of the Okavango delta (Figs 2.1 & 6.2). Haplotypes of both these museum specimens are very similar and identical and represent shared haplotypes to those found in Red lechwe within the Okavango Swamps (Figs 6.2 & 6.3). Unfortunately, a sheer absence of Angolan specimens makes it impossible to ascertain how the genetic diversity of Owambo (Upper Kunene) and Upper Cuanza populations relate to other lechwes in the wetland archipelago. As compared to the estimated expansion of *K. kafuensis* through the Late Pleistocene ($200 > 72 < 35$ Kyr), the short branch lengths, characterized by highly similar (and many shared haplotypes) points to a relatively recent dispersal of *K. leche* from the Okavango depression along endoreic rivers across southern Angola.

This raises further interesting questions. It follows that *K. leche* would have been split into two populations when the Upper Zambezi was impounded in Barotseland (in the Middle Pleistocene, as represented in the Batoka Unconformity). It logically follows that these populations only became linked after the Zambezi was linked directly with the Okavango graben. Such a hydrological link was established at the southwest rim of Palaeo-Lake Bulozhi, and involved diversion of the Cuando into the Okavango graben to attain its modern topology. The Cuando was previously an Upper Zambezi tributary, where its fossil channel is represented today by the Matabele-Mulonga plain. So, the phylogeographic history of these reduncines parallels (yet differs fundamentally) from how alcelaphine and hippotragines were affected during the period represented in the Batoka unconformity. Hartebeest, wildebeest and sable were able to disperse south and north, respectively, during the period when the riverless Zambezi valley was inundated with Kalahari sands (Section 6.4.2.1). I hypothesize that recent panmixia of female Red lechwes would have occurred not just after the Zambezi had reestablished its topology, but more precisely ensued after the Cuando-Bulozhi capture event. It follows that these previously isolated Red lechwe populations began to mix as the Upper Zambezi began to grade the Younger Gravels (YGI) around ~200 Kya (Chapter 5, Fig. 5.3).

Thus, creation of this link between wetlands in the Upper Zambezi valley (upstream of Senanga and Ngonye Falls) with the Okavango graben, places biogeographic significance on dynamics of landscape evolution centred around the Matabele-Mulonga plain, whose affinities were previously considered obscure (Williams 1986). A capture event, where the Cuando (a Palaeo-Lake Bulozzi and thus Upper Zambezi tributary) was redirected into the Okavango graben explains how lechwes dispersed south and west thereafter (Section 4.8.5, Figs 4.7 & 5.6). The diversion of the Cuando into the Okavango graben would have allowed lechwes comparatively easy access (along with many other organisms) between wetlands in the Barotse and Okavango depressions. The isolation of several species of large mammals west of the Cuando places additional significance on this landform as a biogeographical barrier, especially to terrestrial ungulates (Section 6.4.2.1).

By this stage, probably late in the Middle Pleistocene, the Kafue river was assuming its modern topology. It would appear that this southward dispersal of lechwes followed on the draining of Lake Patrick near the end of the Middle Pleistocene. Moreover, the Palaeo-Chambeshi had ceased to exist at least 400 Kya previously (Chapters 4 & 5, Figs 5.3 & 5.6), and so a vast barrier of savanna was already in existence - dividing aquatic biota in the Upper Zambezi from the Upper Kafue drainage systems. This is important, because it appears lechwe did not disperse along the senile drainage across the Machili Flats, whose southwest draining rivers link with the Simalaha Flats on the Upper Zambezi. Although dispersals of lechwes appear to have been contained east and south of the former delta of the Palaeo-Chambeshi, certain fishes (including cichlids) may have dispersed across the watershed between the Ngwezi and Nanzila rivers, which thus persistently linked the biota of the Upper Zambezi and Upper Kafue systems (Fig. 4.10). Nevertheless, tigerfishes have not been able to surmount this barrier between the Upper Zambezi and Kafue rivers, and neither the Buckingham Falls delimiting the mid-Zambezi fish fauna from that of the Upper Kafue (Bell-Cross 1982).

Unresolved Questions

Challenging questions also pertain to the phylogeography of the Red lechwes confined to floodplains on the Kashiobwe Flats, in the Mweru graben. These Luapula Red lechwe remain represented by two specimens only (K136a, NMZB 2751 and K154, NMZB 2754). It is revealing that their CRHV1 haplotypes group within the *K. leche* cluster (Fig. 6.2). The

geological evidence (Dixey 1944) supported by patterns of gastropod diversity (Dudley 2000, Chapter 4) reveals the Kashiobwe Flats are a young landform that only formed in the Late Pleistocene after the Luvua pirated Palaeo-Lake Mweru (and thus the Luapula-Chambeshi) as its headwaters, to create the equally young topology of the Zambian Congo system (Fig. 5.6).

An allied phenomenon in this region pertains to the mystery surrounding the origin and status of the extinct Roberts's Lechwe, historically confined to the Pambashyshe Swamps, Luongo-Kalungwishi drainage system (Chapter 7). All three haplotypes cluster in the *leche* clade (Fig. 6.2). Based on this small sample size, it is difficult to draw firm conclusions about the evolutionary history of this population. Nevertheless, these *K. robertsi* haplotypes group with the *leche* cluster (Okavango and northern Zambia). It follows that their isolation is either relatively recent, or more likely reflects ancestral polymorphisms from when the Proto-Luongo system was linked to the Palaeo-Chambeshi River.

This relationship of *K. robertsi* with other extant lechwes contrasts against *K. smithemani* in important respects. The period when the Luongo-Kalungwishi drainage system was linked with rivers to the south quite possibly facilitated dispersals of lechwe antelope between these drainage systems. Thereafter, the Luongo-Kalungwishi Rivers were isolated by deepening of the Mweru graben (Chapter 4, Figs 4.3 & 4.4). This would account for the isolation of *K. robertsi*. I suggest lechwe dispersed on to the northeast Zambian plateau when the Proto-Luongo River was linked with the Palaeo-Chambeshi, possibly in the vicinity of the Itawa Dambo, with the confluence north of the Mufilira syncline (Chapter 4). Thereafter dichopatric speciation of *K. robertsi* ensued: with its distribution contained along the Upper Luongo River, extending across the Pambashye Swamps to the Kalungwishi River (Figs 2.2 & 4.3).

This reconstructed Pleistocene phylogeographic history of *K. leche s.s* must also acknowledge the fossil lechwes (*K. cf. venterae*) preserved in the Cornelia and Florisbad sediments in the Early and Middle Pleistocene, respectively (Brink 1987, 1988, Chapter 2). Their outlying distribution presumably reflect on separate, yet perhaps allied, dispersal events southwards across the South African highveld. It is assumed these extinct lechwe also originated from wetlands in the Katanga-Chambeshi region. Nevertheless, more evidence is

required to resolve how these Cornelia and Florisbad lechwes were linked to their north with palaeo-drainage dynamics across the Katanga-Chambeshi region.

6.4.2.5 Control of Phylogeographic Processes by Geomorphological Events

It can be concluded that Palaeo-Lake Bulozzi and Lake Patrick appear to have excluded lechwes entirely, or these populations occupied marginal habitat. It is reasonable to expect that these physical controls interacted with predation pressure. Even if floodplains (and thus lechwe habitat) existed around the margins of these fluctuating palaeo-lakes, they would have comprised narrow zones on relatively steeper valley sides. Here, one can speculate that lechwes were more vulnerable to carnivores, especially cursorial canids and hyaenas that flourished through the Pleistocene (see Turner & Antón 2004 for examples). But without fossils, we can only speculate about past colonizations and extinctions in islands across the archipelago. Total absence of lechwes in the Lufira depression is instructive in this respect.

The scenarios raised in the previous paragraph lead on to an important criterion. It is critical to distinguish source habitats where populations of lechwes could persist, and expand to attain high densities, versus those wetlands across which these semi-aquatic antelopes have been able to disperse, but would have struggled to breed successfully. Vast floodplains characterize such source habitats; while river margins and dambos, when seasonally flooded, would have created corridors along which lechwes have been able to disperse. This significance of dambos was emphasized previously (Cotterill 2005, Chapter 4). Up to tens of kilometres wide (but typically several kilometres in width), the largest dambos extend for hundreds of kilometres as drainage lines in their own right. It is reasonable to suggest these landforms formed dispersal corridors when persistently flooded under high rainfall regimes. It should be feasible, and above all fascinating, to model the hydrology of dambos across the Katanga-Chambeshi region in the context of palaeo-climates. The geological antiquity of the African erosion surface, with its deep biomantles (regoliths), mantling the region's vast plateaux, frames evaluation of these most recent dynamics. I hypothesize there is a threshold at which a dambo either tends to gallery forest (Mushitu) or becomes a cyclically flooded wetland. In the latter state, the landform would then become a water meadow, with all attendant attributes of lechwe pastures described in Chapter 2.

6.5 CONCLUSIONS

The principal evolutionary events whereby lechwe antelopes diversified can now be summarized, in order of more recent timing:

1. Dispersal, followed by vicariance of a wide-ranging ancestral lechwe population that occurred contiguously from Katanga, and ranged south to at least northern Zambia. There dispersal was facilitated by links across the Trans-Katanga and Palaeo-Chambeshi drainage systems. This explains why a modern representative, *K. anselli*, preserves the greatest quotient of genetic diversity even though this recent population became narrowly confined within a rift valley in Katanga.
2. The distinct product of the initial vicariance is represented by *K. smithemani* in the Bangweulu-Upper Chambeshi system. A cluster of mixed haplotypes also points to a more subtle signal of an older vicariant event (or more likely an expansion event), as represented by *smithemani* haplotypes, with long branch lengths, clustering within *leche*.
3. The population of *K. leche s.s* in the Okavango graben (that likely extended along the Cuito-Cubango drainage system) was isolated from that in the Upper Kafue and Upper Zambezi systems, when the latter was impounded to maintain Palaeo-Lake Bulozzi through the Middle Pleistocene. These populations only became linked, after the Cuando River became a direct tributary of the Okavango graben ~200 Kya. This was a penultimate event in a pulse of dispersals by several large mammals when the Arid Corridor linked the southern and east African savanna biomes. In distinctly different, albeit contemporaneous, events, lechwes dispersed along - as apposed to across - drainage systems.
4. In an incident of peripatric speciation - estimated to have initiated at ~350 Kya - the lechwe population in central Zambia seeded a population on the Kafue Flats in central Zambia; where they then diverged rapidly into *K. kafuensis*, the youngest, yet most morphologically distinctive population.
5. The significant demographic expansion of *K. kafuensis* followed on the Kafue River establishing its modern topology in the Middle Pleistocene after ~350 Kya. This morphosis from Lake Patrick to Kafue Flats is mirrored in expansion of the Kafue lechwe population (235 > 78 < 35 Kya).

6. In the most recent dispersal event, either *K. leche s.s.* or *K. robertsi* colonized the Kashiobwe floodplains around the southern reaches of Lake Mweru. This followed on lowering of the lake level as the Luvua River incised the northern rim of the Mweru graben, creating the Zambian Congo drainage system.

To answer a central question of this study, combined evidence (the Geomorphic and Biogeographic datasets, Chapters 4 & 5) pointed to strong, if not overwhelming, control by geomorphological events on all these evolutionary events. The coalescent-based analyses (Mismatch and MDIV) reveal that expansions of lechwes populations and principal lineages diverged in episodes that correspond closely to significant changes in water meadow habitats. These events in landscape evolution are hypothesized to have either provided novel habitat (desiccations of palaeo-lakes) or disrupted formerly contiguous lechwe habitat. Thus, all evidence does reveal that principal features of the evolutionary history of lechwe antelopes do indeed exhibit a strong correlation with zones of tectonic activity and associated drainage rearrangements. Not least, each significant event in lechwe evolution correlates closely with distinct events in palaeo-drainage dynamics. Based on the model of landscape evolution, these correlations can be summarized below, in order of more recent age:

1. Although it is concluded that initial dispersals of a widespread ancestral population of lechwes was facilitated by the Trans-Katanga and Palaeo-Chambeshi drainage systems, tenure of this network has still to be precisely constrained. The Palaeo-Chambeshi persisted through the early Pleistocene to grade late ESA tools into its gravels across the Okavango-Kafue graben. It may have persisted into the early Middle Pleistocene; but this could represent actions of the Palaeo-Kafue River (after scission of the Palaeo-Chambeshi across the Mufilira Syncline).
2. Subject to further refined phylogeographic evidence for lechwes and other surrogates of the aquatic biota, it can be concluded that protracted geodynamics, centred on the Mweru graben, initiated dichopatric speciation of lechwes. These have evolved into *K. anelli*, *K. leche*, *K. robertsi* and *K. smithemani*. This complex event, or rather events, entailed rearrangements of drainage systems through the Middle Pleistocene, with isolations of the Upper Luongo, and Bangweulu and Kamalondo, in tandem with rearrangements of neighbouring drainage systems. Such protracted geomorphological dynamics affecting drainage across the Katanga pedicle and Mufilira Syncline

(Chapter 4, Fig. 4.3) evolved progressively, perhaps over tens to hundreds of thousands of years. This would have constituted a relatively broad window of opportunity for persisting gene flow among populations of aquatic biota in neighbouring wetlands. Phylogeographic evidence reveals that lechwes were directly involved in these geobiotic dynamics. Coalescent-based analyses estimate lechwes diverged at ~463 Kya, and probably earlier given variance around theta estimates (Table 6.5).

3. Impoundment of the Upper Zambezi (invoked to explain the tenure of Palaeo-Lake Bulozzi) lead to a prolonged dessication of the Zambezi valley, upstream of Batoka gorge. This had major consequences on continent-wide biogeographical patterns in certain bovids. As characterized in the phylogeography of alcelaphine antelopes, a pulse of dispersal events followed dessication of the Upper Zambezi valley. An allied event entailed disruption of the Cuando-Upper Zambezi link. (The redirected Cuando River was ultimately reconnected to the Upper Zambezi at Kazangula.) This diversion of the Cuando enabled dispersals of *K. leche* into the Okavango depression, to reach the Cuito-Cubango rivers across Angola.
4. The Kafue graben was possibly inhabited by lechwes when Lake Patrick still existed, and thus before the Kafue River attained its modern topology. Nonetheless, phylogeographic signals testify to a relatively recent colonization, most plausibly effected from the Upper Kafue drainage to the north. This occurred long after the link had ceased to exist across the Palaeo-Chambeshi's delta (Machili Flats) to the Okavango graben and its Cuando and Upper Zambezi tributaries.
5. The population expansion of *K. kafuensis* followed on dessication of Lake Patrick late in the Middle Pleistocene; after river piracy by the headwaters of a mid-Zambezi tributary drained this inland lake, beginning ~300 Kya.
6. The level of Lake Mweru dropped significantly as the Luvua River captured this lake as its headwaters, with consequent incision of the Luvua gorge. This initial event culminated in addition of ~700 km of the Chambeshi-Luapula drainage systems to form the principal headwaters of the Congo river. Ultimately, the Kashiobwe Flats formed around the southern edges of Lake Mweru. It is unclear whether this wetland was colonized by Red lechwe dispersing north across the Congo-Zambezi watershed, or a more local dispersal from the Luongo-Kalungwishi, or whether these Red

lechwes represent a discrete, but historically extinct, population in the ancestral catchment of the Lower Luapula drainage system. It may also be possible that palaeo-lake Lufira was temporally linked via the Palaeo-Kafila River with the Lower Luapula and Proto-Lake Mweru.

Reconstruction of this phylogeographic history of the *K. leche* complex sets the stage to address outstanding questions of this study. This is to apply combined genetic and morphological data to reevaluate the taxonomy of these remarkable antelopes. This chapter has linked phylogeographic events to the overall evidence underpinning the model of Plio-Pleistocene landscape evolution. Principal events that modified drainage across the Katanga-Chambeshi region also influenced lechwe populations profoundly through the Pleistocene. It is interesting to compare palaeo-drainage dynamics that affected lechwes to those that affected fishes. In this respect, successive captures of Upper Zambezi tributaries by the Kasai's headwaters (which enabled southward dispersals of Congo basin fishes, Bell-Cross 1968, 1982, Section 5.8) had no effect on extant lechwe antelopes. Further to the west, topological changes across headwaters of the Owambo and Cuanza basins likely influenced lechwe populations; but complete absence of data for these populations means there is scant possibility of resolving this conundrum. Study of the endangered population of lechwes in the Cuanza basin is an urgent priority, especially considering the recent confirmation by Pitra *et al.* (2006) that the Giant sable, *H. variani*, isolated in the Cuanza-Cuando region, constitutes a distinct evolutionary lineage.

CHAPTER 7



▲ Dawn over Kafue Flats at Lochinvar, July 2001. A lek of *Kobus kafuensis*, with sparring males. Resting females are chewing the cud.

Photo: F. Cotterill

▼ The Lukulu River, a major north-flowing tributary of the Upper Chambeshi, Bangweulu Flats Zambia

Photo: F. Cotterill



CHAPTER 7 MORPHOLOGICAL VARIATION IN LECHWE ANTELOPES, AND INSIGHTS INTO THEIR MOLECULAR PHYLOGENY

"While avoiding paraphyletic taxa is essential in the erection of meaningful classifications, forsaking diversity "to avoid paraphyly" is counter to a fundamental goal of biodiversity research, namely, to recognize units of diversity. It is ironic that lineages may be unrecognized because more is known about them (i.e., phylogenetic relationships) and that those studying diversity systematically conceal that which they ostensibly seek to reveal."

D. Kizirian & M. A. Donnelly (2004: 1073)

7.1 INTRODUCTION

This chapter describes and interprets two datasets. One describes the variation in the morphology of the *K. leche* complex, as represented by cranial and pelage characters of 171 specimens, including, and additional to type material. These analyses of morphological characters are followed by the analysis and discussion of variation obtained in a genetic dataset. This comprises sequences of three molecular markers, which act as an extension of the phylogeographic study of Chapter 6. Additional sequenced markers include the mtDNA cytochrome *b* gene region; intron 1 of the nuclear gene B-spectrin nonerythrocytic 1 (SPTBN-1), and a haplotypic Y chromosome marker. The latter comprised the complete sequence of the sex-determining region (SRY) and adjacent non-coding sequence. The combined evidence from these morphological and molecular datasets is compared and discussed to reappraise the diversity of the *K. leche* complex. Here I revise and discuss the taxonomy of these large mammals, with repeated recourse to the philosophical argument presented in Chapter 3. These findings and discussion are structured by the narrative of evolution of the Katanga-Chambeshi region (Chapters 4 and 5).

Scrutiny of published data on the morphology and distributions of south-central African reduncines suggested recognition of four species (Cotterill, 2000). In addition to red lechwe, *K. leche s.s.*, these are: Kafue lechwe, *Kobus kafuensis* Haltenorth 1963 (Kafue Flats); black lechwe, *K. smithemani* Lydekker 1899 (Bangweulu Basin); and the historically extinct Roberts' lechwe, *K. robertsi* Rothschild 1907, restricted to the Pambashye Swamps, Luongo-Kalungwishi drainage system (Cotterill, 2003a,b, Fig. 7.1). Examination of museum specimens of Upemba lechwes, preserved in Chicago and Tervuren, allowed a long overdue assessment of their taxonomic status. Morphological comparisons led to the unexpected discovery that these antelopes are most similar to the black lechwe, *K. smithemani*, and quite distinct from the red lechwes, *K. leche s.s.* of the Upper Zambezi-Okavango drainage system. The dire conservation plight of the Upemba lechwe made its formal description an urgent priority.

7.1.1 Historical Treatment of the Diversity of Lechwe Antelopes

Derscheid (1926) treated the three forms of *K. leche* as subspecies, and this included *K. l. robertsi*. The only serious attempt to clarify the taxonomic status of the lechwe taxa then known was by Barclay (1933). He concluded that no subspecific divisions were warranted in *K. leche*, but his conclusions were weakened by reliance on patterns and colour of pelage' let alone insufficient material. Neither of these authors mentioned *ambolloensis* Sokolowsky 1903 or *notatus* Matschie 1912, described from southeast Angola and the Caprivi, Namibia, respectively. Both these taxa were treated as synonyms of *K. l. leche* by Ansell (1972). Earlier treatments of *K. robertsi* are discussed in the results section below.

The attempt at a taxonomic review by Howard and Sidorowicz (1976) created more problems than it solved. Their *a priori* motivation that all lechwe formed a single taxon led to several errors and remarkable blunders. Erroneous results in this paper followed on misidentifications of specimens; where Kafue lechwes were treated as Red lechwes, and then included in the “pure” sample of *leche*. The overall failure of this study was subsequently demonstrated by Ansell and Banfield (1979). The latter study of morphological variation employed multivariate analysis of nine cranial characters to distinguish four taxa: namely *leche*, *smithemani*, *robertsi* and *kafuensis*. It demonstrated *smithemani* and *leche* to be most similar in skull proportions and size, with *kafuensis* the most distinct population. These taxa were treated as subspecies of *K. leche*.

Prior to completion of sequencing of molecular genetic markers, the morphological dataset compiled in this chapter was analysed and published to support the timely description of *Kobus anselli* (Cotterill 2005). This chapter comprises an expanded analysis that adds additional data and conclusions unavailable to Cotterill (2005). It especially benefits from the signals in the molecular dataset, coupled with the insights obtained in Chapter 6. Overall, the hypodigm (Simpson 1940, 1961, Chapter 3) appears to represent variation of each sampled populations adequately with the exception of four major gaps. These are the obscure populations of Red lechwe in central Angola, central Zambia (Busanga) and around Lake Mweru (Chapter 2) and the enigmatic historically extinct taxon - *robertsi*.

7.1.2 Choices of Cranial Characters and Historical Background

The exact reasons why modern mammalogists employ the morphological characters they do to distinguish and compare variation among large mammals are often unclear. This especially applies to their inaugural use, which might precede the grand works of Buffon, Cuvier and Geoffroy Saint Hilaire. The concept of a character in comparative biology became more formalized when Richard

Owen developed the more encompassing concept notions of homology at the British Museum of Natural History in the early 19th century. Morphometrics developed thereafter to become central in mammalogy; to discern taxa and populations. Thomas (1905) proposed many of the standard cranial measurements still in use today; and these have been endorsed and refined in the multitude of studies (Fristrup 2001).

Ansell (1965) argued for the importance for improved mensural data in African mammalogy, and described a set of standardized measurements of mammals, followed in this study where applicable. This can be seen, in retrospect, to have been influenced by Simpson (1961) emphasis on sampling variation within populations statistically. And it appears this shift to building large museum collections of taxa (mammals included) was a response to the influences of population-thinking on comparative biology.

With respect to lechwe antelopes, Ansell & Banfield (1979) employed a total of nine cranial measurements and also considered variation in pelage in comparing samples of museum specimens. Their results were based on a canonical variates analysis, and distinguished four taxa: namely *leche*, *smithemani*, *robertsi* and *kafuensis*, but did not examine, in deserving detail, any representatives of the population of Upemba lechwe confined in the Kamalondo depression of Katanga. The latter have now been incorporated into this study (Cotterill 2005). Although constrained by a meagre sample size available, Ansell & Banfield (1979) concluded that *K. robertsi* Rothschild 1907 is a valid taxon. Latterly, Vrba *et al.* (1994) applied a dataset of cranial characters to quantify the morphological variation of the Reduncini. This study focused on the patterns of morphological evolution across these antelopes, and concluded that reduncines exhibit distinct paedomorphosis in how horn and skulls morphology has evolved within the clade. Vrba *et al.* (1994) concluded that paedomorphic specialization has reached its extreme manifestation in the waterbucks of the *K. ellipsiprymnus* complex. Compared to the extent reduncini, the lechwes, *K. leche* and *K. megaceros* were considered to represent an intermediate stage in paedomorphosis.

7.1.3 Variation in the Pelage of African Bovids

Variation in the colours and patterns of mammalian pelage have been used widely in mammalian taxonomy, since Linnaeus and early taxonomists in the 1800s. Colours of the fur and patterns in the coats of mammals are challenging to quantify in unequivocal terms; so the more informal delimitations of characters has often been applied to describe variation in these characters. Taylor *et al.* (1990) discussed this problem in detail, in a thorough study that focused on the challenging patterns of pelage

variation in herpestid carnivores belonging to the *Cynictis pencilata* complex in southern Africa. This quantified directly the colorimetric properties of the fur in museum specimens of *Cynictis*. These problems do not appear to have been rigorously considered in the taxonomy of the Bovidae. The challenges entailed in describing variation in coat colour of bovids likely began in hunter gatherer communities in prehistory, probably associated with folk taxonomies (Atran 1990). The ethnographies of herding tribes across Africa reveal the complex tradition that centre on the economic and cultural importance of bovid livestock. This is resplendent in how vocabularies of herding tribes have been enriched to describe the phenotypic variation among their stock. These words have practical uses in animal husbandry as well as underlying complex traditions in use and values of African cattle. Hanotte *et al.* (2002) conclude the extant diversity of African cattle represents the diversification - at the hand of man - has interwoven not just two species, *Bos taurus* and *B. indicus*, but possibly a third endemic North African species.

Poland *et al.* (2003) have documented how Zulu names for the Nguni cattle, of southeast Africa evoke analogies with natural patterns to characterize pelage patterns. The speckled, banded, and stippled colourations of birds's plumage and eggs, snakes, and insects, are examples of three broad classes, respectively. Two examples for especially variably coloured beasts are the names Imasenezimpukane ('Sour Milk with Flies') and Inkunzi edabulumhlambi ('Bull that went right through the Herd'). Both denote kaleidoscopic variation in pelage pattern, in which all the populations' colours are stochastically expressed. The French term, brun-argente, invoked to describe the silver-brown dichromatic pattern of alcelaphines antelopes of the *Damaliscus lunatus* clade (Hughes 1933; Cotterill 2003a) is a rather lame comparison in European descriptions. More intriguingly, these appellations that form part and parcel of the lexicon of Zulu herdsman invariably extend beyond characters of pelage, to describe nuances in the individual cow's behaviour. Similar traditions have evolved in each of the numerous cattle herding tribes across Africa (Poland *et al.* 2003). These are practicable solutions, evolved over millennia to quantify variations in mammalian pelage resplendent in bewildering manifestations of phenotypic plasticity. No serious academic study of pelage variation in wild bovids has extended what are in all respects time-worn and thus practicable taxonomies – this is likely due to the fact that in many instances of colour variation among organisms has not been detectable when using neutral mtDNA markers. Thus, many biologists have tended to treat colour variation as a phenotypically plastic character, and so of limited evolutionary signal.

Compared to the extreme variation in fur colour and pelage patterns of domesticated bovids, those of wild antelopes are far more conserved. This is true of the *K. leche* complex, in which the principal

colour of the pelage ranges from the grey-browns, and bright reddish-browns of *K. anseli* and *K. leche* s.s. to the dark-brown and coal-black coat patterns of mature *K. smithemani* males. The dichromatic property of the fur of the *K. leche* complex is not as marked as that evident in many antelopes, such as alcelaphines (Ansell 1968, Cotterill 2005). In the case of *Damaliscus*, this variation necessitated quantification of both extremes in this dichromatic sheen - the brun-argente - against standardized colour codes (Cotterill 2003a).

7.1.4 Selection of Molecular Characters

The first studies that utilised direct sequences of genetic markers to study the diversity of the Artiodactyla focused on coding and non-coding genes of the mitochondrial genome. Applications of portions of the non-coding, relatively fast-evolving Control Region are discussed in the previous chapter (the subject of a detailed study of variation in this marker in the *K. leche* complex). The ribosomal and cytochrome *b* (*cyt b*) mtDNA regions have become commonly utilized marker and have also been applied with some success to this group (Gatesy *et al.* 1997; Matthee & Robinson 1999a). The *cyt b* marker was also employed by Birungi & Arctander (2001) to obtain a molecular phylogeny of the Reduncini. This study sequenced the entire 1140 bp of *cyt b* to conclude diversification among the *K. leche* complex confers with interpretations of the morphological evidence and the subspecific classification was recognized.

Matthee *et al.* (2001) developed several complementary nuclear markers to resolve uncertainties in the deeper topology of bovid phylogeny. These leant on the burgeoning genomic study of *Bos taurus* to detect QTL's (quantitative trait loci) in the cow genome, which in turn enabled the development of primers to sequence introns of nuclear genes. Typically of nuclear markers, these have all evolved approximately three times slower than mtDNA protein coding markers (Matthee & Davis 2001). Based on variation among other reduncine taxa, only intron 1 of the SPTBN gene was judged a possible candidate marker to sequence in this study. Reading of the literature revealed three candidates that appeared to exhibit comparatively rapid rates of evolutionary divergence. Two of these candidate markers included Intron-7 of the β -Fibrinogen as applied by Seddon *et al.* (2001) in a phylogeographic study of Palaearctic insectivores (Hedgehogs, *Erinaceus europaeus* and *E. concolor*) and Protamine 1 (Van Den Bussche *et al.* 2002). A concerted effort was applied to sequence a male haplotypic marker in lechwes, and in the present study it was decided to target the 3' portion of the protein-coding SRY gene on the Male-Specific-Region of the Y-chromosome. The SRY of the Bovidae has received attention with respect to its control on sex determination, and comparative variability exhibited across mammals (Payen & Cotinot 1994; Daneau *et al.* 1995; Pamilo & O'Neill 1997; Cheng *et al.* 2001).

Whitfield *et al.* (1993) suggested that SRY has evolved relatively rapidly in mammals. Clawson *et al.* (2004) quantified slight variation in SRY amongst breeds of North American cattle, and the paternal marker demonstrated male introgression between Asian cattle (Kikkawa *et al.* 2003). This previous research on domestic bovids motivated a review of variation in the SRY of reduncine antelopes, to establish if it could reveal complementary aspects of evolutionary history in the *K. leche* complex, characterized by maternally inherited mtDNA markers.

7.2 SPECIMENS AND METHODS

7.2.1 Type Material and Taxonomy

It is pertinent to first review type material and type localities for named taxa of the *K. leche* complex, especially given historical uncertainties attached to the provenance and locations of critical specimens. Pertinent taxa are listed in order of time of publication. For convenience, this nomenclature follows the taxonomic scheme of Cotterill (2005) and the conclusions of this study, further explicated in this chapter.

Order **ARTIODACTYLA** Owen, 1848

SubOrder **RUMINANTIA** Scopoli, 1777

Family **BOVIDAE** Gray 1821

Tribe **REDUNCINI** Knottnerus-Meyer 1907

Genus ***Kobus*** A. Smith, 1840 [= *Cobus* Buckley 1876]

(includes *Adenota* Gray 1847; *Hydrotragus* Fitzinger 1866; and *Onotragus* Gray 1872)

***Kobus leche* Gray**

Adenota lechè Gray 1850 *Gleanings Menagerie Knowsley Hall* 2: 23

The reliable provenance of this taxon is well established (Spinage 1995), but *K. leche* is historically extinct at the type locality, after dessication of Lake Ngami (Smithers 1971, Chapter 2). The Holotype comprises a nearly complete flat skin, in excellent condition; and skull base of an adult male, with horns (BM 1850.7.4.2). The nearly complete skull of an historical specimen of *leche* (CUMZ H22.682 adult %) constitutes a Topotype; as does the complete skull (MNKB 3501 adult %) preserved in the Von Humboldt Museum, Berlin (Appendix 1). The latter was collected by pioneer ornithologist S. Wahlberg. Another pioneer ornithologist C. J. Andersson visited Lake Ngami in August-September 1853 (Dean *et al.* 2006), where he collected lechwe specimens around Lake Ngami and along the Taoghe River (Andersson 1856); but the locations of these specimens await discovery, if they indeed still exist.

***Kobus smithemani* Lydekker**

Cobus smithemani Lydekker 1900 *Proc. Zool. Soc.* 1899: 982

The prospector F. J. Smitheman travelled in the Bangweulu region in 1897-1898, where he collected the first specimen of the Black lechwe. It was shipped from Barotseland to the BM(NH) to be described by Russell Lydekker, who gave the type locality as "...the neighbourhood of Lake Mweru". Erroneous references to *K. smithemani* occurring around Lake Mweru persisted in early literature, but this is quite wrong. Ansell (1968) concluded there was convincing historical evidence that in August 1898, Smitheman travelled around Chitambo, where the explorer David Livingstone had died in 1873. There is no evidence that Smitheman collected anywhere else in northeast Zambia. As Hughes (1933) recorded Black lechwes in abundance further north of Chitambo in the early 20th century, the type locality of *smithemani* was further restricted to the vicinity of Chitambo in the grid square 1230a1, southwest Bangweulu basin (Ansell 1978: 58).

***Kobus leche amboellensis* Sokolowsky**

Adenota amboellensis Sokolowsky 1903 in Baum, *Kunene-Sambesi Expedition* pg 535.

Sokolowsky (1903) described this taxon from southern Angola, considering it distinct from nominate *leche*. Ellerman *et al.* (1953: 195) restricted the type locality of *amboellensis* to "The Kubango River, between the Kueio and the Quatiri (approximately 17° S., 18° 30'E), southern Angola". Crawford-Cabral & Mesquitela (1989) stated the type locality to be: "Confluencia do Luassingua com o Longa", and Crawford-Cabral (1967) earlier suggested *amboelloensis* could be a valid subspecies. As discussed below, *amboellensis* is treated as a synonym of *K. leche* Gray.

***Kobus robertsi* Rothschild**

Cobus robertsi Rothschild 1907 *Proc. Zool. Soc* 237

The provenance and type material of *Kobus robertsi* has been the source of mystery soon after its original description. Ansell (1974) recalls how as a young lieutenant, Colonel O. E. Wynne was tasked in January 1913 by Lydekker and Blaine to collect a specimen of Robert's lechwe for the BM(NH) mammal collection as the original type had been lost. Wynne subsequently collected BM 13.11.27.1 on 7th October 1913 from the Luongo River (Appendix 1). Thus, the type locality was restricted to 10° 35'S, 28° 59'E by Ansell (1974).

The identity, provenance and current whereabouts of the Holotype (a mounted head) lies at the centre of persisting mystery. Recent research by Dr P. J. Grubb on Lord Rothschild's correspondence, archived in the BM(NH) has clarified the identity of the collector, Mr Frederick Russell Roberts who

collected and sold the original specimen to Rothschild (through the taxidermists Rowland Ward). Nonetheless, the holotype cannot be traced as of 2004 (P. J. Grubb *in litt*). A mounted head, this Holotype was exhibited at Tring, where it was seen by Ansell (1974) who identified as a mis-labelled specimen of *K. smithemani*. This specimen appears to have been moved from Tring to the Wandsworth storeroom of the BM(NH) in London (P. J. Grubb *in litt*). It is listed in the BM(NH) catalogue (Tring mammal collection) as “*Cobus robertsi* %head 39.4671”. This is presumably the same specimen, that Ansell (1974: 20) mentioned that he saw labelled “Robert’s Kob, *Cobus robertsi*, N. E. Rhodesia” (his misquoted number BM 39/3671). This specimen cannot now be located in the BM(NH) collections (P. J. Grubb *in litt*). All literature sources reiterate that the type of *robertsi* came from between Lakes Mweru and Bangweulu. Lydekker (1908) considered *robertsi* an immature *smithemani*; but later noted that Lord Rothschild has informed him that “*C. robertsi* appears, indeed, to come closer to *C. leche* than to *C. smithemani*; and is found in company with the former, from which it differs” Lydekker (1911: 12). This conclusion was reinforced by Blaine’s and Wynne’s specimens from the Kalungwishi and Luongo rivers, respectively (Lydekker & Blaine 1914: 249).

The practicable solution to this problem has been to continue to follow Lydekker (*op. cit.*) and Ansell (1974), and apply *robertsi* as the name available for the now extinct population of lechwe that occurred through the Luongo-Kalungwishi drainage systems (collectively named the Pambashye Swamps). Nevertheless, the Holotype of *robertsi* might still exist, and is presumably the mounted head seen at Tring by Ansell (1974), but identified as a *smithemani*, which cultivates the suspicion that Rothschild’s *robertsi* might indeed be a synonym of *smithemani*. This would mean that the extinct population of the Pambashye Swamps has actually vanished undescribed! On going historical research on Joseph Edward Hughes (1876 - 1935) who wrote the classic *Eighteen Years on Lake Bangweulu* (Hughes 1933) might hopefully clarify where F. R. Roberts travelled and collected in northeast Zambia. This was probably in 1903 (P. J. Grubb *in litt*). The Neotype (BM 13.1.7.11) formed the single representative of this taxon in morphometric comparisons of male lechwe in this study, following on Ansell & Banfield (1979). Two flat skins were also studied. DNA from BM 13.1.7.11 was successfully amplified for markers used in the genetic section of this study, and in the phylogeographic study alongside two other specimens (Chapter 6).

***Kobus leche notatus* Matschie**

Onotragus leché notatus Matschie 1912 Deutsche Jger-Zeitung 59: 119.

The type locality was given as “Caprivi Zipfel, which requires further restriction to either the Okavango or Cuando rivers. Matschie (1912) did not specify which specimens amongst at least two

candidates constituted the type of *notatus*. Neither could the actual holotype be identified in the MNKB in February 2004. I examined skulls of two males (MNKB 23374 and 23399) collected by Kaufmann, as described by Matschie (1912). Although type material obviously exists, the holotype could have been designated separately (on a label) as the mounted head of the Red lechwe illustrated in Fig. 83 of Matschie (1912: 117). It would be premature to designate one of these skulls as a Lectotype until further archival research clarifies this situation. This might also restrict the type locality with respect to Kaufmann's collecting localities. As discussed below, *notatus* is treated as a synonym of *K. leche* Gray.

***Kobus kafuensis* Haltenorth**

Kobus leche kafuensis Haltenorth 1963 *Klassifikation der Säugtiere, Artiodactyla* 1 (18): 93

Based on the middle figure of an adult male depicted on Plate V in Ansell (1960), Haltenorth (1963) named the Kafue lechwe as *kafuensis*, but designated no other type material. Ansell (1969) subsequently designated as Lectotype the flat skin of the adult BM 61.727 % from which was painted the illustration in Ansell (1960). Naming biological taxa after rivers can propagate considerable nomenclatural and biogeographical confusion. Names such as *congolensis*, *zambeziensis*, and pertinently *kafuensis* are cases in point. So the type locality of *kafuensis* is restricted to the collecting locality of the lectotype at Lochinvar Ranch ~15°48'S, 27°16'E.

***Kobus kafuensis grandicornis* Ansell**

Kobus leche grandicornis Ansell 1964 *The Puku* 2: 10

Prior to elucidating their respective status, Ansell (1960) originally thought *robertsi* might be the available name for the Kafue Flats population. Ansell (1964) described the variation of *grandicornis* based on a representative hypodigm of specimens and closely studied populations. The Holotype is the flat skin and complete skull of an adult male (NMZB 5001), with the type locality fixed at ~15°48'S, 27°16'E. It is quite clear that *grandicornis* is a synonym of *K. kafuensis* Haltenorth 1963.

***Kobus anselli* Cotterill**

Kobus anselli Cotterill 2005 *J. Zool., Lond.* 265: 119

Cotterill (2005) provided a full description based on the hypodigm totalling 35 specimens, including the Holotype - a complete skull and flat skin, FMNH 27571 % (erroneously typeset as a / in the original description). The type locality is fixed at Katobwe 8°44'S, 26°05'E in the Kamalondo depression.

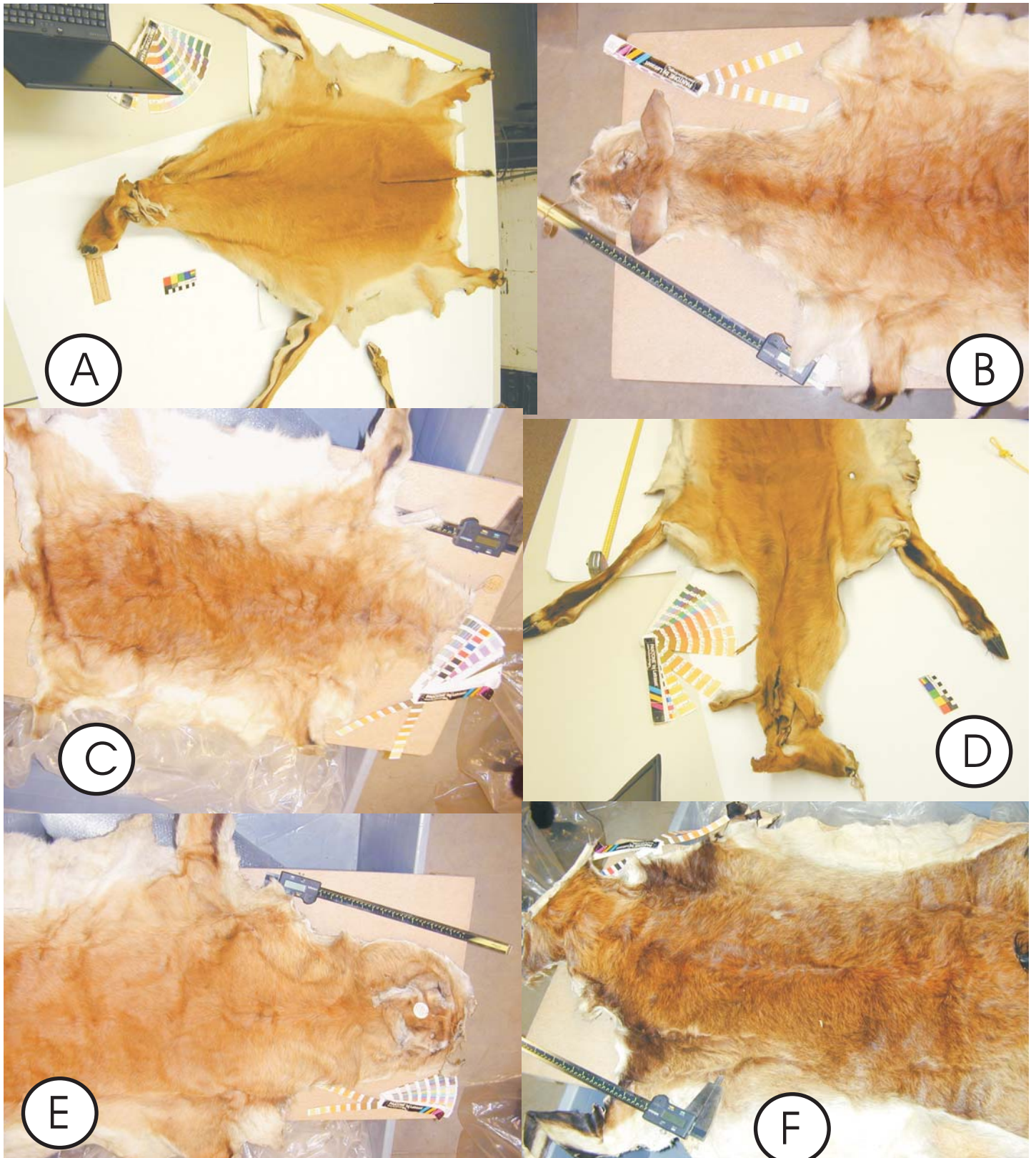


Figure 7.1. Comparisons of flat skins of five specimens of Upemba lechwe, *Kobus anselli* (A FMNH 27571 ♂ Holotype; B, MRAC 18275 ♀; C 18277 ♀ & D, FMNH 27574 ♂; E MRAC 18281 ♂) and one specimen of *K. robertsi* (F, RMAC 8811 ♂). Note that the white throat stripe is reduced or entirely absent in *K. anselli*, and the leg stripes are reduced in the latter compared to *K. leche*. Specimens in FMNH and RMAC photographed by courtesy of the Field Museum of Natural History, Chicago and the Royal Museum of Central Africa, Tervuren, Belgium, respectively.

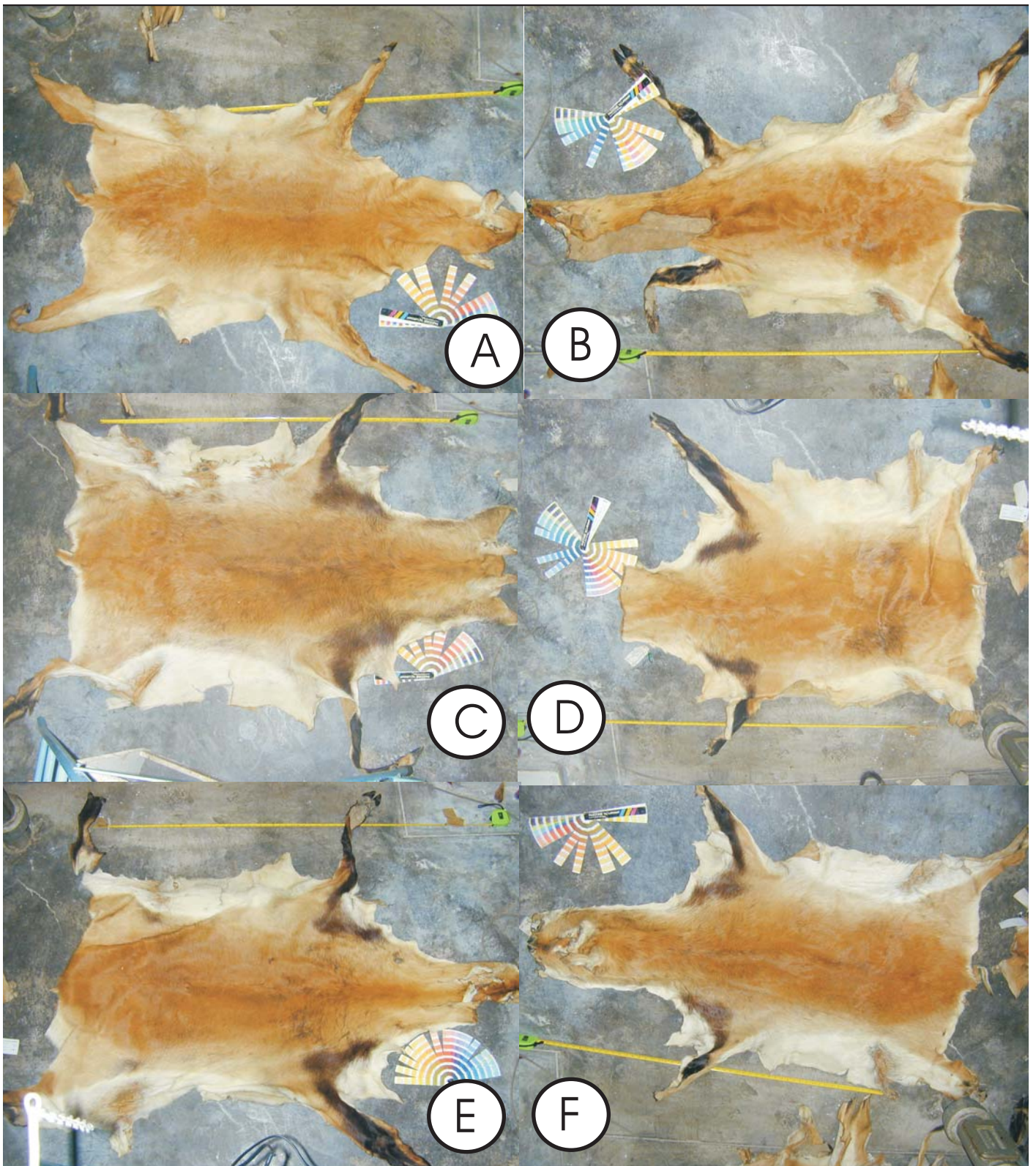


Figure 7.2. Comparisons of flat skins of six specimens of Kafue lechwe, *Kobus kafuensis* (A, NMZB 5003 ♀; B, NMZB 13651 ♂; C, NMZB 4613 ♂; D, NMZB 5008 ♂; E, NMZB 5004 ♂; and F, NMZB 8830 ♂). Note the sexual dimorphism in the dark shoulder patches, absent in the adult female.

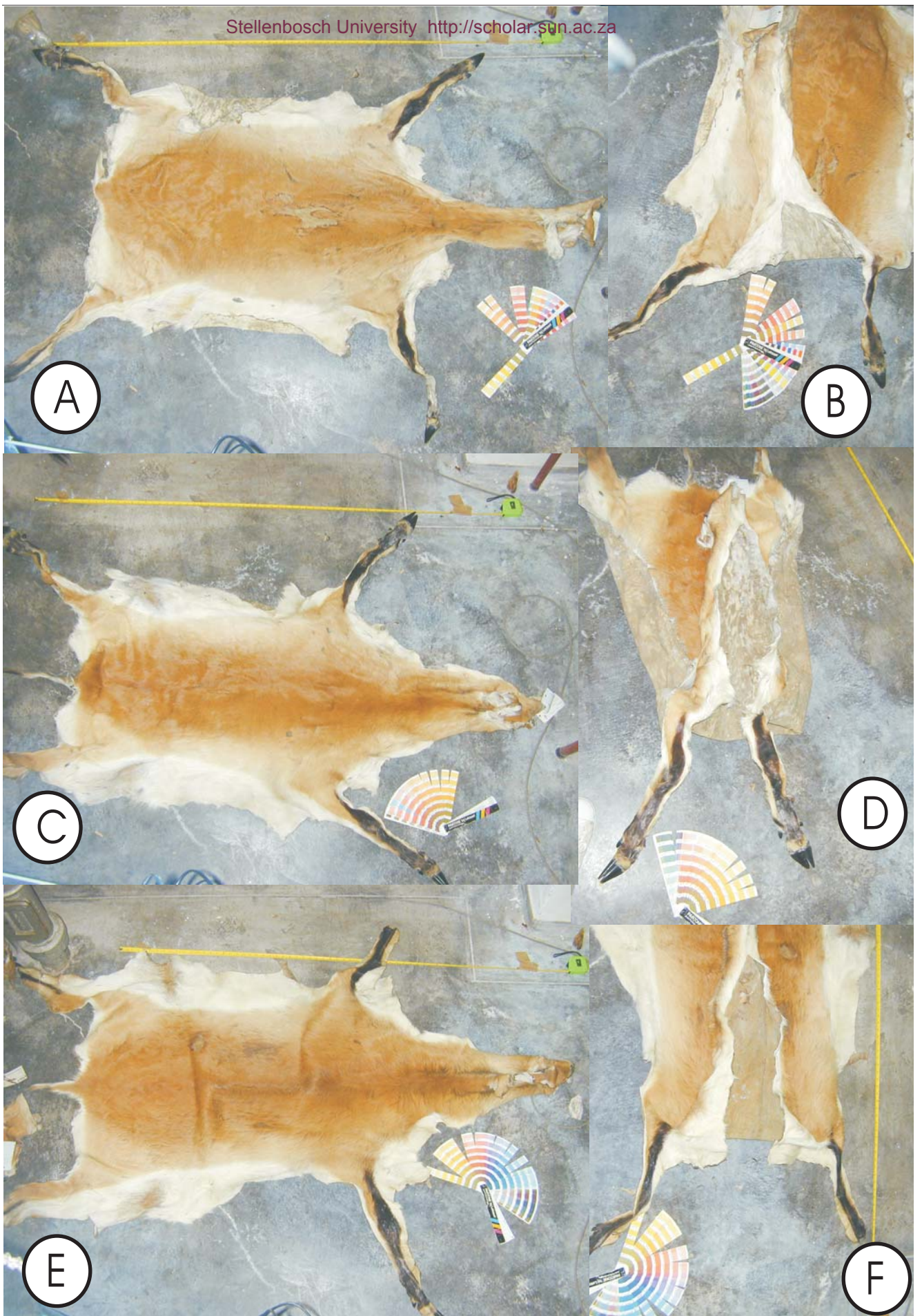


Figure 7.3. Comparisons of flat skins of three specimens of Red lechwe, *Kobus leche* (A & B, NMZB 50588 ♂; C & D, NMZB 56370 and E & F, NMZB 5067). The white throat stripe is quite distinctive in each specimen.

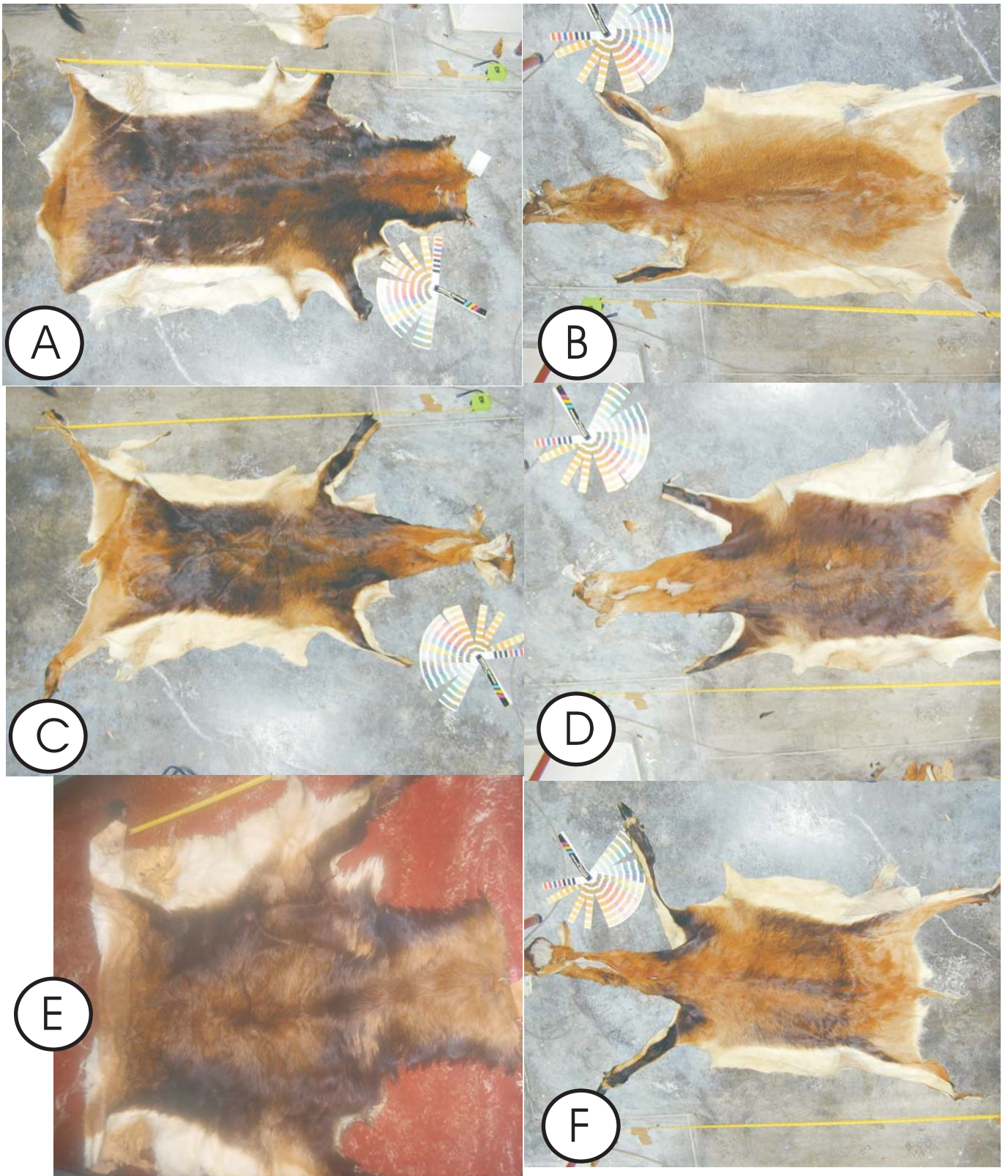


Figure 7.4. Comparisons of flat skins of six specimens of Black lechwe, *K. smithemani* (A, NMZB 11142 ♂; B, NMZB 5224 ♀; C, NMZB 1776 ♂; D, NMZB 1777 ♂; E, BM(NH) 99.2.22.1 ♂ Holotype; and F NMZB 2757 ♂).

7.2.2 Morphology - Museum Specimens and Cranial Characters

I examined lechwe specimens (*Kobus leche* complex only) in the collections of the Amathole Museum (KM, formerly Kaffraian Museum), American Museum of Natural History, New York, USA (AMNH), Cambridge University Museum of Zoology, Cambridge, UK (CUMZ), Field Museum of Natural History, Chicago, USA (FMNH), Royal Museum of Central Africa (Musée Royale d'Afrique Centrale), Tervuren, Belgium (MRAC), Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe (NMZB), The Natural History Museum (BM(NH)), National Museum of Natural History, Smithsonian Institution (USNM) and the Transvaal Museum (TM). These are preserved as flat skins or skulls, or both. Statistical analyses focussed on the far more abundant material available for adult male lechwes (due to trophy hunting). Sample sizes were reduced further by incomplete skulls, damaged by broken braincases, nasals, or premaxillae. Adult males were categorized by completeness of horn growth, and complete eruption of premolars, following Ansell & Banfield, (1979). Out of 343 specimens examined, skulls of 171 adult males were selected (subject to age and their relative completeness) for univariate and multivariate analysis. Females were not considered in morphometrics, given very patchy representation in collections. Also no less than 30 full taxidermic mounts of males were also excluded. (Taxidermists are notorious for interchanging capes, horn sheaths, and skulls of antelopes to create trophies of composite provenance!) The total sample of measured skulls thus included 15 *anselli*, 76 *kafuensis*, 42 *leche*, 1 *robertsi*, 37 *smithemani* and 15 *anselli* from: Angola, northeast Botswana, Zambia, and Katanga, DRC. Localities are cited as quarter degree squares, or where possible as degrees and minutes of latitude and longitude (Fig. 2.1, Appendix 1). Fifteen cranial measurements were taken with digital callipers to the nearest 0.1 mm (Table 7.1). An additional four horn measurements were taken to the nearest mm with a flexible steel tape measure. Horn Length (H) was measured along the front curve of the longest horn from lowest edge of the base to the tip, following Rowland Ward's Method 7 (Smith, 1990). Care was exercised to pass the tape over horn ridges and not press it into the crenulated horn grooves (Table 7.1). Records of Body mass, Body Length and Shoulder Height were collated from (Williamson 1979) and the field journal of Zimmer (1926-1927). This has allowed comparisons of the overall body proportions and body masses of four populations.

7.2.3 Quantification of Pelage Variation

Comparisons of the pelage patterns and fur colours of lechwe antelopes sought out an objective measurement that was repeatable across continents and under different light conditions. The apparatus developed by Taylor *et al* (1990) was not considered for this study, given its cost and lack of mobility. Where present, the extent of the darker blazes on shoulders or legs were scored, as were patterns of

pale and/or dark markings on the ears. The presence and extent of the paler throat stripe was scored on flat tanned skins and its narrowest width measured to the nearest 1 mm. Pelage colours reported for Upemba lechwes were also scored against a coded Letraset Pantone® colour chart under a fluorescent white light source, because the Munsell and Ridgway charts were not obtainable. Separate colour scores were recorded for: the dorsal region of the neck, the mid-back and rump, the contrasting colouration of the head, the darker markings along the legs, and shoulder patches (when present).

7.2.4 Statistical Analyses of Morphological Data

Statistical analyses used Statistica 6.0 (StatSoft). The mensural data was explored with univariate methods first to assess patterns of variation within and among taxa. Data were transformed to natural log values to meet standards for parametric statistical testing. Principal Components Analysis (PCA) of standardized data investigated patterns of variation within and among populations (Sharma, 1996; Tabachnick & Fidell, 1996). These PCAs differed in their inclusion of selected variables, allowing maximization of sample sizes, whilst comparing how PCAs differed in their retrieval of taxonomic patterns from the dataset. Comparisons of measurements used Multivariate Analysis of Variance (MANOVA) to test for significant differences within and between populations, and to assess contributions of morphometric variables and quantify morphological variation (Sokal & Rohlf, 1995; Tabachnick & Fidell, 1996). Stepwise Discriminant Function Analysis (DFA) discriminated taxonomically relevant variation among characters. Significant characters were selected from those that contributed little to the DFA, and thus could obscure useful signal from the data (Sharma, 1996; Tabachnick & Fidell, 1996).

7.2.5 Taxonomic Representation and Sequencing of Molecular Genetic Markers

DNA was obtained using the methods described previously. All procedures to amplify, sequence and process chromatograms of the selected gene regions utilised in this chapter follows those described in Chapter 6. Representative samples of the described taxa were selected for this study of phylogenetic relationships. These selected individuals of the *K. leche* complex are listed in Appendix 2. To improve the historic signal in the data, multiple representatives drawn from different geographic areas were included. In addition, I targeted museum specimens representing outlying localities and extinct populations. This included representative samples of Upemba lechwe, *K. anselli*. A number of Reduncines were used as outgroups; these included puku (*Kobus vardoni*), Defassa's waterbuck (*K. defassa*), common waterbuck (*K. ellipsiprymnus*) and the Nile lechwe (*K. megaceros*) (Birungi & Arctander 2001).

Table 7.1. Descriptions of cranial and horn measurements (with abbreviations) obtained from museum specimens of the *Kobus leche* complex.

Measurement	Abbreviation	Description
1 Horn length	H	Total length along the front curve of the longest horn, from lowest edge of the base to the tip (following Rowland Ward's Method 7, Smith 1990)
2 Horn spread	HS	Width across tips of horns
3 Horn curve	HBC	Direct length from horn tip to anterior base of horn sheath
4 Horn width	HW	Greatest width across horns
5 Greatest Skull	GSL	Total length of skull from anterior of premaxilla to posterior occipital condyles
6 Condylobasal	CBL	Posterior of occipital condyles to front of premaxilla
7 Basal Horn Width	HBW	Greatest thickness of right horn core measured at parietal
8 Basal Horn Spread	HBS	Outside width across horn cores measured across parietals; measured at bases of horn sheaths
9 Inner Horn Width	IHW	Width of separation between horn cores measured across parietals between horn cores
10 Interorbital	ITB	Minimum width across lachrymals measured across inside rim of orbits
11 Supraorbital Width	SW	Inner width between supraorbital foramina measured across inner edges of foraminae
12 Braincase Width	BW	Maximum width of braincase measured at parietal-temporal suture
13 Braincase length	BH	Minimum distance between coronal (fronto-parietal suture) and occipital processes
14 Nasal Width	NW	Maximum width of nasal bones - measured at posterior portion of nasals across frontal sutures
15 Nasal Length	NL	Length of nasal bones from posterior suture with lachrymals/frontals and premaxillary-maxillary suture
16 Zygomatic width	ZW	Greatest width across zygomatic arches perpendicular to longitudinal axis of cranium
17 Maxillary breadth	MB	Greatest width across buccal surfaces of maxillary tooth row
18 Maxilla Length	ML	Greatest length of maxillary tooth row; from rear of M ³ to anterior edge of P ²
19 Maxillary	CL	From front of anterior premolar (P ²) to tip of premaxilla
20 Premaxillae Width	PW	Greatest width across anterior portion of premaxillae perpendicular to longitudinal axis of cranium

Table 7.2. Details of the primer sequences used to amplify the mtDNA *cyt b* and nDNA SRY, SPTBN, α -fibrinogen and Protamine 1 genes of the *Kobus leche* complex

Gene Region	Primer Name	Sequence
Cyt <i>b</i> ¹	L14724	5'- CGAAGCTTGATATGAAAAACCATCGTTG -3'
	L14841	5'- AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA -3'
	H15915	5'- GTCATCTCCGGTTTACAAGAC -3'
	H15494	5'- GTGTAGTTGTCAGGTCTCC -3'
	H15149	5'- AAAGTGCAGCCCCTCAGAATGATATTTGTCCTCA -3'
	BvCyt <i>b</i> R*	5'- CTTTTCTGGTTTACAAGACCAG -3'
SPTBN ²	SPTBN 1F	5'- TCTCAAGACTATGGCAAACACGAAGACCTGTTACAGAAGCA -3'
	Int1F*	5'- GATTTAACAAGATGCTATAGGGTGG -3'
	Int2F*	5'- GTTCCTrAGTGACCsAAAAGAAAATAATAC -3'
	SPTBN 1R	5'- CTGCCATCTCCCAGAAGAA -3'
	Int1R*	5'- GTACTrAAGGrAAAGATrGGTCCATTTcAGAAAwG -3'
	Int2R*	5'- CCATTCATrCAAAGTGCAGGGyCAC -3'
SRY ³	SRY-F 26404	5'- ACAGAGACTACTAGCCATACAC -3'
	HMGFnew*	5'- GAGACAAATACCCGGGCTATAAATATCGACCTC -3'
	CDSF*	5'- GAKTTCCTTACTCTCGCTAACAAAGGCrCkC -3'
	SRY-2200F*	5'- CTAGCTACTTTCCACCTCyTTGTAAATTGCAGG -3'
	SRY-R 26414	5'- CAATTTTTCTACTTTAGCCTA -3'
	SRY-1900R*	5'- CTTmkTATAAAATTAAGTCGsAGGTGAAAyTGTAG -3'
	SRY-2200R*	5'- GGCTTTTTcACAGTGGGAACAAAAGrCTATAAACTG -3'
	SRY-ERnew*	5'- CCAAAAAAGKGAKGCTTYCTTTGCAAGCTG -3'
Beta-fib ⁴	BFIBR1	5'- ATCACAACGGCATGTTCTTCAG -3'
	BFIBR2	5'- AANGKCCACCCAGTAGTATCTG -3'
Protamine 1 ⁵	Prot1F	5'- ACCTGCTCACAGGTTGGCTG -3'
	Prot1R	5'- GTGGCAAGAGGNTCTTGAAG -3'

¹Irwin *et al.* (1991); ²SPTBN Matthee & Davis (2001); ³SRY Clawson *et al.* (2004); ⁴Seddon *et al.* (2001); ⁵Adroer *et al.* (1992); *designed in this study

complete mitochondrial cytochrome *b* (mtDNA *cyt b*) gene (1140 bp); intron 1 of the B-spectrin non-erythrocytic (SPTBN) nuclear gene (815 bp); intron 7 of the α -fibrinogen gene (657 bp); the nuclear coding region of Protamine 1 (355 bp); and the nuclear coding region of the sex-determining region (SRY) gene and its adjacent 3' non-coding region (totaling 1278 bp).

In order to reconstruct phylogenetic relationships within the *Kobus leche* species complex, I targeted both mitochondrial and nuclear DNA (nDNA) gene regions in order to carry out a combined analysis using data derived from two genomes. To this end I sequenced the following gene regions: the Sequencing of *cyt b* employed the universal primer sets of Irwin *et al.* (1991). In addition, a lechwe-specific reverse 3' primer, BvCytbR, was developed to amplify DNA from museum specimens that failed with H15915 (Table 7.2). The primers SPTBN1F and SPTBN1R were employed to amplify the entire sequence of intron 1 of SPTBN, following Matthee *et al.* (2001). Internal primers were designed to facilitate amplification of SPTBN-1 from museum DNA (Table 7.2). Sequencing of intron 7 of the γ -fibrinogen gene followed Seddon *et al.* (2001), while the coding region of the Protamine 1 gene followed Adroer *et al.* (1992) reported in van den Bussche (2002).

Sequencing of the SRY gene of lechwe proved more challenging. Trials with the published primers (Clawson *et al.* 2004) only worked for the 5' section below the HMG box. An alignment was assembled, using representative Genbank sequences of the SRY (~700 bp) and adjoining 3' stretch of non-coding sequence (~1000 bp). The taxa represented by SRY sequence comprised one representative of the Perissodactyla, *Equus caballus* and six species of Cetartiodactyla, *Bos taurus* (AB039748 and AF148462), *B. bubalis* (AY189027), *B. grunneus* (AF148463) *Capra* (D82963), *Ovis aries* (Z30265) and *Sus scrofa* (AY842547). In the penultimate products of this development, three primer pairs were designed to bind to the most highly conserved regions in this alignment. The initial set of primers (20-25 bp) lacked specificity; and in fact only non-target DNA amplified after concerted effort. It was found that longer primers (30-35 bp), with higher annealing temperatures (Table 7.2), proved successful in the amplification of this single-copy, haplotypic marker in the nDNA genome. Matching the latter set of primers using the BLAST program against GenBank sequences confirmed their specificity for the target Y chromosome region.

Statistical Analyses of Molecular Characters

Multiple overlapping sequences were read from both forward and reverse strands and manually aligned against reference sequences from GenBank for each data set. Pairwise comparisons of observed sequence differences, nucleotide composition and the number of transitions and transversions in each sequence set were calculated in MEGA version 3.1 (Kumar *et al.* 2004). Where appropriate, sequences were translated into amino acids in MEGA version 3.1.

Due to the lack of parsimony informative sites in the SRY, γ -fibrinogen and Protamine 1 gene regions for the *K. leche* complex (see Appendices for sequence alignments G2-6), phylogenetic analyses used

the *cyt b* and SPTBN data sets (see further comments in Results). The alignment of *cyt b* sequences was augmented by complementary CRHV1 sequences (Chapter 6) for each of the 48 individuals in a Bayesian analysis. An ILD test was performed in PAUP* 4.0b10 to confirm the feasibility of combining the *cyt b* and SPTBN alignments. Maximum parsimony and neighbour-joining (NJ) distance methods were used for phylogenetic analyses. Maximum parsimony analyses used the full heuristic search option with 100 replicates and TBR branch swapping in PAUP* 4.0b10. The distance analysis incorporated maximum likelihood parameters, the optimal evolutionary model and model parameters were first estimated applying Akaike information criteria (AIC, Akaike 1974) in MODELTEST 3.06 (Posada & Crandall 1998). Genetic distance matrices were then generated using the optimum model parameters and used to estimate distance trees by the neighbour-joining method (Saitou & Nei 1987) in PAUP* 4.0b10. Levels of node resolution were evaluated by 1000 bootstrap iterations.

Based on inconclusive results of the maximum parsimony and NJ analyses, a Bayesian analysis employed MrBayes 3.1.1 (Huelsenbeck & Ronquist 2001) in an attempt to resolve relationships within the *K. leche* complex, with *K. megaceros* as outgroup. The partition function was applied in MrBayes to analyse a composite dataset combining 48 *cyt b* sequences (1140 bp) and complementary CRHV1 sequences (561 bp) for selected individuals (Appendix 2). The analyses employed 6 rate changes, a proportion of invariable sites and a gamma distribution. Based on the average standard deviation of the split frequencies, convergence was reached only after 30 million generations. This analysis was repeated twice, but only two runs reached 35 million generations, where the standard deviation dropped under ~0.07. An overlay plot of the log-likelihood values from separate chains was obtained, and the burn-in estimated from the beginning of the plateau. Against this criterion, the first 40 000 runs were discarded as burn in. A NeighbourNet network analysis was also performed on this dataset, using the software program SplitsTree 4.3, as described in Section 6.2.6.

7.3 RESULTS

7.3.1 Fur Colours and Pelage Patterns

The pelages of tanned skins of adult specimens were compared. These totaled 18 *anselli*, 22 *kafuensis*, 38 *leche*, 2 *leche* (Luapula), 2 *robertsi*, and 35 *smithemani*, of which detailed quantification of colour variation compared the similarities and more subtle differences between *anselli* and *leche* (Table 7.3). This is considered a representative hypodigm given the skins available in museums. The extreme differences between *smithemani* and all other taxa confirm the conclusions of earlier authors (Allen 1963; Ansell 1968). Adult males of *K. kafuensis* are especially distinctive from all other populations, as

concluded by Ansell (1964) and Ansell & Banfield (1979). Representative individuals are compared in the colour plates (Figs 7.1 - 7.4). A standardized comparison of all available skins of *anselli* was compared against a sample of *K. leche* (Table 7.3a). Subject to constraints of sample size, the fur of the neck of *K. anselli* appears more uniform red, compared to topotypical *leche*, which tends to grey laterally and ventrally. The adult male *robertsi* (Fig. 7.1f) is readily distinguishable from all other lechwe taxa. Although represented by very few skins, the rich chocolate-red fur of *robertsi* is distinctly longer on the back and withers compared to all other lechwes. Moreover, both skins of adult male *robertsi* exhibits pronounced darkly coloured shoulder patches similar to adult *kafuensis* males (Figs 7.1 & 7.2).

7.3.2 Overall Morphological Comparisons

The overall proportions of the four taxa can be compared in Table 7.4 (no data is available for *K. robertsi*). Only meagre data are available for *K. anselli*, despite search of field and museum catalogues (W. Wendelen, *in litt.*). The information archived for the two FMNH specimens is part of detailed external measurements that had been preserved in the field by the collector to facilitate their taxidermy as full mounts (Zimmer 1926-1927: 116, 140-141). It is clear that *K. kafuensis* and *K. leche* are similar in overall size, with male *leche* on average slightly heavier (Williamson 1979). As pointed out by Allen (1963) and Ansell (1963), both sexes of *smithemani* are distinctly lighter in mass compared to *kafuensis* and *leche*; moreover, sexual dimorphism is not so pronounced in *smithemani*. Overall, *K. kafuensis* stands apart from all other taxa on account of the much longer horns of mature males (Table 7.5). Only three specimens of the Red lechwes on the Busanga Swamps (central Zambia) were found in collections, and only two are males included in this study. Nonetheless, the impression of observing several hundred live animals is that males present a distinct horn profile, and their horns are longer overall, compared to the Red lechwes of the Okavango and Linyanti systems. Insufficient specimen numbers has obviated testing this hypothesis in this study.

7.3.3 Cranial Variation

Comparisons of cranial characters reveal that the four populations of lechwes form distinct groups, which overlap in cranial and horn characters (Table 7.5). Scatterplots reiterate this pattern, although each population clusters into a recognizable group. But these are poorly defined by relatively high variation in these characters (Fig 7.5), which exhibit more distinct clustering in the PCA (Fig. 7.6). MANOVA demonstrated that all four populations are significantly different (Table 7.6). PCA (Table 7.7, Fig. 7.6) and DFA (Table 7.8, Fig. 7.8), confirm that *kafuensis* is the most morphologically distinctive lechwe in south-central Africa, as shown originally by Ansell (1964) and Ansell & Banfield,

(1979) contra Howard & Sidorowicz (1976). Comparisons using PCA demonstrated that *kafuensis* is most distinct compared to all other taxa, because this mainly reflects their distinct horn morphology. In addition to the MANOVA results (Table 7.6), Kafue lechwes are larger in all respects, especially when compared against *anselli* and *smithemani* (Tables 7.4-5, Figs 7.5-8). Subsequent analyses compared the four more similar taxa (*anselli*, *leche*, *robertsi* and *smithemani*). A coherently similar phenetic pattern was retrieved repeatedly in the series of PCAs (Fig. 7.6, Table 7.7). These differed in included variables, and their sample sizes of taxa varied. It is clear that *anselli* forms a distinct phenetic entity, which is most similar in skull shape and size to *smithemani*, and quite distinct from *leche*. It is interesting that the single specimen of Luapula *leche* clusters with topotypical *leche*, whilst *robertsi* appears more similar in cranial shape and size to *anselli* and *smithemani* (Figs 7.6-7). Mirroring the MANOVA results, the distinctiveness of *anselli*, *leche* and *smithemani* is especially apparent in a stepwise DFA (Table 7.8). Classification of the Luapula *leche* and *robertsi* specimens in the DFA corresponds with PCA results, albeit singular samples prohibit testing their significance (Fig. 7.8).

Multivariate analyses of skull morphology, notably PCA, reveal that *robertsi* is of equivocal status with respect to *anselli* and *smithemani*. Deficiencies of the singular sample aside, the Neotype of *robertsi* is clearly distinct in the cranial shape, and overall size, from *leche*, while the DFA suggested that *robertsi* is most similar to *anselli* with respect to cranial morphology (Figs 7.6-8). Nonetheless, based on comparisons of adult males representing all these taxa, the pelage of *robertsi* differs from *smithemani* distinctly (as originally confirmed by Ansell 1974) and is quite distinct from *anselli* (Figs 7.1-4). Above all, preserved material evidence (summarized above, see Ansell, 1974, 1978) confirms that an isolated population of “red lechwes” occurred in the Pambashye Swamps into the 20th century, isolated in the Pambashye Swamps (Upper Luongo and Kalungwishi drainage systems, Fig. 2.1). It is also interesting that all three skins of *robertsi* are quite distinct from the two preserved from the Luapula population. The single male specimen of the latter is more similar to large males of *leche* from the Okavango and Busanga Swamps, than to *robertsi*, *smithemani* or *anselli* (Cotterill 2005, Figs 7.6-8). It is, nonetheless, premature to draw firm taxonomic conclusions from such small samples.

7.3.4 Diagnostic Cranial Characters

Table 7.6 quantifies the relevance of single variables to distinguishing pairs of compared taxa. As is apparent when comparing live animals, the long horns of Kafue lechwe, with their sweeping profile, are diagnostic of adult males. This is demonstrated in the MANOVA comparing *kafuensis* against *leche*, which has significantly larger horns compared to *anselli* and *smithemani* (Tables 7.4 & 7.6).

Table 7.3a. Colours of the fur of selected flat skins of *K. anseli* and 1 specimen of *K. robertsi* against a selected sample of *K. leche*, compare scores against Letraset Pantone® colour chart.

Specimen	Taxon	ears red- brown	face red-brown	neck greyish-brown - red	mid back red-brown - red
RMAC 18281	<i>anselli</i>	465u	146u	1385u to 131u	1385u to 131u
FMNH 27571	<i>anselli</i>	124u	131u	145u to 131u	1385u to 139u
RMAC 18280	<i>anselli</i>	467u dark tips	146u	1395u	1395u
RMAC 18285	<i>anselli</i>	-	1395u to 153u	466u	1395u
RMAC 17959	<i>anselli</i>	-	-	466u	139u
RMAC 18284	<i>anselli</i>	-	-	138u	145u
RMAC 18282	<i>anselli</i>	-	-	146u to 131u	146u to 131u
RMAC 18282	<i>anselli</i>	-	-	145u	153u
RMAC 18274	<i>anselli</i>	139u	154u	153u to 131u	153u
RMAC 17958	<i>anselli</i>	145u	139u	145u	153u
RMAC 17960	<i>anselli</i>	-	-	145u	154u
RMAC 18275	<i>anselli</i>	465u	464u	465u	154u
RMAC 18565	<i>anselli</i>	465u	146u	1385u	154u
RMAC 18278	<i>anselli</i>	-	-	466u	154u
RMAC 18276	<i>anselli</i>	465u darker tips	464u	466u	154u
RMAC 18277	<i>anselli</i>	-	-	465u	1615u
RMAC 8209	<i>anselli</i>	-	-	146u to 161u	161u to 154u
RMAC 18279	<i>anselli</i>	465u	1395u	1395u	464u
FMNH 27574	<i>anselli</i>	131u to 125u	139u	139u to 131u	
FMNH 34469	<i>leche</i>	146u	139u	139u	139
FMNH 34466	<i>leche</i>	466u	146u	1395 to 452u	139u
FMNH 34468	<i>leche</i>	125u to 146u	139u	1395u to 465u	139u
FMNH 34467	<i>leche</i>	451u	146u	1395 to 452u	139u to 145u
FMNH 34471	<i>leche</i>	125u	1395u grizzled	145u	145u to 139u
RMAC 3057	<i>leche</i>	465u	139u	139u red-brown	145u to 139u
RMAC 8211	<i>robertsi</i>	-	-	139u	139u to 161u

Table 7.3b. Comparisons of pelage colouration and patterns of *Kobus leche* and *Kobus anselli*. Dichromic colours were scored for six different regions of tanned skins: head; throat; front legs; dorsum; flanks/belly. Samples size of specimens examined in parentheses.

Pelage	<i>leche</i> (n=30)	<i>anselli</i> (n=18)
Specimen details	FMNH 34461; 34466; 34469; 34468; 34467; NMZB 4434; 5066; 5067; 5492; 5493; 5494; 8359; 10166; 10167; 10167; 11933; 11934; 11967; 18729; 22518; 50586; 50587; 50588; 56370; 56372; 56373; 5491; 4613; 2751; 2753	MRAC 17958; 17959; 17960; 18274; 18275; 18276; 18277; 18278; 18279; 18280; 18281; 18282; 18283; 18284; 18285; FMNH 27574; 27571; 34471
Head	Red head (21) Light brown head (2) White eyebrow (3) White rings around eye (16) [No head (9)]	Red head (9) White eyebrow (9) White chin (9) [No head (9)]
Throat	Broad white stripe: 4-8+cm (24) [Missing (6)]	Narrow white stripe: 1-2cm (7) Red (11)
Front legs	Broad black strip up whole leg (22) Thin black stripe halfway up leg (8)	Thin black stripe halfway up leg (15) Thin black stripe up whole leg (3)
Dorsum	Pale red (5) Golden red (19) Red-brown (6)	Pale red (1) Red-brown (19) Pale red-brown/white belly (4)
Flanks/belly	Red-brown/grayish brown belly (30)	Red-brown/white belly (14)

FMNH - Field Museum of Natural History; NMZB - National History Museum of Zimbabwe, Bulawayo;
RMAC – Musée Royale d’Afrique Centrale

Table 7.4. Summary of cranial measurements (in mm) of 15 *Kobus anselli*, 75 *K. kafuensis*, 41 *K. leche* and 37 *K. smithemani*. All are adult males, including the neotype of *K. robertsi* and the single known male specimen from the isolated population of red lechwe south of Lake Mweru. Means \pm 1 SD, ranges, and sample sizes (in parentheses) are given for each variable for each population. For abbreviations see Table 7.1.

Measurement	<i>anselli</i>	<i>kafuensis</i>	<i>leche</i>	Luapula <i>leche</i>	<i>smithemani</i>	<i>K. robertsi</i>
H	546 \pm 74 410-667 (15)	712 \pm 49 588-812 (75)	575 \pm 47 500-694 (39)	520	529 \pm 40 412-600 (37)	449
HS	315 \pm 93 194-474 (15)	443 \pm 98 181-756 (74)	292 \pm 77 125-539 (39)	384	359 \pm 82 208-517 (35)	254
HBC	465 \pm 54 335-539 (13)	604 \pm 50 454-700 (60)	464 \pm 42 395-552 (32)	468	461 \pm 44 324-528 (35)	381
HW	404 \pm 56 339-520 (15)	513 \pm 69 357-756 (70)	397 \pm 50 282-545 (39)	400	402 \pm 53 317-550 (35)	332
HBW	35.2 \pm 2.6 32.0-40.0 (15)	43.3 \pm 2.4 37.2-49.7 (75)	42.2 \pm 3.1 35.6-49.0 (40)	43	36.3 \pm 2.1 31.6-40.6 (37)	35.9
HBS	112.1 \pm 2.9 107.7-117.0 (15)	123.2 \pm 5.5 110.7-136.4 (75)	126.0 \pm 5.2 115.8-139.8 (40)	134.9	113.8 \pm 7.3 100.0-128.2 (37)	119.3
IHS	50.9 \pm 7.1 40.0-62.8 (15)	55.7 \pm 6.1 41.9-69.3 (75)	61.1 \pm 5.9 51.3-75.5 (40)	60.4	56.6 \pm 7.8 47.2-73.4 (37)	69.6
ITB	87.2 \pm 3.8 78.7-91.5 (13)	97.1 \pm 6.0 85.0-113.6 (76)	95.0 \pm 5.7 84.3-107.3 (36)	104.1	91.9 \pm 4.5 82.8-105.2 (33)	88.5
SW	41.7 \pm 2.3 37.7-46.1 (13)	46.6 \pm 3.8 38.0-54.6 (76)	45.5 \pm 3.7 35.5-52.3 (41)	47.5	44.5 \pm 3.6 36.8-51.4 (36)	47.3
GSW	121.2 \pm 2.3 117.2-125.6 (13)	132.2 \pm 4.7 118.7-143.2 (59)	131.5 \pm 3.6 125.0-142.8 (31)	132.7	124 \pm 4.5 115.8-133.4 (31)	122
NW	29.9 \pm 2.0 27.6-33.4 (12)	36.1 \pm 3.6 28.3-43.4 (62)	31.0 \pm 3.0 24.6-40.0 (32)	26.7	32.3 \pm 2.6 26.9-36.8 (30)	25.8
NL	110.4 \pm 3.9 104.7-116.7 (13)	110.6 \pm 5.5 97.7-122.3 (58)	108.4 \pm 7.3 95.9-125.6 (30)	106.6	108.2 \pm 7.0 97.3-122.6 (28)	104.2
BW	77.7 \pm 3.0 73.0-84.5 (13)	80.8 \pm 3.2 72.3-89.9 (73)	80.6 \pm 3.3 75.6-88.5 (35)	79.5	75.9 \pm 3.5 68.9-82.2 (34)	74.4
BH	61.0 \pm 3.1 57.4-66.0 (10)	64.2 \pm 3.6 57.5-76.9 (69)	66.5 \pm 4.4 53.4-74.2 (32)	66.9	62.9 \pm 4.6 49.7-71.1 (33)	61.9
GSL	280.6 \pm 7.1 268.7-292.0 (10)	300.3 \pm 8.3 282.1-316.8 (54)	298.1 \pm 10.2 286.5-319.8 (28)	305.5	286.0 \pm 7.9 271.0-302.8 (28)	281.3
CBL	270.9 \pm 4.5 266.2-280.6 (12)	292.8 \pm 7.7 276.4-311.8 (54)	293.5 \pm 10.8 275.3-316.5 (26)	296.7	278.3 \pm 9.9 251.4-297.6 (28)	264.8
ZW	118.8 \pm 3.5 114.3-124.5 (10)	126.4 \pm 4.0 116.1-134.2 (73)	124.6 \pm 3.7 116.1-131.2 (34)	127.4	119.1 \pm 4.7 107.6-126.8 (32)	113.5
MB	68.9 \pm 2.3 66.0-73.6 (13)	74.1 \pm 3.0 66.9-81.2 (75)	72.1 \pm 2.7 65.9-77.6 (33)	77.1	69.3 \pm 2.6 64.6-73.6 (31)	63.3
ML	72.4 \pm 3.0 68.0-77.1 (13)	73.6 \pm 2.8 66.4-81.1 (75)	76.0 \pm 3.3 69.8-83.0 (34)	77.3	69.1 \pm 4.1 59.0-77.1 (32)	70.4
CL	82.8 \pm 2.8 78.8-87.0 (13)	90.2 \pm 3.8 82.4-96.8 (57)	87.6 \pm 4.5 80.3-97.6 (31)	90.5	87.2 \pm 3.5 80.7-93.3 (28)	82.8
PW	36 \pm 1.6 33.1-38.3 (12)	38.1 \pm 2.2 33.4-42.6 (53)	39.4 \pm 1.7 33.8-43.4 (28)	42.5	38.3 \pm 2.2 33.7-43.7 (26)	31.2

Table 7.5. Mean body masses and external body measurements of four species of lechwe antelopes, *K. leche* complex, summarized for each sex. Where possible only adults are reported, as these characters obviously vary with age and condition. Sources of data: Robinette & Child (1964); Grimsdell & Bell (1975), Ansell (1964), and Williamson (1979). The only data available from *K. anselli* were collected by J. T. Zimmer for FMNH 27571 and 27574. (Total range in parentheses.) [Sample size in square parentheses.]

Variable	Kafue lechwe		Red lechwe		Black lechwe		Upemba lechwe	
	<i>K. kafuensis</i>	%	<i>K. leche</i>	%	<i>K. smithemani</i>	%	<i>K. anselli</i>	%
Sex	//	//	//	//	//	//	//	//
Body Mass	78.7	102.9	71.3	112.7	70.1	89.3	-	-
	(61.6-96.9)	(86.5-127.7)	(52.0-89.0)	(87.5-135.0)	(64.1-73.2)	(76.4-102.3)		
Body Length	[83]	[38]	[54]	[22]	[137]	[23]		
	153	161	150	162	154	163	-	149, 157
Shoulder Height	[81]	[25]	[86]	[49]	[138]	[22]		[2]
	(150-164)	(161-169)	(134-162)	(150-175)	(149-158)	(153-173)		
Shoulder Height	97	104	95	104	89	94	-	93, 94
	(90-106)	(99-112)	(87-101)	(94-112)	(87-91)	(91-97)		
	[80]	[24]	[60]	[30]	[138]	[17]		[2]

Table 7.6. Breakdown of contributions of individual variables to significant differences in MANOVAs which compared 15 *Kobus anselli* against 75 *K. kafuensis*, 41 *K. leche*, and 37 *K. smithemani*. (Actual samples varied subject to representation for each variable, see Table 1). Overall tests of significance (Wilk's Lambda) are in square brackets. Levels of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; # $p < 0.0001$; NS not significant. For abbreviations see Appendix 2.

Character	<i>anselli</i> / <i>leche</i> [0.0267*]	<i>anselli</i> / <i>kafuensis</i> [0.0531#]	<i>anselli</i> / <i>smithemani</i> [0.0255**]	<i>kafuensis</i> / <i>leche</i> [0.1#]	<i>leche</i> / <i>smithemani</i> [0.0835***]
H	0.60 NS	48.62 #	5.27 *	63.3#	15.48 **
HS	1.09 NS	7.16 *	0.54 NS	31.7#	6.15 *
HBC	1.37 NS	40.90 #	2.67 NS	112.3#	1.03 NS
HW	0.74 NS	10.81 **	0.33 NS	34.5#	0.11 NS
HBW	67.3 #	112.38 #	13.77 *	0.777 NS	62.19 #
HBS	90.18 #	31.78 #	2.91 NS	7.16*	32.65 #
IHS	27.32 #	6.01 *	10.80 **	10.2***	0.35 NS
ITB	23.00 #	18.54 #	23.37 #	1.07 NS	4.17 *
SW	10.40 **	13.03 **	6.10 *	0.352 NS	0.94 NS
GSW	98.29 #	32.99 #	8.72 **	0.0139 NS	39.01 #
NW	3.37 NS	30.72 #	13.91 ***	17.6 ***	1.36 NS
NL	2.77 NS	0.75 NS	3.00 NS	2.31 NS	0.04 NS
BW	1.99 NS	2.68 NS	1.99 NS	0.0117 NS	13.49 ***
BH	23.31 #	5.39 *	3.62 NS	12.8***	8.57 *
GSL	26.95 #	43.47 #	4.95 *	0.794 NS	21.01 ***
CBL	33.98 #	62.47 #	7.73 **	0.0647 NS	24.14 #
ZW	27.47 #	29.21 #	1.04 NS	0.637 NS	21.74 #
MB	11.41 **	17.79 ***	0.69 NS	2.42 NS	10.16 **
ML	6.93 *	3.51 NS	3.65 NS	2.04 NS	29.47 #
CL	11.55 **	33.83 #	14.17 ***	3.72 NS	0.38 NS
PW	25.71 #	2.93 NS	11.39 **	4.46*	1.09 NS

Table 7.7. Factor loadings for 7, 11 and 5 selected variables, respectively, in the three different Principal Component Analyses (PCA) of *Kobus leche* specimens plotted in Fig. 4. Variance component of each variable in parentheses. The first PCA (Fig 7.6a) analysed 141 specimens including *K. kafuensis*. The second (Fig. 7.6b) and third (Fig. 7.6c) analysed totals of 59 and 67 specimens, respectively, from five populations of lechwe antelopes (excluding *kafuensis*). For abbreviations see Appendix 2.

Variable	PCA 1			PCA 2			PCA 3		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
H	0.123 (0.101)	-0.083 (0.247)	0.018 (0.022)	-	-	-	-	-	-
HS	0.288 (0.560)	0.095 (0.326)	-0.023 (0.037)	-	-	-	-	-	-
HBC	0.143 (0.137)	-0.064 (0.148)	0.027 (0.049)	-	-	-	-	-	-
HW	0.162 (0.176)	-0.036 (0.046)	-0.017 (0.021)	-	-	-	-	-	-
HBW	0.043 (0.012)	-0.069 (0.170)	-0.018 (0.022)	-0.0802 (0.194)	0.0691 (0.375)	0.0208 (0.065)	-0.0781 (0.245)	-0.0703 (0.479)	-0.0003 (0)
HBS	0.006 (0)	-0.036 (0.047)	-0.038 (0.098)	-0.0661 (0.131)	0.0060 (0.002)	0.0139 (0.029)	-0.0666 (0.178)	-0.0078 (0.006)	0.0060 (0.011)
IHS	-0.043 (0.0125)	-0.021 (0.0156)	-0.106 (0.752)	-0.1019 (0.312)	-0.0710 (0.396)	0.0238 (0.085)	-0.1096 (0.482)	0.0672 (0.438)	-0.0027 (0.002)
ITB	-	-	-	-0.0448 (0.060)	0.003 (0.001)	-0.023 (0.079)	-	-	-
SW	-	-	-	-0.0629 (0.119)	-0.0325 (0.083)	-0.0344 (0.177)	-	-	-
GSW	-	-	-	-0.0379 (0.043)	0.0151 (0.018)	-0.0005 (0)	-	-	-
ZW	-	-	-	-0.0306 (0.028)	0.0166 (0.022)	-0.0085 (0.011)	-	-	-
MB	-	-	-	-0.0239 (0.017)	0.0195 (0.030)	-0.0197	-	-	-
ML	-	-	-	-0.0359 (0.039)	0.0222 (0.039)	0.0295 (0.131)	-0.0386 (0.060)	-0.0207 (0.041)	0.0340 (0.335)
CL	-	-	-	-0.0268 (0.022)	0.0069 (0.004)	-0.0286	-	-	-
PW	-	-	-	-0.0337 (0.034)	0.0198 (0.031)	-0.0403	-0.0295 (0.035)	-0.0192 (0.036)	-0.0473 (0.652)

Table 7.8. Squared Mahalanobis Distances shown above the respective diagonals; and unbiased Mahalanobis distances (corrected for uneven sample sizes) below the respective diagonals for stepwise Discriminant Function Analyses (DFA) of lechwe specimens. These included (Fig. 7.8a), and excluded *Kobus kafuensis* (Fig. 7.8b), respectively. Single samples of *K. robertsi* and Luapula *leche* are excluded. Sample sizes in round parentheses. All values significant at $P < 0.0001$. Unbiased Mahalanobis distances were calculated using the formula of Marcus (1993) following Singleton (2002).

Discriminant Function Analysis 1 (Fig. 7.8a)				
[12 variables: HBW, HBC, ML, PW, IHS, HBS, MB, H, CL, HS, SW, HW]				
Taxon	<i>anselli</i> (n = 12)	<i>leche</i> (n = 22)	<i>smithemani</i> (n = 21)	<i>kafuensis</i> (n = 40)
<i>anselli</i> (n = 12)	-	22.4	8.51	30.92
<i>leche</i> (n = 22)	20.7	-	17.03	12.03
<i>smithemani</i> (n = 21)	7.78	15.73	-	24.53
<i>kafuensis</i> (n = 40)	20.75	11.1	22.7	-

Discriminant Function Analysis 2 (Fig. 7.8b)				
[10 variables: HBW, ML, GSW, IHS, HBS, PW, ZW, HS, HW, H]				
	<i>anselli</i> (n = 12)	<i>leche</i> (n = 22)	<i>smithemani</i> (n = 21)	-
<i>anselli</i> (n = 12)	-	25.71	12.25	-
<i>leche</i> (n = 22)	22.8	-	16.91	-
<i>smithemani</i> (n = 21)	10.82	14.98	-	-

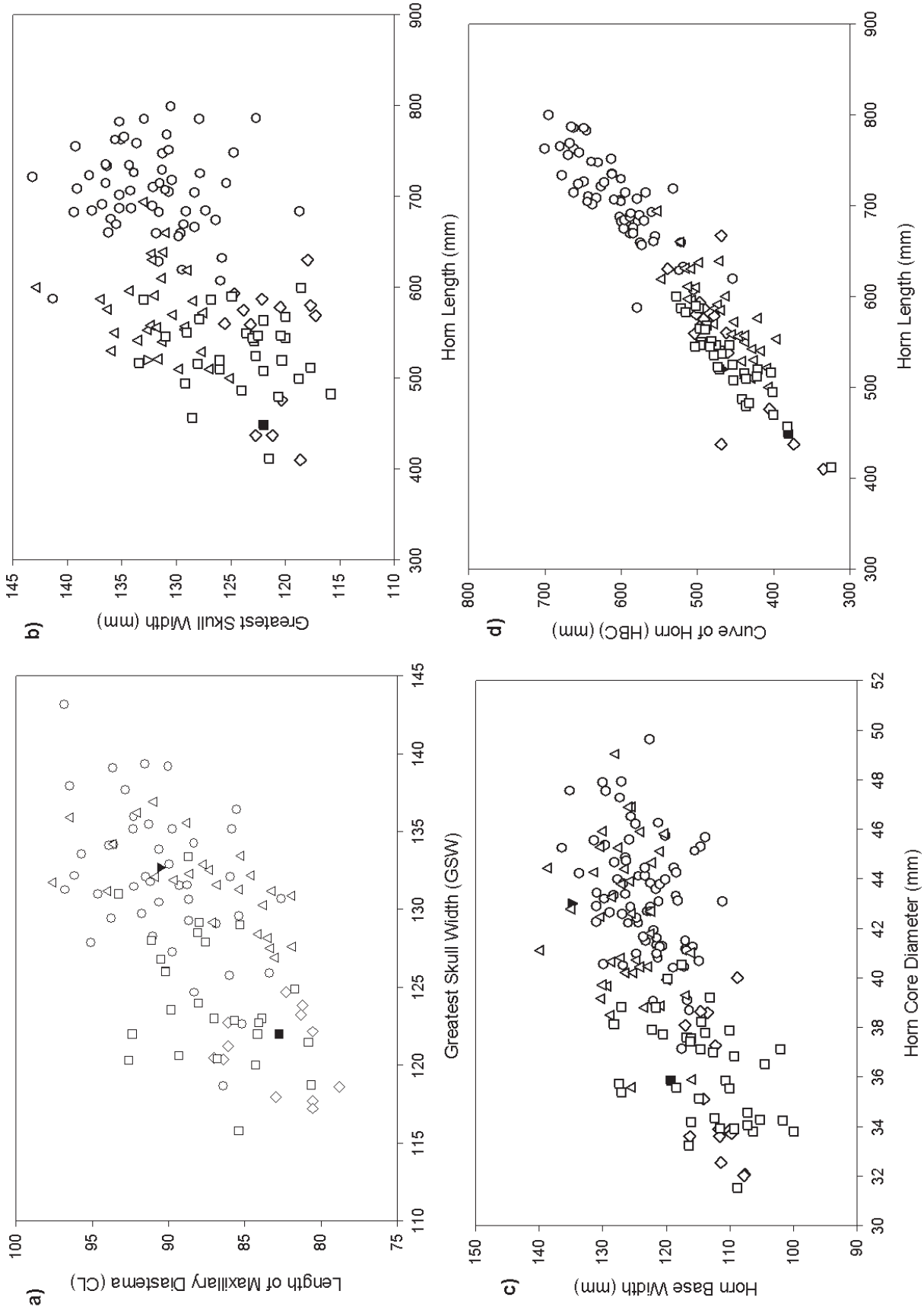


Figure 7.5. Scatterplots of selected variables for a total of 170 lechwe specimens. a). Length of Maxillary Diastema (CL) vs Greatest Skull Width (GSW). b). Greatest Skull Width (GSW) vs Horn Length (H). c). Horn Base Width (HBS) vs Horn Core Diameter (HCD), and d). Horn Curve (HBC) vs Horn Length (H).
 ○ *kafuensis*; ◇ *anselli*; △ *leche*; ▼ *robertsi*; ■ *leche*; and □ *smithemani*.

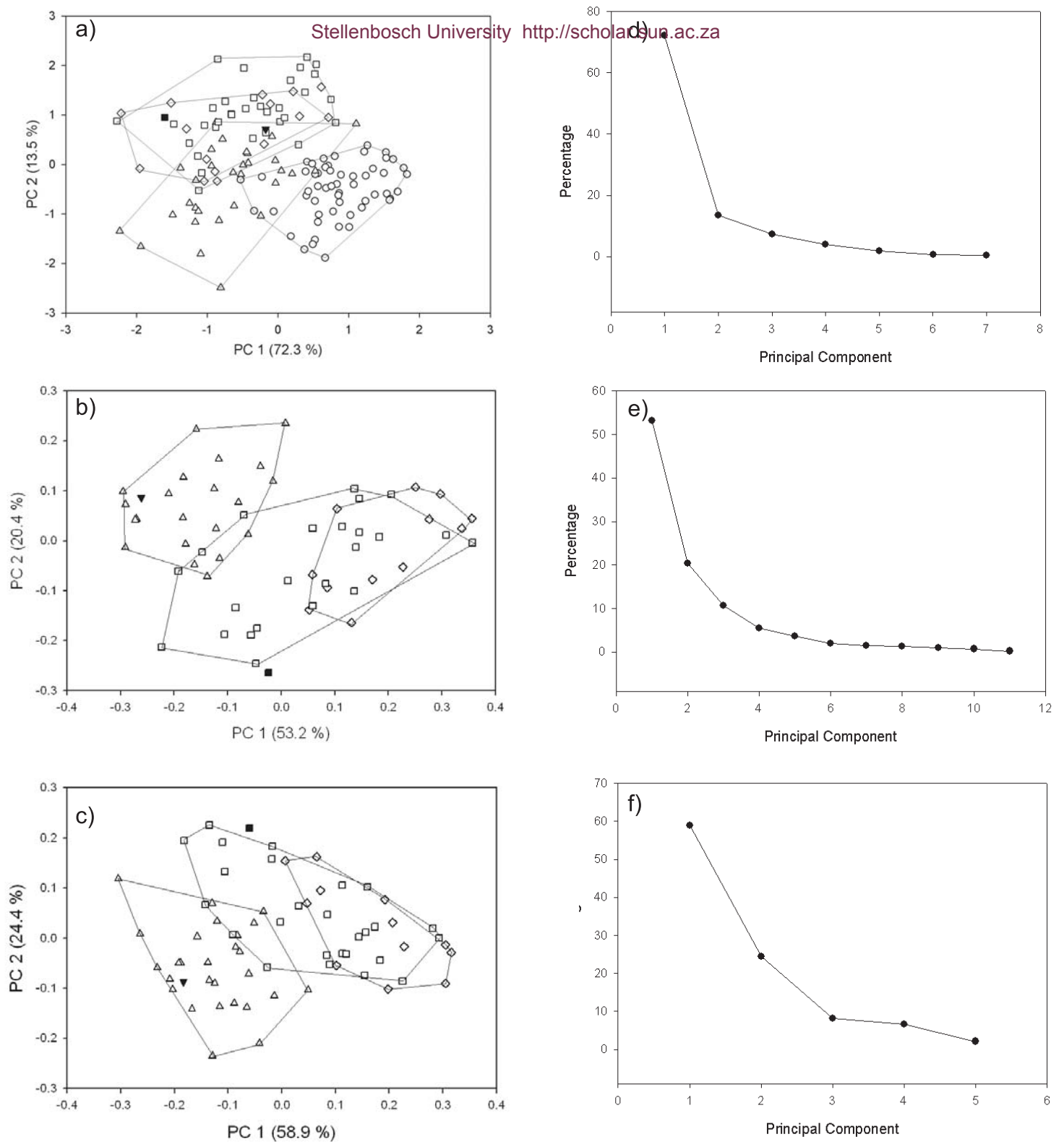


Figure 7.6. Plot of scores from Principal Component Analyses (PCA) of standardized log transformed data for selected taxa of lechwe antelopes. Factor loadings for variables listed in Table 7.5.

a). Scores for first two principal components accounting for a total of 80.3 % of the variation in 108 specimens from a PCA of six selected horn variables (H, HS, HBC, HW, HBS, IHS) for all six populations, including *kafuensis*, and all 15 *anselli*.

b). Scores for first two principal components accounting for total of 85.8% of variation in 59 specimens from a PCA of significant variables (HBW, HBS, IHS, ITB, SW, GSW, ZW, MB, ML, CL, PW) for five taxa, excluding *kafuensis*.

c). Scores for first two principal components accounting for a total of 83.3% of variation in 67 specimens from a PCA of significant variables (HBW, HBS, IHS, ML and PW) for five taxa, excluding *kafuensis*.

○ *kafuensis*; ◇ *anselli*; △ *leche*; ▼ *Luapula leche*; ■ *robertsi*; and □ *smithemani*.

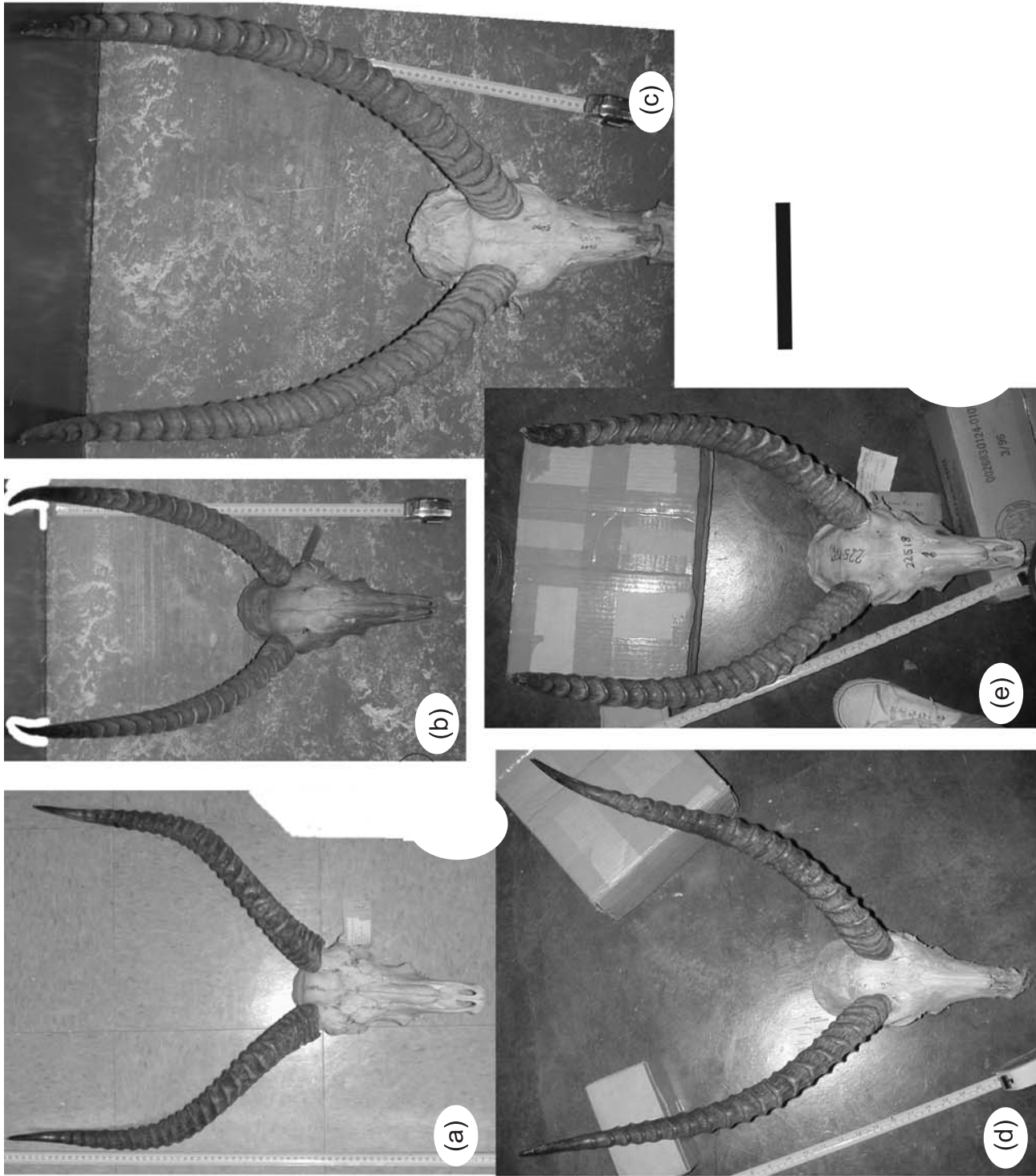


Figure 7.7. a) Comparisons of skulls of adult males of the *Kobus leche* complex: *K. anselli* (FMNH 27571 Holotype); b) *K. robertsi* (BM 13.11.27.1 Neotype); c) *K. kaffuensis* (BM 61.727, Lectotype); d) *K. smithemani* (NMZB 1776); and e) *K. leche* (NMZB 22518). Scale bar = 20cm. BM(NH) and FMNH specimens photographed by courtesy of The Natural History Museum, London, and Field Museum of Natural History, Chicago, respectively.

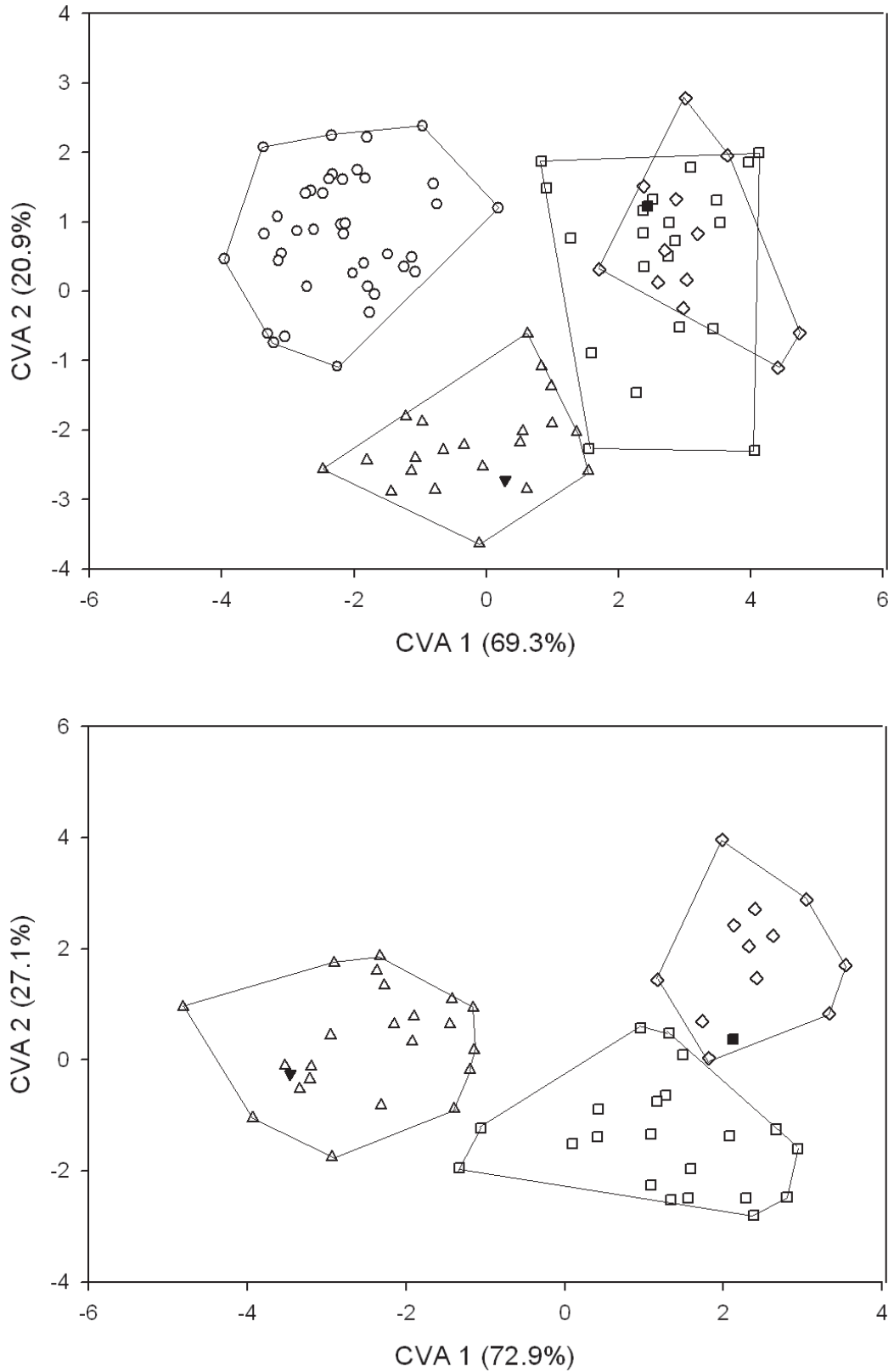


Figure 7.8. Plot of scores from Stepwise Discriminant Function Analysis (DFA) of standardized log transformed data for selected taxa of lechwe antelopes.

a). Scores for first two canonical variates accounting for total of 89.0% of variation in 97 specimens with eight selected variables (H, HBW, HBS, IHS, GSW, NW, ML and PW) for all six populations, including *kafuensis*.

b). Scores for first two canonical variates accounting for total of 95.5% of variation in 57 specimens with eight variables (H, HBW, HBS, IHS, GSW, NW, NL, ML and PW) for five populations, excluding *kafuensis*.

○ *kafuensis*; ◇ *anselli*; △ *leche*; ▼ Luapula *leche*; ■ *robertsi*; and □ *smithemani*.

Compared to *smithemani*, mean width and length of the skull of *leche* is significantly larger, especially across the zygoma and maxilla, and the braincase of *leche* is significantly higher than that of *smithemani* (Tables 7.4 & 7.6). The skull of *anselli* is in all respects more gracile. On average the skull of *anselli* is shorter and narrower, with a narrower premaxilla (PW), and significantly shorter maxillary diastema (CL) compared to both *leche* and *smithemani*. In addition to narrow horn pedicel and horn cores, narrowness is exhibited in the width across the lacrymals (ITB) and zygoma (GSW). The skull of *anselli* averages 10 mm narrower in these characters compared to *kafuensis* and *leche*. The horns of *anselli* are also more slender than those of all other taxa. Average horn length of 15 adult *anselli* is significantly longer than *K. smithemani*; and the horn profile of *anselli* is more similar to that of *leche* in the tips being closer together (Table 7.4, Fig. 7.7).

In conclusion, the characters HBW, HBS, IHS and SW reflect the widths across the horn cores and parietals; and alongside ITB and GSW, these measurements can be taken even from greatly damaged skulls. Pertinently, these taxonomically informative characters are often present even in “trimmed” trophies, and also fossils. These mensural characters are potentially of great value to classify fossil and subfossil bovids recovered from archaeological and palaeontological sites.

7.3.5 Diagnostic Pelage Characters

The pelage of *smithemani* is most distinct. The pelage of *K. anselli* is similar in general colouration to *K. kafuensis* and *K. leche*. All three taxa lack the suffusion of darker hairs characteristic of *K. smithemani*, which is resplendent in darker hairs along the face, neck, shoulders and flanks. The pelage of *K. anselli* does not exhibit any conspicuous sexual dimorphism. The dorsum, from withers to rump, and top of the neck ranges from light to a bright red-brown (Pantone scores range for these shades of red range from 1385u to 158u), with paler red hair on the sides of neck and flanks. The belly and groin are pure white: as are the lips and chin, and hair around the eyes and ears. Forehead and upper muzzle suffused with darker red hairs. The latter contrasts with the light brown, or light-red of the muzzle, head and back of the ears. The ears of four of ten specimens have black tips. Hair on inner and anterior of ears conspicuously pure white; and this extends on to the back of the ears. In contrast, the back of the ears of *K. leche* tend to be uniform light-red or tan-brown (Figs 7.1-4).

Darker striping along the anterior of the foreleg of 18 skins of adult *K. anselli* is reminiscent of *K. leche*, albeit with marked reduction in its extent. These darker markings are characteristically reduced to a thin stripe on the lower leg, or a small patch on the knee (Table 7.3). In contrast, the homologous character in *K. leche* is much broader, a very dark stripe from hoof to elbow. The white throat stripe is

also reduced in *K. anselli*. In 15 of 18 skins, it is entirely absent from the upper third of the neck; the throat of 11 individuals is entirely red, extending from below the chin approximately halfway down to the chest. In all other populations of red lechwes (*K. leche s.s.*), the white throat stripe is contiguous with the white hair of the chin and belly (Fig. 7.1-4). Both sexes exhibit this character. These skins of *K. anselli* all lack the dorsal ridge of hair discussed by Ansell (1974), occasionally exhibited in *K. leche s.s.* As described by Ansell (1964, 1968), mature males of *kafuensis* develop large dark shoulder patches; while *smithemani* males tend to a considerably darker pelage which achieves its maximum development in adults over four years old (Figs 7.1-4). Nevertheless, *K. kafuensis* and *K. smithemani* also exhibit a contiguous white throat stripe, which is edged by black hair in *K. smithemani* (Ansell 1968). The two known adult male specimens of *K. robertsi* have dark shoulder patches extending on to the throat; and also exhibit a white throat stripe (Ansell 1974, Fig. 7.1). Two specimens from Chisenga, Luapula, Lake Mweru are similar to *K. anselli* in their reduced leg stripes; but the skull morphology of the adult male (NMZB 2753) is indistinguishable from *K. leche s.s.* (Cotterill 2005, Figs 7.5, 7.6, & 7.8).

7.3.6 Summary of Morphological Dataset

This analysis of morphological characters across sampled populations of lechwes has revealed that the lineages appear similar in certain of the selected characters, yet diagnostic characters in both pelage and crania distinguish these described lechwes as distinct taxa. It therefore follows that their populations represent distinct lineages. These patterns revealed, in morphological variation of the *K. leche* complex, sets the stage to establish how the phylogenetic information relates to this finding; and furthermore, how the combined data presented in this chapter relate to the phylogeographic patterns revealed in Chapter 6. The following section presents molecular genetic data, which then enables discussion of the evolutionary significance of the combined findings.

7.3.7 Molecular Genetics

Due to the highly conserved nature of the SRY, α -fibrinogen and Protamine 1 gene regions in the *K. leche* complex, all results reported are based on the Cyt *b* and SPTBN gene regions only. This was supplemented by the Bayesian analysis of Cyt *b* and CRHV1 toward resolving the recent relationships among lechwe taxa. Despite the extensive taxonomic coverage achieved for each aforementioned nuclear gene region, all three presented a lack of parsimony informative sites (PIS). I therefore decided to discontinue screening the sample set for these markers. In summary, comparisons of 1278 bp of the SRY and adjacent non-coding region, identified only 7 PIS (of 14 variable sites) within the *Kobus leche* complex; across 355 bp of the Protamine 1 gene only 3 PIS (of five variable sites) were

identified; whilst 657 bp of the α -fibrinogen gene failed to present any PIS (within six variable sites). Initial attempts at reconstructing the phylogenetic relationships within the *Kobus leche* complex failed to produce resolved nodes. See Appendices 4-8 for alignments of all gene regions sequenced as part of this study.

7.3.7.1 Composition and nucleotide variation of the mtDNA *cyt b* and SPTBN sequences

The aligned data sets for the *cyt b* and SPTBN gene regions comprised 1140 bp and 815 bp, respectively. Due to difficulties in amplifying the target regions in museum specimens, it proved impossible to produce fully complementary data sets for the two gene regions (i.e. *cyt b* and SPTBN intron, which combined into one matrix), which dictated analysis of a subsample of paired *cyt b* and SPTBN sequences. Five sequences from museum specimens discarded from analyses as they were incomplete. Each *cyt b* sequence analysed constituted a distinct haplotype.

The two different DNA regions were characterised by variation in base composition and modes of evolution (Table 7.9). Within the 1140 bp of the *cyt b* gene no insertion/deletions were observed, and the sequences translated according to the expected mammalian amino acid composition for this mtDNA gene (380 amino acids). Base composition for the *Kobus cyt b* gene follows that described by Irwin *et al.* (1991) for mammals and characterised by a deficiency of guanine: T=26.7%, C=29%, A=31.8% and G=12.4%. Of the 286 variable sites, 152 sites (53.1%) were parsimony informative. Within the *Kobus leche* complex 53 amino acid positions of *cyt b* were variable, and 9 of these were parsimony informative changes. Mean uncorrected sequence divergence at *cyt b* across all taxa within the *K. leche* complex was 1.9% (range 0.3 - 10%), and contrasts with that of 3.8% (range 0.3 - 13%) for all nine of the reduncine taxa compared, of which the *K. leche* complex comprised five taxa (Table 7.10).

A total of 815 bp were sequenced and aligned across the *Kobus leche* complex for intron 1 of the SPTBN gene. Base compositions were consistent for all four nucleotides: T=26.5%, C=25.0%, A=22.7% and G=25.8%. Within the region sequenced, 104 variable sites were identified and of these 28 (26.9%) were parsimony informative. Mean uncorrected sequence divergence for SPTBN over all for all the reduncine taxa compared (including the *K. leche* complex) was 2.6% (range 0.1 to 8%).

7.3.7.2 Phylogenetic analysis

A comparison of the two analysed data sets shows that the mtDNA *cyt b* gene contained a higher proportion of both variable and phylogenetically informative sites than the nuclear intron SPTBN

Table 7.9. A summary of the patterns of sequence variability in the *cyt b* and SPTBN data sets of selected taxa of Reduncini.

DNA region	Total (bp)	Variable characters (% parsimony informative)	Best-fit model and Gamma distribution (" value)	Nucleotide frequencies			
				%A	%T	%C	%G
<i>cyt b</i>	1140	286 (53.1%)	GTR+G+I 0.6076	31.8	26.7	29.1	12.4
SPTBN	815	104 (26.9%)	K80 (K2P)+G 0.2674	22.7	26.5	25.0	25.8

Table 7.10. Comparisons of pairwise, uncorrected p, genetic distances (lower left of diagonal) with Standard Errors (upper right of diagonal) calculated for *cyt b* between the five taxa comprising the *Kobus leche* complex, and four taxa of Reduncini.

	<i>anselli</i>	<i>leche</i>	<i>kafuensis</i>	<i>robertsi</i>	<i>smithemani</i>	<i>megaceros</i>	<i>vardoni</i>	<i>defassa</i>	<i>ellipsiprymnus</i>
<i>anselli</i>		[0.1]	[0.2]	[0.1]	[0.2]	[0.6]	[0.8]	[0.8]	[0.8]
<i>leche</i>	0.8	-	[0.2]	[0.1]	[0.2]	[0.6]	[0.8]	[0.8]	[0.8]
<i>kafuensis</i>	1.1	1.1	-	[0.2]	[0.2]	[0.6]	[0.8]	[0.8]	[0.8]
<i>robertsi</i>	0.006	0.6	1.0	-	[0.3]	[0.6]	[0.8]	[0.9]	[0.8]
<i>smithemani</i>	0.018	1.8	2.0	1.7	-	[0.6]	[0.7]	[0.8]	[0.8]
<i>megaceros</i>	0.071	0.071	7.3	7.2	7.2	-	[0.7]	[0.5]	[0.5]
<i>vardoni</i>	0.079	0.079	8.1	8.0	8.1	8.4	-	[0.8]	[0.8]
<i>defassa</i>	0.085	0.084	8.7	8.6	8.2	5.5	7.9	-	[0.2]
<i>ellipsiprymnus</i>	0.084	0.083	8.6	8.5	8.1	5.2	8.0	0.007	-

region (Table 7.9). However, in spite of this, the retention (RI) and consistency (CI) index values (Table 7.11) of the *cyt b* gene were on average higher (0.8065 and 0.5385 respectively) than those for the SPTBN intron data (0.7724 and 0.7282 respectively). When treated separately the *cyt b* and SPTBN data sets, along with the limited taxa within the combined partition, produced largely congruent tree topologies for both the maximum parsimony and distance analyses. Nonetheless, a distance analysis using maximum likelihood model parameters on the *cyt b* data resolved the greatest number of relationships relative to the total number of taxa included in each data set; the maximum parsimony analyses was particularly poor at resolving relationships. Therefore, I have only reported the topology of the distance tree as best reflecting the phylogenetic relationships of the *Kobus leche* complex (given the current data set) and traced on the SPTBN and partition bootstrap values for shared

Table 7.11. Summary of the topologies obtained from phylogenetic analysis of the mtDNA *cyt b* and nDNA SPTBN independent gene regions of the *Kobus leche* complex and reduncine outgroup taxa (see Fig. 7.9).

Data Partition Method	No. of pars. informative characters	Tree length	CI	RI	Nodes											No. of nodes with ~70% bootstrap support/total no. of nodes resolved
					A	B	C	D	E	F	G	H	I	J	K	
Cyt <i>b</i> 1140bp n=40	Parsimony 152	273	0.7385	0.8065	100	71	74	74	62	63	61	73	72	72	100	9/17
	Distance ML				100	100	74	68	X	68	55	X	51	X	72	12/22
SPTBN 815bp n=24	Parsimony 69	103	0.7282	0.7724	100	-	-	100	X	-	X	X	67	-	-	4/6
	Distance ML				100	-	-	72	X	-	X	X	73	-	-	6/6
Combined matrix	Parsimony 125	196	0.6633	0.6140	100	-	-	-	-	-	88	-	-	80	-	4/7
1955bp n=10	Distance ML				95	-	-	-	-	-	94	-	-	82	-	7/7

The number of parsimony informative characters, optimal tree length, consistency index (CI) and retention index (RI) values are given for each parsimony tree for the three data sets. NJ distance trees estimated using maximum-likelihood model distances. Nodes A-K correspond to those in Fig. 7.9; bootstrap values (>50%) are reported; X indicates where a node was not retrieved while '-' indicates that sequence data was not available for samples represented by the node.

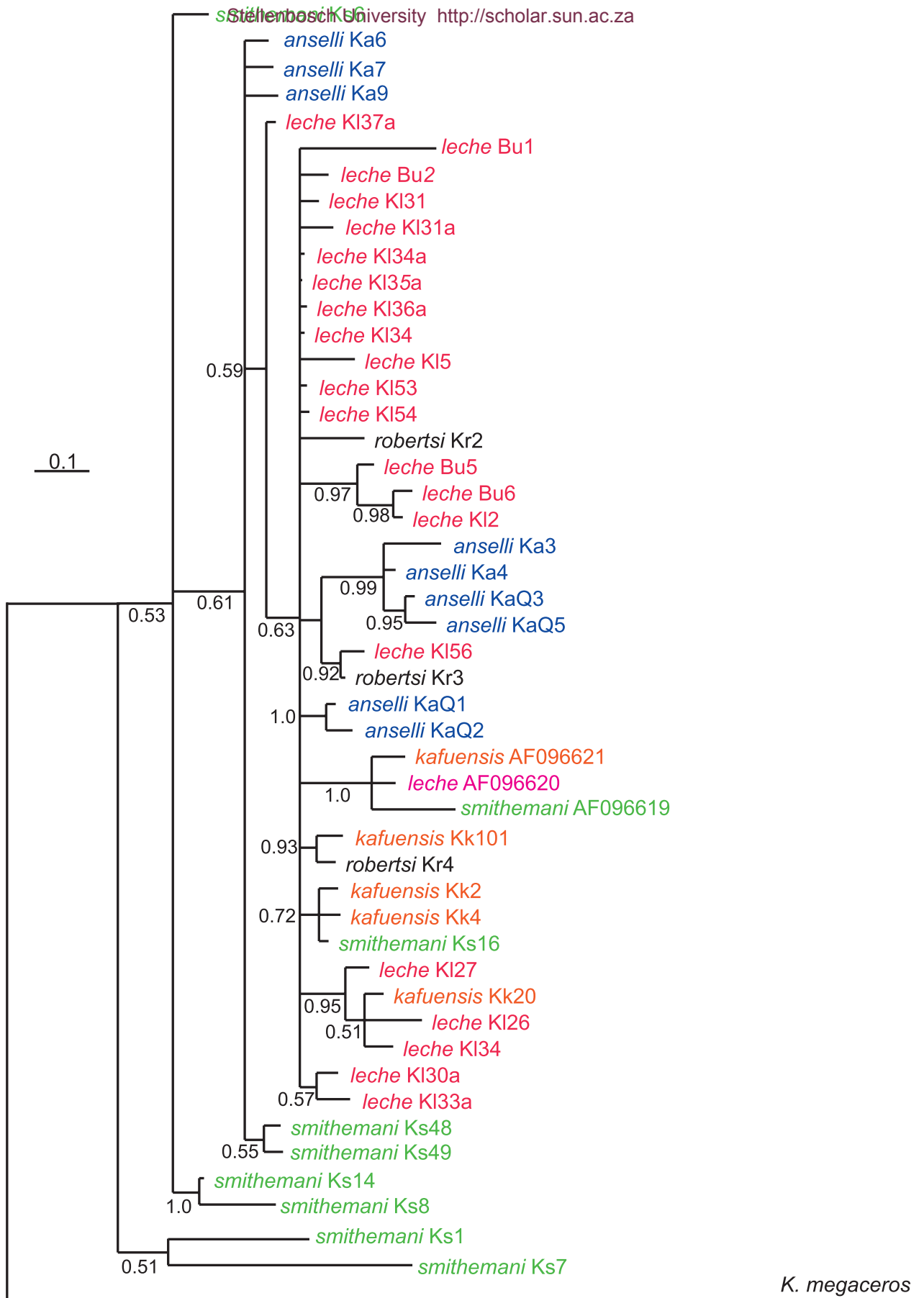


Figure 7.10. Topology retrieved by a Bayesian analysis of the *cytb* gene and CRHV1 (see Chapter 6) of 48 specimens of the *Kobus leche* complex, with *K. megaceros* as the outgroup taxon. Values given below the branches represent posterior probability support values for nodes.

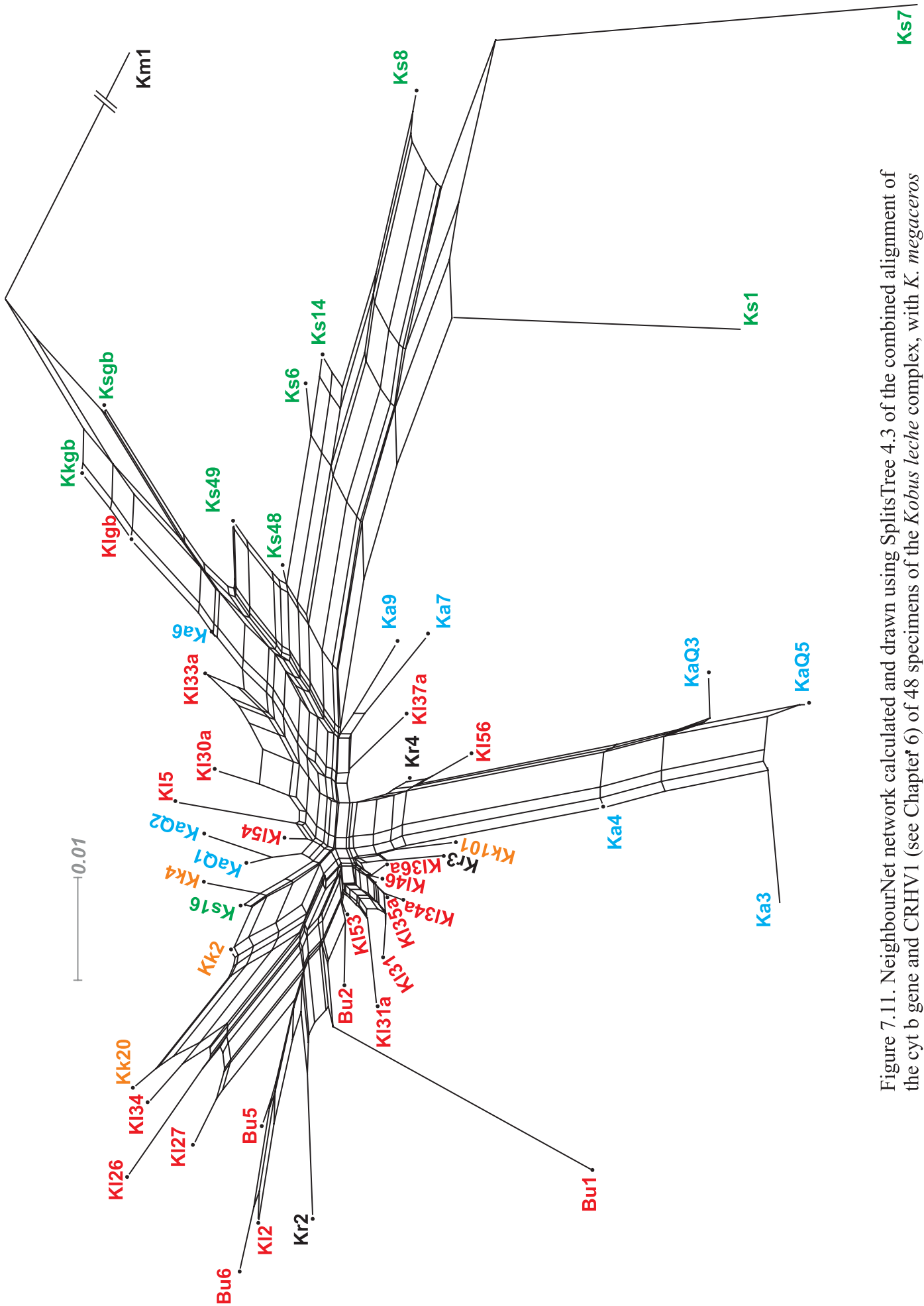


Figure 7.11. NeighbourNet network calculated and drawn using SplitsTree 4.3 of the combined alignment of the *cyt b* gene and CRHV1 (see Chapter 6) of 48 specimens of the *Kobus leche* complex, with *K. megaceros* as the outgroup taxon.

resolved nodes. Whilst the *cyt b* data set represented the largest number of *Kobus leche* samples, I have tried to compare how well each data set recovered phylogenetic relationships within the *Kobus leche* complex by identifying 11 nodes of interest from the *cyt b* tree topology (labelled A-K in Fig. 7.10). This is because, despite their reduced taxa sets, both the SPTBN and combined matrix analyses were able to resolve a number of nodes in common with the *cyt b* data (Table 7.10).

Bayesian analysis of the partitioned *cyt b* and CRHV1 data exhibits a similar topology to SPTBN and *cyt b* presented above (Fig. 7.10). The bulk of the *K. leche* complex (37/49) comprise a heterogeneous clade, with comparatively low posterior probability support. It is interesting that this tree nests this composite clade with deeper clades comprising *K. smithemani* and *K. anselli*. This topology points to *smithemani* and *anselli* as representing the ancestral lineages in the species complex, as suggested by variation exhibited in the larger sample of CRHV1 sequences (Chapter 6). The NeighbourNet network of this combined alignment (*cyt b* and CRHV1) also reveals the closer clustering of *K. leche* and *K. kafuensis* (and the two *K. robertsi*) while *K. smithemani* is the most divergent (as suggested by Birungi & Arctander 2001). The latter taxon comprises a distinct cluster in the NeighbourNet network (Fig. 7.11), and its relationships to *kafuensis* and *leche* reflect the findings of Chapter 6 (Figs 6.2 & 6.3).

By retrieving a single origin for the *Kobus leche* complex, this data set has confirmed the findings of Birungi & Arctander (2001). In all analyses the outgroup taxa, representing four recognized taxa of the Reduncini (genus *Kobus*), were consistently well supported as a sister clade to lechwe antelopes. Within the *Kobus leche* complex, patterns of relationships are multifarious. This topology appears to reflect the intricate patterns reported for the mtDNA control region data set, presented in Chapter 6.

7.4 DISCUSSION

A robust body of evidence about the genetic and morphological variation of the *K. leche* complex is compiled into this and the previous chapter. My strategy is to now discuss the genetic findings first, and progress to interpret the morphological evidence.

7.4.1 Genetic Variation in Lechwe Antelopes, and the genus *Kobus*: Cytochrome b

Compared to Birungi & Arctander (2001), the greatly expanded database for variation of Cyt

b in this study incorporates the three taxa (*kafuensis*, *leche* and *smithemani*) they sequenced for single individuals. In addition, museum specimens have enabled comparison of *K. anseli* (5 individuals) and the extinct *K. robertsi* (3 individuals). Moreover, museum specimens of *K. leche* from western Angola (K146), Cubango River, Namibia (K156), Mambova Flats (K131, K131a, K137a), Lukanga Swamps (K135a), Kasempa, northwest Zambia (K130a) and the Kashiobwe Flats (Lower Luapula, K136a and K154) were also sequenced. Nearly all these sequences represent historically extinct populations (Fig. 2.1). The heterogeneous composition of these clades (notably F, Fig. 7.9) mirrors findings of the control region dataset (Chapter 6). One sees a pattern of deeper structure (principally *smithemani* and some *anselli*) within which are nested clades of heterogeneous composition. These comprise a mixture of taxa. Overall, these data reveal that there is very little difference among the representatives of lechwe sequenced for *cyt b*. According to this tree (Figs 7.9), all south-central African lechwe antelopes form a single taxonomic unit. Furthermore, the Bayesian analysis of this *cyt b* alignment augmented by respective CR sequences (Fig. 7.10) did not modify these results markedly.

7.4.2 Genetic Variation in Lechwe Antelopes: nDNA markers

The low resolution of the nDNA markers sequenced in this study can be interpreted to represent recent divergence in the *K. leche* complex. The low variation exhibited in the SRY data is interesting in light of recent discoveries in other mammals. This lack of variation in the haplotypic Y chromosome marker among lechwe populations is reminiscent of a recent study of Hamadryas baboons, *Papio hamadryas* in northeast Africa and western Arabia, where no nucleotide variation was found among 16 males sequenced for 3 kb of the SRY intron DBY13. Neither did 97 male baboons exhibit any variation in a total of 1.1 kb represented in four shorter introns. This lack of variation in these Y chromosome markers contrasts starkly against other primates (Lawson Handley *et al.* 2006). Low variation is also exhibited in *Lynx* and *Bos taurus* (Hellborg & Ellegren 2004). In the human Y one SNP / 0.5-1 kb of sequences is the norm, and similar levels are exhibited in *Pan paniscus* and *P. troglodytes* (Stone *et al.* 2002) and among shrews (Brändli *et al.* 2005). Lawson Handley *et al.* (2006) invoked three explanations for the origin of this dearth of genetic variation. These include: 1) low effective population size (N_e) of males (a skewed Operational Sex Ratio, OSR), 2) a consequent on demographic history (one or more bottlenecks), and 3) selection modifying variation of Y chromosome markers directly.

All three phenomena could feasibly explain the low nucleotide diversity exhibited among the *K. leche* complex. One can argue that N_e can be expected to be low in male lechwes, because the OSR is indeed highly skewed (Chapter 2). This reaches its extreme in *K. kafuensis*, in which a minority of males dominate matings (Nefdt 1995). The polygynous mating systems of *K. leche* (Williamson 1979, 1992, 1994) and *K. smithemani* (Thirgood *et al.* 1992; Nefdt & Thirgood 1997) can also be expected to manifest in a low N_e in their male populations. Low genetic variation can also follow on severe and prolonged bottlenecks that dominate a population's demographic history. Yet, levels of mtDNA diversity are relatively high in all four populations of the *K. leche* complex. *K. kafuensis* has indeed experienced a recent expansion event, but any associated bottleneck is an unlikely explanation, considering the high levels of genetic diversity exhibited in mtDNA markers (CRHV1, Chapter 6, and Cyt b) in these extant populations.

Selective sweeps can manifest in low genetic variation in extant populations. This has been demonstrated in primates, where the demonstration of positive selection for Y-linked genes. Selective sweeps are suggested for the reproductive proteins, lysin and sp18, with very low variation within species of abalone (Metz *et al.* 1998). The recent conclusions of Gerrard & Filatov (2005) confirm other studies in which Y chromosome genes feature prominently as candidates for positive selection (Swanson & Vacquier 2002; Swanson *et al.* 2003). Interestingly, mammalian SRY exhibits evidence for pronounced positive selection, as compared among primates (Whitfield *et al.* 1993) and between *Mus domesticus* and *Homo sapiens* (Makalowski & Boguski 1998).

To conclude, the lack of genetic variation in the nDNA markers, including Protamine 1, and Intron 7 of α -Fibrinogen, reveals that divergence between the lineages comprising the *K. leche* complex has simply been too recent for mutations to have fixated across extant populations. These patterns corroborate findings of Chapter 6, with respect to the rapidly evolving CRHV1 marker. Several factors underlie what molecular characters we apply to investigate the evolutionary histories of organisms, populations and encompassing taxa (Schlötterer 2004). Certainly in this study, the now time-proven value of mtDNA markers has fostered many phylogeographic and taxonomic insights into some of the Bovidae, greatly facilitated by universal mammalian primers. The ease of amplifying mtDNA markers continues to underlie their popularity. With respect to this study, the far less commonly used ND5 gene might be more suitable. It evolves distinctly faster than cyt b (Tserenbataa *et al.*

2004; Roca *et al* 2005). Nevertheless, one needs to consider the costs and benefits of such research. Any such novel approach requires much investment in the resources to develop primers and explore patterns of genetic variation. Future studies might employ AFLP (Amplified Fragment-Length Polymorphic) markers to elucidate the more recent evolutionary relationships amongst these lechwes, as applied to certain African fishes. Such studies (e.g cichlids, Albertson *et al.* 1999) and mormyrids, Sullivan *et al* 2002, 2004) require high quality DNA, which was unavailable to this study. Amplification of microsatellites require fresh tissue to provide DNA of sufficient quality. So, the dependence on museum specimens in this genetic study would have obviated using either microsatellites or AFLPs.

7.4.3 Morphological Variation in Lechwe Antelopes in the Context of Genetic Evidence

Patterns of variation in cranial and pelage characters reveal that four distinct lineages have evolved within the *K. leche* complex. Based on the distinct pelage of two adult males, *K. robertsi* also appears to be as morphologically distinct as any of the other four taxa. All evidence places the more scattered populations of Red lechwes into a single species, *K. leche s.s.* One needs to observe a caveat with this taxonomic decision, because sampling of the latter taxon was not fully completed in this study. Obviously, the lechwes of Angola's Upper Kunene floodplains have vanished forever, but special conservation attention needs to be paid to the population confined in the Cuanza-Luando region of northwest Angola (described in Chapter 2). This is an urgent conservation action. The Red lechwes of central Zambia (especially the population conserved in the Busanga Swamps) appear to exhibit longer horns with a distinct profile. In the field, they are readily distinguished from *K. leche s.s.* of the Okavango Delta. This population needs to be more thoroughly studied. Ideally, a sample size of 30 + adult skulls could be used to test if this suspected morphological difference is meaningful. Moreover, the few specimens sequenced of these Busanga lechwes exhibited the greatest genetic variation in the *cyt b* analysis (Fig. 7.9), within which the Red lechwes of Angola and the Okavango are clustered. Correspondingly high variation is exhibited among the 11 control region sequences of Busanga lechwes (Chapter 6). This combined evidence reinforces the need to evaluate the population with due seriousness.

The demographic and phylogeographic history of *K. kafuensis* reveals this taxon represents the most recent speciation event in the complex. Overall, it constitutes a distinctly unusual phenomenon with respect to evolution in the *K. leche* complex. In important respects, *K.*

kafuensis is the most morphologically distinctive of the *K. leche* lineages (Ansell 1964; Cotterill 2005, Section 7.3.6). Yet, the three representatives of *K. kafuensis* are distributed across the Cyt b trees (Figs 7.9 & 7.10), although CR variation of this taxon does exhibit a tight cluster compared to other lechwe taxa (Chapter 6). Their diversification can be explained as rapid evolution to local ecological conditions, where the pronounced sexual dimorphism of males has been integral to the evolution of a lek mating system (Chapter 2). As argued in Chapter 3, these morphological characters can be interpreted as the rapid origin of a distinct SMRS in this lineage, isolated on the Kafue Flats. The history of dispersals is most plausibly explained as the ancestral population colonizing the Kafue Flats from the Lukanga and Busanga basins to the north.

The uncertainties attached to applying molecular markers to assign lechwe taxa, with any confidence to clades, equally applies to *K. anselli* and *K. robertsi*. In all respects, morphological characters provide the most reliable criteria with which to identify lechwe specimens. Besides differences in pelage markings, the most informative are cranial characters, especially dimensions of the horn cores, and horn profiles (Section 7.3.6). Improved resolution into the evolutionary relationships of the *K. leche* complex clearly demands more appropriate genetic characters. Sequencing of genetic markers influenced directly by sexual selection offer a promising avenue, as argued for birds (Edwards *et al.* 2005) and demonstrated for several model organisms (Swanson & Vacquier 2002; Swanson *et al.* 2003). Protein components of mammalian seminal fluid, pertinently seminogelin II (SEMG2) exhibits rapid positive selection in primates, where species with promiscuous matings systems exhibits the highest rates of genetic divergence in SEMG2 (Dorus *et al.* 2004). It is suggested that sequencing of such candidate markers in polygynous bovids, especially populations where multiple matings occur, is well worth exploring. These could be more feasibly characterized than the more complex genetic determinants of pelage characters.

The overall pattern of phylogeographic and phylogenetic diversity exhibited in the *K. leche* complex exhibits interesting parallels to that revealed amongst the species-rich flocks of cichlid fishes in Africa's great lakes (Albertson *et al.* 1999; Sturmbauer *et al.* 2001; Verheyen *et al.* 2003; Salzburger *et al.* 2005), and recently in the riverine cichlids of south-central Africa, whose greatest diversity is centred within the Katanga-Chambeshi region (Joyce *et al.* 2005, Chapter 4). Persistence of ancestral polymorphisms characterizes these

clades of recently evolved species, each of which is morphologically distinct (Nagl *et al.* 1998). Speciation of cichlids has been geologically recent (Salzburger *et al.* 2005). It is interesting that coalescent-based analyses of selected species complexes revealed a high level of recent gene flow between morphologically and behaviourally distinct species (Won *et al.* 2005), which contrasts against the findings of this study, which revealed negligible levels of gene flow as opposed to ancestral polymorphisms as a function of large effective population sizes (Chapter 6). As with Africa's cichlid fishes, characterization of the lechwe antelopes of south-central Africa is more feasible with morphological characters. The similarities exhibited between the evolutionary histories of lechwe antelopes and cichlid fishes highlights weakness in taxonomies structured on operational-founded concepts of the species category. Strict adherence to the criterion of reciprocal monophyly of mtDNA and nDNA markers (as in ESUs or the GSC, Chapter 3, Table 3.1) would reject the taxonomic significance of such morphologically distinct taxa.

The morphological characters reveal that each of these cichlid and lechwe populations has experienced a history of evolutionary independence; and the ancestral polymorphisms testify to their recent divergences. The AMOVA and MDIV analyses in Chapter 6, confirmed these lechwe populations have indeed been isolated. Clearly, the genetic markers available cannot resolve finer details in this recent evolutionary history. The logical approach is to sequence genes related directly to the heritable morphological synapomorphies that distinguish taxa in the *K. leche* complex. Taxonomic incongruities presented in the *K. leche* complex also exhibit interesting parallels with the lava lizards (*Microlophus albemarlensis* species complex) that have evolved across the Gálapagos archipelago. These morphologically distinct populations of *Microlophus* are geographically isolated, yet their mtDNA gene trees have only partially diverged, which was inferred to reflect admixture across islands (Kizirian & Donnelly 2004; Kizirian *et al.* 2004). Further testing of this hypothesis should apply coalescent-based techniques (e.g. MDIV as in Chapter 6, or IM, Won *et al.* 2005). It is also not coincidental that these species complexes of lava lizards and lechwes have both evolved across archipelagos.

7.5 CONCLUSIONS

A comprehensive analysis of morphological variation preserved in museum specimens has provided otherwise unavailable data with which to scrutinize the trinomial taxonomy inaugurated by Ellerman *et al.* (1953). Analyses of genetic markers reveal how divergence of

the *K. leche* species complex has been relatively rapid. The extant diversity of lechwe antelopes in south-central Africa has received conflicting treatment by taxonomists (see Section 7.1 for details of this history and taxonomic authorities). One can treat all available evidence of genetic and morphological variation amongst recent lechwe antelopes to classify these young evolutionary products in two contrasting treatments.

One approach is to apply a trinomial taxonomy, and continue to treat these taxa all as subspecies. The latter approach would then continue to recognize a single polytypic species, *Kobus leche* Gray represented by five geographically isolated subspecies. These would comprise: *K. l. leche* (Botswana, southern Angola, and western and central Zambia, Kashiobwe Flats), *K. l. kafuensis* (Kafue Flats only), *K. l. robertsi* (Pambashye Swamps), *K. l. smithemani* (Bangweulu depression and Upper Chambeshi) and *K. l. anseli* (Upemba Swamps). One could try and camouflage the subjectivity of the subspecies category by calling each of these five taxa Evolutionary Significant Units (ESUs). The taxonomic treatment developed through Chapter 3 argued against both ESUs and subspecies, not least because resultant classifications misrepresent real evolutionary history. Moreover, Fraser & Bernatchez (2001) advocated classifying ESUs within one's species concept of choice. Yet, "[a] lineage demonstrating highly restricted gene flow from other such lineages within the higher organizational level (lineage) of a species" (Fraser & Bernatchez 2001: 2742, Table 3.1) cannot be segregated out as a distinct ontological entity when classified under the ESC. Here, we encounter an ontological paradox. As argued by Frost *et al.* (1991), this problem mirrors that bedeviling attempts to characterize any subspecific entity, contained within a populational lineage, which, in its own right, has evolved along an independent evolutionary trajectory. Such classifications are challenged to treat young segments of individuated lineages as distinct ontological entities in their own right. Segments of populational lineages can be divvied up into as many different kinds (categories) for as many operational criteria as we employ. Subjective treatment of fragments of individuals makes for taxonomic chaos (Chapter 3).

The second treatment must first acknowledge how critical aspects of the evolutionary history pertaining to the divergence of these lechwes await elucidation, especially the heritable mechanisms of lineage-specific pelage and skull characters in each morphologically distinct lineage. As argued above, it is suggested that sequencing of these genes should characterize divergent molecular characters. Nonetheless, telltale phylogeographic signals revealed in the

histories of these lineages (Chapter 6); testify to formative events whereby lechwes diversified across a wetland archipelago. Not least, they reveal how each lineage has evolved as a distinct populational lineage. Following Cotterill (2005) and founded on the argument in Chapter 3, comparisons of suites of morphological characters corroborate that each population is not merely a deme in one evolutionary lineage. With respect to their geographical isolation summarized above, each represents an evolutionary distinct lineage, and in terms of the ESC is a distinct species:

Kobus anselli Cotterill

Kobus kafuensis Haltenorth

includes *grandicornis* Ansell

Kobus leche Gray

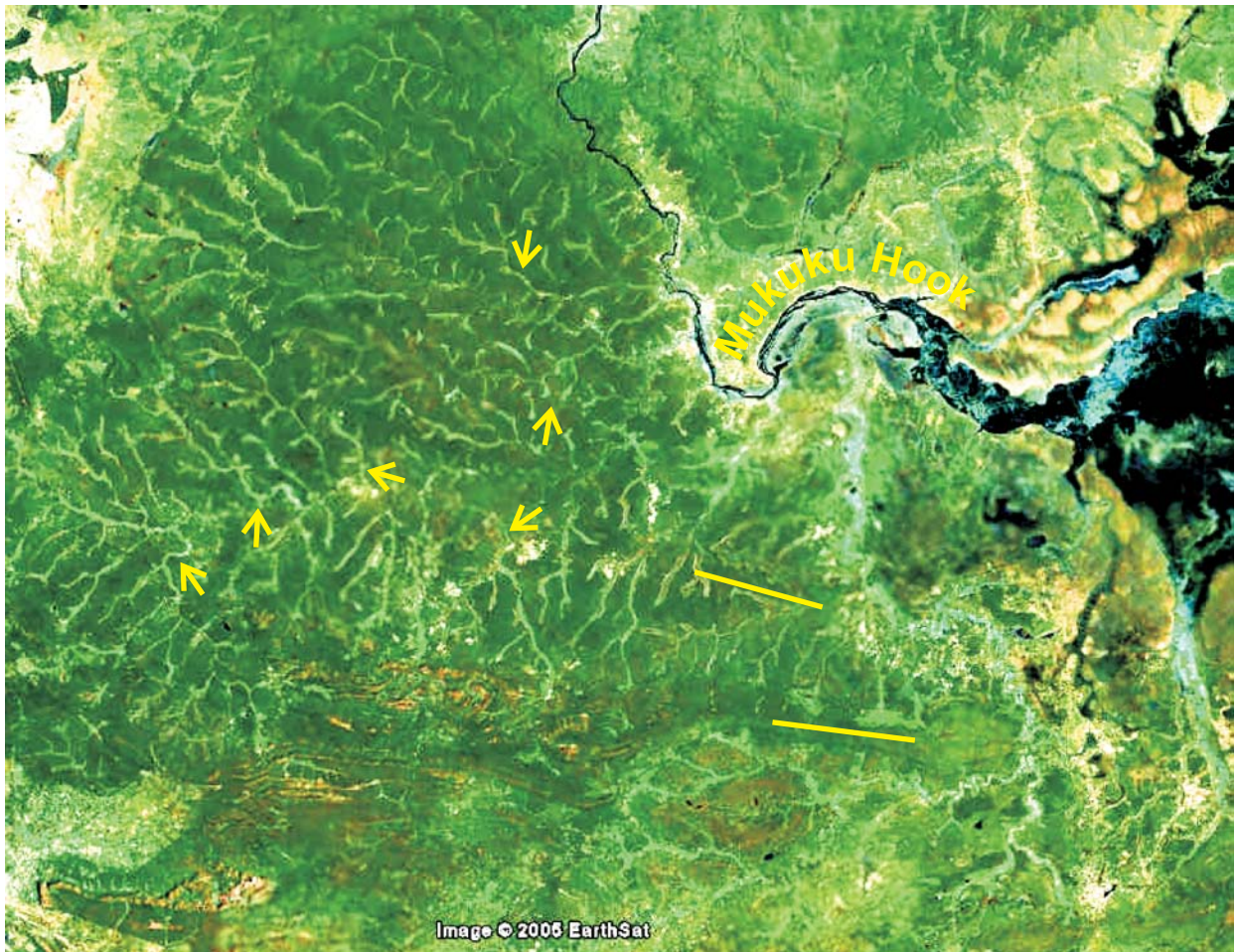
includes *ambolloensis* Sokolowsky and *notatus* Matschie

Kobus robertsi Rothschild

Kobus smithemani Lydekker

For decades through the 20th century, the distinctiveness of two of these species - namely *K. anselli* and *K. robertsi* - escaped deserving attention from mammalogists and thus biogeographers. The consequences of treating them as merely “Red lechwes” was to camouflage (albeit inadvertently) their importance as distinct evolutionary entities. Lamentably, dire threats to the continued existence of both living populations failed to receive due attention from conservation authorities. It is interesting to acknowledge, in retrospect, how *K. kafuensis* suffered similar typological treatment (as a Red lechwe e.g. Ansell 1955; Mitchell & Uys 1961) until the early 1960s! Fortunately, its taxonomic distinctiveness was suspected, and the conservation plight of these Kafue lechwes attracted international attention (Chapter 2). There is an analogous risk that the distinctiveness of the Busanga Red lechwes could also be overlooked. This error can be avoided by a detailed study of this isolated population against the databases assembled in this study. Taxonomic review of the endangered Cuanza population is an even more urgent priority.

CHAPTER 8



[Top] View over the Katanga Pedicle and southwest corner of the Bangweulu basin. Note the acute bend in the Luapula River at the Mukuku Hook, and remarkable topology of the extant drainage, reflecting effects of tectonism and strong fault control over vestiges of the Trans-Katanga and Palaeo-Chambeshi drainage systems. Yellow lines parallel the more obvious abandoned channels (Section 4.7). Yellow arrows single out especially marked evidence of drainage anomalies

Photograph: GoogleEarth

[Bottom] A surviving vestige of the immense Palaeo-Chambeshi drainage system, but still a significant wetland, nonetheless: the Upper Kafue River at Chunga, central Kafue National Park.

Photograph: F. Cotterill

CHAPTER 8 CONCLUDING SYNTHESIS

“In Nature’s infinite book of secrecy
A little I can read” William Shakespeare (*Anthony and Cleopatra*) 1606

As a synthesis, this final chapter discusses the principal findings of this study. It focuses on how the evolutionary history of the *Kobus leche* complex relates to the biogeography of south-central Africa, and seeks to place causes of lechwe evolution into context. It begins by addressing the three sets of key questions, posed at the beginning of Chapter 1, and reiterated on pg 56:

1. What are the products of the vicariant evolution of lechwe antelopes? Can specimens of currently unclear taxonomic affinities be identified using molecular and morphological techniques? These historical specimens vouch for outlying populations in eastern Angola, north Zambia, the southern Congo Basin and Chisenga Island, Lake Mweru.
2. How has the vicariance of wetland habitats influenced lechwe evolution across south-central Africa? For example, did timings of evolutionary events in lechwe populations correspond to geological evidence of changes in wetland habitats? How do distributions of extant lechwes relate to landscape vicariance - notably invoking rearrangements of drainage systems across south-central Africa?
3. How can patterns and processes revealed in the evolutionary history of the *K. leche* complex, and their habitats, inform conservation plans and actions?

I begin by summarizing findings of Chapters 6 and 7, and frame the taxonomy and phylogeography of lechwe antelopes within the philosophical argument of Chapter 3. Thereafter, these taxonomic and phylogeographic patterns are discussed in terms of more encompassing aspects of evolutionary history. I examine how the *K. leche* complex has evolved in relation to palaeo-environments. Special attention is paid to dynamics of palaeo-drainage systems across the Katanga-Chambeshi region. Lastly, I draw on this study’s findings to discuss conservation plans and actions, and implications for future studies.

8.1 TAXONOMIC TREATMENT

The central taxonomic conclusion of this study is that the *Kobus leche* complex comprises five distinct species. Three of these taxa were described between 1850 and 1907, with belated recognition of *K. kafuensis* in 1963/1964. Most recently, the description of the Upemba lechwe, *K. anselli*, as a distinct

taxon is an important discovery in this study. It has not been feasible to apply statistically robust methods, and compare the historically extinct *K. robertsi* against representative hypodigms of the other four taxa in morphometric or phylogeographic analyses. Nevertheless, the three surviving flat skins confirm *robertsi* to be a distinct taxon (Chapters 6 & 7). All other populations of lechwes across southern and eastern Angola are assigned to *K. leche*, which is by far the most widespread taxon and also includes all western and central Zambian specimens. The Kashiobwe Flats population (represented by two Chisenga Island specimens) is, tentatively, also assigned to *K. leche*. Unfortunately, the lack of specimens made it impossible to ascertain the taxonomic status of the extinct Owambo (Upper Kunene) and endangered Upper Cuanza populations in western Angola.

Classification of these young antelope species evoke controversies over microtaxonomic categories, and they indeed exemplify challenges entailed in classification of recently evolved vertebrates. Chapter 3 set the stage in defending a stance on the species problem grounded in metaphysics. Here a poignant lesson gained from the critique of evolutionary biology by Rose (1997, 2005) is that great misinterpretations flow from doing biology - in the broadest sense of the verb - in the absence of a coherent philosophy. Taxonomy especially requires ontological resolution of taxonomic categories with respect to the biodiversity we are challenged to classify and conserve. The solution to the species problem (argued through Chapter 3) hinges on solid ontological foundations that structure epistemological pluralism. This is a critical, empowering advance toward credible scientific interpretations of complex historical patterns. Taxonomic treatment in this study is structured on the Individuality Thesis, following Ghiselin (1984, 1997), Wiley (2002) and Mayden (1997, 1999, 2002) as detailed in Chapter 3. Couched in a philosophy of Absolute Realism (*sensu* Ghiselin 1997), it distinguishes a fundamental dichotomy between the ontology of the species category versus epistemic operations used to discover individuated species. This ontology recognizes that evolution has populated the species category with billions of unique lineages, whose heterogeneous properties reflect speciation events caused by many different processes. It further follows that a spectrum of evidence is required to characterize any of these individuated species accurately and precisely.

The Evolutionary Species Concept (ESC) of Simpson (1951, 1961), Wiley (1978, 2002) and Mayden (1997, 1999, 2002) constitutes the only universal concept of the species category with respect to patterns and processes of speciation. Fulfilling demands on a universal concept (De Queiroz 2005), the ESC provides us with the best available guide to discover real species, that evolved as individuated lineages: each the legacy of at least one evolutionary significant event. All other purported species

concepts actually constitute species criteria. Attempts to reify any one of the latter as a “species concept” and thus a definition of the species category inflates its particular ontological biases. And efforts to characterize biodiversity are correspondingly constrained by its operational limitations. The philosophy and practice structured by the ESC avoids these operational biases and errors, whereby such species criteria are applied as “species concepts”, in singular roles, to try and categorize biodiversity. When framed under the ontological aegis of the ESC, these species criteria (notably the RSC and PSCs) provide the “epistemic toolkit” (evidence permitting) to compare sampled populations. This enables comparisons of hypodigms of two or more populations, to test whether they constitute one or more lineages with independent evolutionary histories. The critical question is whether apparently similar populations are parts of a metapopulation or represent evolutionary species.

The taxonomic treatment applied to the *K. leche* complex (Section 7.5) minimizes the three categories of errors, where taxonomies fail to characterize biodiversity accurately and precisely. Either way, the categories of subspecies and Evolutionary Significant Units (ESUs) divvy up lineages into artificial, and thus subjective categories. Entrenched tendencies to reify such entities, as real evolutionary products, weakens scientific understanding of evolutionary history and its application to other theatres of knowledge (Chapter 3). Polytypic classifications of lechwe antelopes (Ellerman *et al.* 1953; Ansell 1972; Bronner *et al.* 2003) exemplify Type II errors. Their lumping of evolutionarily distinct lineages emplaced “a glass ceiling” over knowledge of lechwe diversity. Persistence of these errors in taxonomies extend to undesirable consequences, where knowledge of particular evolutionary products is obscured (Chapter 3). A polytypic taxonomy failed to accommodate the uniqueness of *K. robertsi* as an endangered species. This is more than likely an important reason why critical conservation intervention did not target the Pambayshe Swamps. It is hopefully not too late to prevent the extinction of *K. anselli* due to a parallel mistake (Chapters 6 & 7).

All five taxa comprising the *K. leche* complex differ unequivocally in morphological characters - in diagnostic pelage, and discontinuous variation in skull morphology, whilst screening of nuclear markers revealed scant variation in the *K. leche* complex among the heterogeneous clades recovered by mtDNA markers. Some authorities might argue against treating these morphologically distinct populations of *Kobus* as full species (nor even ESUs!) because their mtDNA trees do not exhibit reciprocal monophyly. These findings are most plausibly explained by relatively recent speciation events across a wetland archipelago, where ancestral polymorphism and lineage sorting of mtDNA markers disguise divergence amongst lineages of lechwes (Chapters 6 & 7). Molecular and

morphological evidence reveals each lechwe population to be a mosaic of characters. A critical question is whether recent evolutionary history should be represented by neutral characters; or should recently evolved phenotypes structure a taxonomy of lechwe antelopes? Here, priority is accorded to characters inferred to reflect actions of recent evolutionary causes. So it can be seen how aetiological criteria structure a classification, with respect to relative weighting of taxonomic characters. Thus, respective morphological adaptations signify the recent divergence of each populational lineage of lechwes across which neutrally evolving mtDNA haplotypes have only been partially parsed, and nDNA markers have scarcely diverged. I interpret these divergent horn morphologies and pelage as synapomorphic characters (*sensu* Coddington 1988) specific to each allopatric lechwe population. To conclude, under the aegis of the ESC, evidence combined from morphological and phylogeographic analyses has revealed that at least five recently individuated species of lechwes have evolved across south-central Africa. The converse approach is to treat all extant populations of these lechwes as representatives of a single species. Such a taxonomic stance can be applied, if one ignores not only taxonomic evidence but also significant evolutionary events in the Middle Pleistocene of south-central Africa, in which lechwes were key players across a wetland archipelago.

8.2 SPATIAL CONTEXTS OF SPECIATION EVENTS AND THEIR TIMINGS

The phylogeography of lechwe antelopes across south-central Africa reveals how two processes structured their extant diversity. I consider the role of peripatric speciation first. Consilient evidence points to *Kobus kafuensis*, isolated on the Kafue Flats, as the product of a peripatric speciation event. It is, furthermore, reasonable to invoke sexual selection to explain how the Kafue lechwe has evolved into the most morphologically divergent of all extant species (Chapters 6 & 7). Following the Peripheral Isolates Model, the most likely scenario for this dispersal event entailed a “budding-off” event, into the Kafue graben, from the more widespread *K. leche* lineage. This conclusion is supported by the phylogeography of *K. kafuensis* (Chapter 6) and timings of geological events constrained by archaeological evidence and Uranium Series dates at Twin Rivers (Chapter 5). Its interpretation as peripatry is, nonetheless, subject to further testing, perhaps using MHC markers (Klein & Talahata 2002): as applied to Lake Victoria cichlid fishes (Nagl *et al.* 1998) and Darwin’s finches (Vincek *et al.* 1997).

More prevalent than peripatry, dichopatry is invoked to explain how *K. anselli*, *K. leche* and *K. smithemani* evolved from a more widespread ancestor. This complex of events occurred closely together in time; so it is difficult to discern their finer-scaled patterns. The composite events most

plausibly reflects scission of the Bangweulu-Upper Chambeshi drainage system from the Trans-Katanga system. Thereafter the Kamalondo depression was isolated from these eastern drainage systems, and wetlands south of the Southern Equatorial Divide. The total range of this ancestral population probably extended southeast along the Trans-Katanga drainage: inclusive of the Bangweulu-Upper Chambeshi and Proto-Luongo systems as part of the Palaeo-Chambeshi River. Tentative evidence suggests the endangered *K. anselli* represents this original lineage that seeded all extant lechwe taxa across the Katanga-Chambeshi archipelago. High genetic diversity (subject to a small sample size, $n = 26$) supports this suggestion, especially as the 24 haplotypes of *anselli* manifest across all extant lineages (Chapter 6). Timings of speciation events, estimated from coalescent-based comparisons of CRHV gene trees, reveal that all four lineages of the *K. leche* complex diverged during the Middle Pleistocene, where these estimates of lineage divergence and population expansions overlap within and among species (Section 6.3.5). Combined evidence from the geomorphological model points to these speciation events corresponding to significant changes in drainage topologies; these began with alterations of the Trans-Katanga and Palaeo-Chambeshi systems (possibly ~600-500 Kya), and extended to the formation of the extant Kafue Flats (initiated ~300 - 200 Kya, Fig. 8.1).

Cotterill (2000, 2003c, 2004) proposed that margins of major palaeo-lakes provided optimal habitats for prehistoric populations of lechwes. This can now be seen to be a naive interpretation, because phylogeographic evidence does not support this hypothesis, when evaluated against the drainage model (Chapters 5 & 6, Fig. 8.1). Ecological studies have revealed how extant lechwes thrive optimally on vast, shallow floodplains, characterized by high amplitudes in seasonal flooding regimes; where their demographic dynamics exhibit sensitivities to the subtleties of flooding regimes (Chapter 2). Demographic expansions of each population have been preserved as informative phylogeographic signals; and aspects of the natural history of extant lechwes are invoked to explain these expansions as responses to contractions of palaeo-lakes. Thus, dessications of palaeo-lakes are invoked as the most plausible cause of these phylogeographic signals. One example entailed a population expansion of *K. leche* that corresponds with the end of the tenure of Palaeo-Lake Makgadikgadi. A second was when *K. kafuensis* expanded after the tapping of Lake Patrick by a Mid-Zambezi tributary. The latter expansion is interpreted as accompanying morphosis of the Kafue graben from palaeo-lake to floodplain.

Diversification of lechwes has occurred across an archipelago of islands; but this study has discerned only some of these events. Only more robust and representative data can detail - more precisely and

completely - how often, and where, lechwes have speciated through the Quaternary with respect to evolving wetlands (Figs 2.1 and 8.2). This will enable one to test whether island number has been a rate-limiting determinant on speciation of semi-aquatic lechwes and other aquatic biota, as suggested for Galápagos finches (Grant & Grant 1996, 2002) and *Nothonotus* fishes across drainage systems of the Nearctic Central Highlands (Near & Keck 2005). Beyond precise dates of both landforms and phylogeographic patterns, testing of this hypothesis requires complete sampling of all islands. This requires fossil data. AFLP markers can resolve such finer-scaled relationships, as applied to particular Bovini (Buntjer *et al.* 2002), cichlid fishes (Albertson *et al.* 2002; Barluenga *et al.* 2006) and mormyrid fishes (Sullivan *et al.* 2004). Unfortunately, AFLP distance data lacks the informative evolutionary signals implicit in DNA sequence data, when interrogated by coalescent-based and molecular dating methods. So, as applied to the phylogeography of *Loxodonta* (Roca *et al.* 2005), the logical conclusion is to screen longer sequences of nuclear markers that represent paternal and maternal patterns of descent.

Detailed attention to intricacies of the archaeological record and the evolution of the Victoria Falls Formation (VFF), in Chapter 5, proved essential to resolve finer-scaled details in the evolutionary history of lechwes. Previously, as exemplified by cichlid fishes, resolution of biogeographical patterns in relation to landscape evolution was hamstrung by imprecise conjectures as to when palaeo-lakes existed in northeast Botswana (postulated at anywhere since the late Pliocene to early Holocene). Uncertainties still remain, but resolution obtained for tenures of three key landforms (the principal focus of Chapter 5) provide sufficient precision to explicate origins of several lineages of antelopes, as revealed in the phylogeography of alcelaphines and reduncines (Section 6.4.1, Fig. 8.1). Hewitt (2004) interpreted key events in these phylogeographic histories (revealed in studies by Arctander *et al.* 1999 and Flagstad *et al.* 2000) as driven by increased aridity across Africa during the last Glacial Maximum (MIS 2). This pulse of Pleistocene diversification is more precisely delimited as late Middle Pleistocene, when the Zambezi River stopped flowing for ~200 Kyr, corresponding to MIS 12 - 8 (Chapters 5 & 6, Figs 5.3 & 5.6). This is an interesting period in the Quaternary history of Africa, not least because dispersals of these large mammals corresponded to an equally critical period in human evolution - the transition from the Early to Middle Stone Age (Chapter 5). It is important to acknowledge that these events represented in phylogeographic patterns (coinciding with the Batoka Unconformity) could represent the most recent events that followed on antecedent dispersals. Other taxa may have dispersed even earlier in the Early Pleistocene or late Pliocene. For example, Herron *et al.* (2005) detected a relatively deep divergence between the Ground squirrels (*Xerus* spp) of northeast

and southwest Africa (but were unfortunately unable to constrain this event against a *cyt b* molecular clock). Future studies need to test whether indeed any such phylogeographic signals reflect the earlier break in erosion of the Batoka Gorge (Early Pleistocene) during the tenure of Palaeo-Lake Makgadikgadi (Section 5.4, Fig. 8.1).

Beyond the constraining philosophies of cladistic biogeography and panbiogeography, which argue that peripatric speciation has a negligible role, if any, in biotic evolution (criticized by Van Veller *et al.* 2003), evidence collated in this study - not least the *K. leche* complex - reveals how episodes of dispersal were complemented by vicariance to forge Africa's extant biota. Nevertheless, subject to far more comprehensive phylogeographic and phylogenetic patterns (studying more surrogate indicators), it appears that vicariance has indeed exercised dominant control over the evolution of biota across the Katanga-Chambeshi region.

8.3 KEY EVENTS IN EVOLUTION OF LECHWES AND WETLANDS

This study has clarified important events of landscape evolution through the Pleistocene across south-central Africa (Chapters 4 & 5). Although one large mammal was described as new to science, explorations of landscape evolution, aimed at elucidating how *Kobus anselli* and its sister taxa evolved, has discovered no less than six extinct landforms. Their tenures received central attention in a narrative of relatively recent geological history of complex palaeo-dynamics, whereby drainage topologies changed and tenures of palaeo-lakes waxed and waned on High Africa (Chapters 4 & 5). Details of these palaeo-lakes and antecedent drainage systems (listed on pages vii-viii) occupied Chapters 4 through 5. Lechwes are definitely not the only organisms to have been buffeted across these active zones because patterns of endemism, coupled with biogeographical disjunctions in ranges of other aquatic and terrestrial vertebrates, point to broad impacts of palaeo-drainage dynamics on biota across the entire Katanga-Chambeshi region. Thus, structured by the ESC, the extant diversity of lechwes comprise one set of biotic signatures reflecting how palaeo-drainage dynamics influenced aquatic biota across High Africa (Chapter 4, Appendix 2).

Combined phylogeographic and taxonomic patterns have been extended to elucidate aspects of landscape evolution. These abiotic and biotic patterns are mutually reinforcing, where they help resolve important puzzles as to when antecedent drainage systems and palaeo-lakes existed. The insights obtained into the evolutionary history of lechwe antelopes reveal intricate aspects of palaeo-environments, and reinforce estimated timings of changes in palaeo-drainage. Pertinently, a synthesis

of all knowledge explicate key events in lechwe evolution. The vicariance of *K. anselli* is a case in point, with respect to ancestral affinities extending from the Kamalondo depression across Zambia to Botswana and westwards. Explication of these historical associations must acknowledge antecedent links between these drainage systems. And these lechwes are no isolated case. Key aspects of their biogeographical history are congruent with those of other indicator taxa across the Katanga-Chambeshi region. These endemics in the Zambian Congo and Katanga's wetlands (including Upemba) not only share affinities with Okavango-Zambezi taxa, but further with those in the Cuanza and Upper Kunene systems. Partial temporal resolution is also provided where the biogeographical histories of key indicators reveal when certain landforms existed with respect to each other. The evolutionary patterns (and inferred processes) exhibited among extant lechwes point to antecedent geomorphological controls on their demography and speciation. As presented through Chapter 4, key findings can be summarized in order of decreasing age:

1. The existence of the Trans-Katanga and Palaeo-Chambeshi drainage systems explains a strong biogeographical signal preserved in extant biota across south-central Africa. Not least, it explains formerly widespread distribution of lechwes from Katanga, across Zambia and northeast Botswana, to the Cuanza and Owambo basins.
2. The timing of dessication of Palaeo-Lake Makakgadikgadi (PLM) is suggested by a demographic expansion of *K. leche* approximating the Early - Middle Pleistocene boundary. Constrained by archaeological evidence, its timing corroborates with reconstructions of the erosion history of Batoka Gorge and the VFF. All these data colligate into the consilient evidence for two discrete events when the Okavango depression was inundated ~ 500 Kyr apart (Fig. 8.1).
3. Dessication of the Upper Zambezi River is reflected in the Batoka Unconformity; while Palaeo-Lake Bulozzi formed upstream of the N'gonye Falls. Influences of this tectonism extended beyond landforms to control key events in the evolution of not only lechwes, but also several other indicator species. Dating of the Batoka Unconformity testifies to an episode of ~200 Kyr through the Middle Pleistocene. Phylogeographical patterns conform with the timing of this geomorphological event, which controlled dispersals of some large mammals across the Arid Corridor between southwest and northeast Africa (Fig. 8.1).

4. The draining of Lake Patrick, around the end of the Middle Pleistocene, followed on a critical piracy event whereby the Kafue River attained its modern topology. Here, the recent individuation of *K. kafuensis* not only concurs with this event, but further reveals that scission of the Palaeo-Chambeshi's link with the Okavango and Upper Zambezi systems (and equally scission of the Upper Chambeshi from the Proto-Kafue around Mukuku Hook) had occurred before morphosis of Lake Patrick to the Kafue Flats (Fig. 8.1). Sufficiently precise knowledge reveals how the Kafue and Okavango depressions have evolved along separate trajectories within the larger Okavango-Kafue graben (Chapter 5).

5. Available biogeographical data reveals that the Kasai River's piracy of Upper Zambezi headwaters did not influence lechwe populations. Yet it was critical to dispersals of Congo fishes across the Zambezian region. Moreover, modern distributions of dispersant fish species (from the Congo system), pertinently absence of tigerfish from the Upper Kafue, suggests these Kasai River piracies occurred after the scission of the Palaeo-Chambeshi River. Equally, elucidation of why the otherwise widespread Northern Barred-Minnow, *Opsaridium zambezense*, is absent from the Upper Kafue stands to reveal when the Trans-Katanga drainage was linked with the Upper Zambezi.

6. The occurrence of lechwes in the Upper Kunene and Upper Cuanza drainage basins represents the westward extent in distribution of the *K. leche* complex, which embraced the Owambo basin. These lechwes point to direct links that extended from these wetlands, abutting the Atlantic seaboard, across the Katanga-Chambeshi region. Beyond lechwes, distributions of certain fishes constitute more speciose evidence for dispersals and speciation across this part of High Africa (Bell-Cross 1982; Section 4.11). These dynamics reflect hydrological links that extend from the Owambo-Cubango and the Cuanza-Cubango systems across Botswana and Zambia to Katanga (Section 4.10, Fig. 8.1).

7. Centred around the Mukuku Hook, complex geodynamics rearranged palaeo-drainage systems to culminate in the Zambian Congo system: lengthening the Congo River by ~700 km. Thus, this suite of geomorphological events culminated in not only regional, but continental effects. Colonization of the Kashiobwe Flats by lechwes followed on the lowering of Lake Mweru after it became the headwater of the Luvua River. This presumably also enabled many species of Congo fishes (including tigerfish) to invade the Zambian Congo system. Admittedly,

constrained by a very small sample size, the lechwes on the Kashiobwe Flats do not appear to have differentiated genetically to any marked degree. Perhaps they colonized the Kashiobwe Flats quite recently, but this contrasts against the high endemism of the mollusc fauna persisting in the comparatively shallow Lake Mweru.

8. To update Dixey's (1943a) pioneering review, the Southern Equatorial Divide can now be recognized as a composite landform. The Congo-Zambezi watershed comprises ancient and very young watersheds that can be interpreted as both buffered and geomorphologically active landforms, respectively. This heterogeneity reflects the complex geomorphological history entailed in the evolution of the Congo-Zambezi watershed. These buffered and geomorphologically active appear to have contained and facilitated biotic dispersals respectively in the basins they divide (Fig. 8.2).

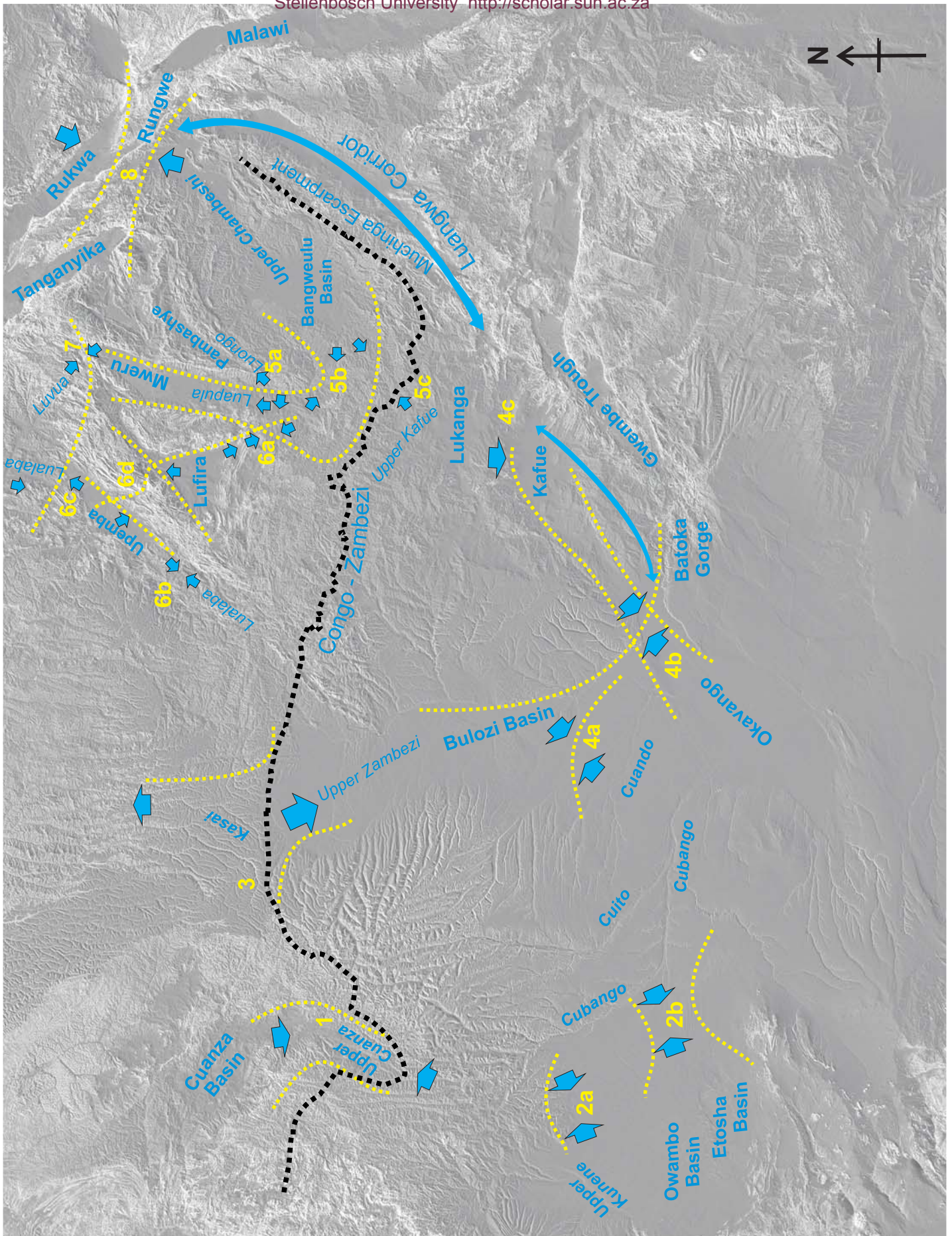
8.4 BIOGEOGRAPHIC SPECULATIONS

Tantalizing questions pertain to when large, herbivorous vertebrates first began to exploit the rich grazing of water meadows in ancient endoreic drainage basins on High Africa. An important conclusion of Chapter 2 is that lechwes are important ecological engineers in water meadows, besides dominating trophic dynamics; so it follows that their recent population of these landforms had profound consequences for the ecology of wetlands. Only excavations of fossils under these wetlands can reveal when reduncine antelopes (genus *Kobus*) first began to exploit water meadows, but these sediments have barely been searched for fossils. The way forward is to study relationships amongst *K. leche s.l* and *K. megaceros* with respect to fossils (including the extinct *K. venterae*) associated with palaeo-drainages across Africa.

Chapter 7 confirmed a singular origin for the ancestral lineage of the *K. leche* complex, whose subsequent diversification extended across the Katanga-Chambeshi archipelago. Any biogeographical scenario incorporating deeper history is thus speculative. Questions pertain to when and where ancestors of these extant lechwes diverged, and the more ancient origins of these specialized antelopes. At present, one can only speculate about dispersals and vicariance of lechwe antelopes in Neogene Africa. The evolution of drainage systems north of the Palaeo-Chambeshi archipelago is very poorly understood, with geomorphological evolution across the Congo basin understood only in the barest but most fascinating of details (Stankiewicz & De Wit 2006; Chapter 4). The model of an east-flowing Congo River (Stankiewicz & De Wit 2006) did not consider Palaeo-lake Congo (Peters & O'Brien 2001;

Chapter 4, Fig. 4.1), which possibly influenced biotic evolution in the Miocene and thereafter. Jackson (1986) hypothesized that many Zambezi fishes originated in the Congo basin, which is confirmed by preliminary results for African cichlids (Salzburger *et al.* 2005). The detailed biogeographic data necessary to test this hypothesis continue to accrue, and the emerging picture of cichlid biogeography points to ultimate origin of these fishes in the Neogene Congo basin (Joyce *et al.* 2005; Salzburger *et al.* 2005). Perhaps a semi-aquatic reduncine antelope - represented by the extant *K. megaceros* and the *K. leche* complex - also evolved in concert with the same palaeo-drainage dynamics in the Congo basin. Following Peters & O'Brien (2001), one can speculate that aspects of late Neogene palaeo-drainage dynamics entailed in the tenure and demise of Palaeo-Lake Congo had significant consequences for biotic evolution, which ramified through to the Katanga-Chambeshi region and elsewhere in Africa. We also cannot discount palaeo-drainage dynamics across the Sahara basin through the Miocene, which saw a radiation of semi-aquatic large mammals (Lithoreau *et al.* 2006)

Figure 8.2 [Following Page]. Map of the Katanga-Chambeshi region depicting foci of significant evolutionary events entailing dispersals of aquatic vertebrates, semi-aquatic lechwe antelopes, and other Bovidae (discussed in Sections 4.11 & 6.4). The black dotted line denotes the Southern Equatorial Divide: the composite landform of ancient and actively evolving watersheds demarcating the Congo-Zambezi watershed. Key parts of this composite landform have changed rapidly around geobiotic congruities, which have respectively contained and abetted dispersals in adjacent basins (Section 8.6.2). Dotted yellow lines approximate the boundaries and/or extent of geobiotic-contiguities. Geobiotic dynamics have been focussed around, within, and across these landforms - containing dispersals of organisms and/or controlling vicariant speciation. The Choma Ridge and Luangwa Corridor are hypothesized to approximate the principal axis of the Arid Corridor, which intermittently facilitated dispersals of biota between the savanna biomes of southwest and east Africa. Geobiotic congruities are numbered: 1 Cuanza-Cubango; 2a Cubango-Kunene; 2b Cubango-Owambo; 3 Cameia-Kasai; 4a Buluzi-Cuando; 4b Okavango-Kafue; 4c Lukanga-Kafue; 5a Luongo-Luapula; 5b Bangweulu-Mweru; 5c Chambeshi-Kafue; 6a Lufira-Kafila; 6b & 6c Lualaba-Upemba; 6d Upemba-Lufira; 7 Luvua-Mweru; 8 Rukwa-Rungwe.

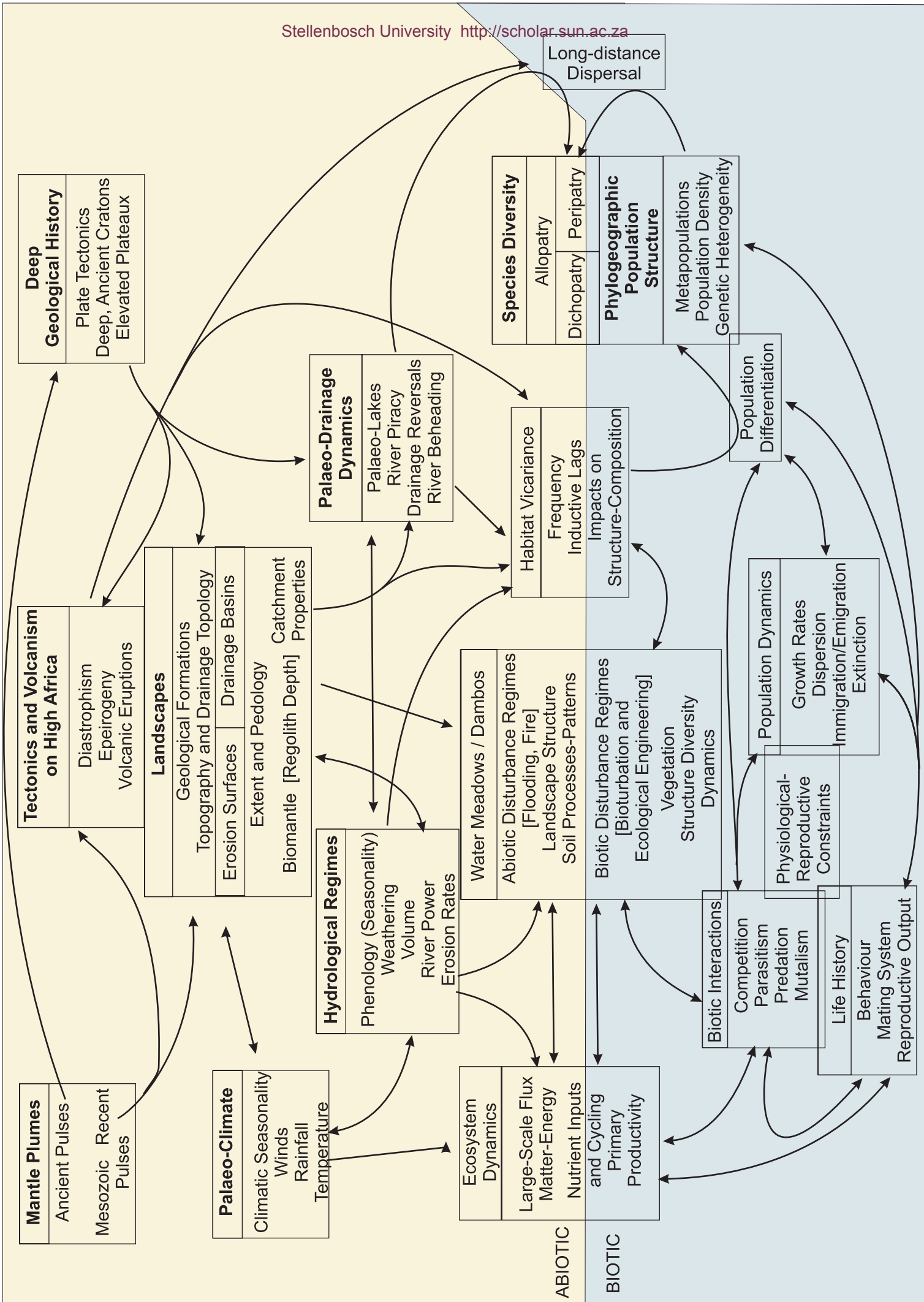


The persistence of truly ancient landforms that constitute the African plate are the most ancient controls (emplaced over 1 billion years ago) that have continued to influence evolution of biota (including lechwes) through the Quaternary. The craton rich African plate has exercised primary control over the basin and swell topography of High Africa, and thus ultimately controlled drainage across the continent for millions of years. This set of geological controls occupies the highest tier of causative agents. So all proximate causes either propagated directly from within this geological template, or, as exemplified by dynamics of climate, have been framed across its structures. Episodes of tectonism have modified certain landforms repeatedly across the ancient landscapes of High Africa. As an ultimate control, structured and manifested in Africa's ancient geology, tectonism has framed and focused more proximate controls over the evolution of wetlands and their biota. In the latter category, dynamics of palaeo-drainage form one cluster of dominant controls that have affected lechwe populations most profoundly. Consideration of these events featured prominently through the preceding chapters. At the other end of this spectrum, behavioural and ecological factors appear to have exercised the most proximate controls on lechwe evolution. This is exemplified by how mating systems - adaptive responses to local ecological conditions in their own right - have underlined the evolution of species-specific characters within lechwe taxa: notably adaptations resplendent in sexually dimorphic, breeding males.

8.5.1 Geologically Ancient Landforms

For many crores of years through the Cenozoic, and equally the Mesozoic, ancient geological formations stringently delimited the nature of palaeo-environments across Africa. They continue to dominate modern attributes of topography and pedology. Amalgamation of the Congo craton with the Kaapvaal and Zimbabwe cratons, ~1.8 billion years ago, individuated a stable portion of lithosphere that formed parts of continents thereafter. Moore & Larkin (2001) revealed how the broad-scale topology of the modern Cuando, Cubango and Upper Zambezi rivers represent landforms of at least Mesozoic age. These ancient lineaments were established when the African plate formed part of the Gondwana supercontinent. Persistence of these drainage channels testifies to an even older, antecedent, control by Africa's bimodal topography established in the Phanerozoic long before Gondwana times (Doucouré &

Figure 8.3. [Following Page] Interrelationships among mechanisms of causation invoked to explain evolution of the *Kobus leche* complex and floodplain grasslands (including water meadows) across the Katanga-Chambeshi region. The nature of causative mechanisms, and their interrelations, are discussed through Section 8.5.



de Wit 2003; McCarthy & Rubidge 2005). Thus, recurrences of epeirogenic flexuring, expressed under landscapes and drainage systems across High Africa, appear to have a truly ancient heritage (Du Toit 1933, 1939; Moore 1999; Chapter 4).

These geological controls account for ancient erosion surfaces, and also aspects of their unique biota. Integral to vast expanses of Zambebian grasslands - and an especially pertinent example - are the Underground Forests confined to seasonally flooded wetlands (White 1976b; Chapters 2 & 4). Their evolution testifies to persistent controls on biotic diversification by pedological conditions on ancient landforms. These plants have evolved on ancient erosion surfaces, preserved across High Africa, whose soils cap the deep regoliths integral to these landscapes. Mantling much of the region, regoliths control drainage in fundamental ways. Their geophysical determinants can be invoked to explain major patterns in evolution and diversity of both aquatic and grassland biota. Dambos exemplify how the majority of wetlands on High Africa constitute buffered landforms in which peculiar abiotic conditions account for interesting aspects of biotic diversification (Chapter 4). This especially applies to the islands of water meadows, where lechwes have speciated. It is pertinent to note that the hydrological and structural controls exercised by regoliths underlying these water meadows have yet to be studied in deserving detail.

8.5.2 Diastrophism and Tectonics in the East African Rift System (EARS)

The body of evidence collated in this study reveals how tectonism has altered landscapes across High Africa. Repeatedly, incidents of faulting and flexing initiated cascades of events: modifying existing landscapes and creating new landforms. Marked effects on wetlands and thus lechwes, are attributed to the Mid-Pleistocene Rukwa-Rungwe diastrophism. Considered overall, these geological dynamics constitute a set of ultimate controls that have caused significant evolutionary changes. Poignant examples of their effects include: drainage evolution within and around Katanga (especially across the Katanga Pedicle, and the Kamalondo and Mweru depressions); Palaeo-Lake Buluzi; control over drainage into the Kafue and Okavango basins in their shared graben; and associated control over the flow regime of the Zambezi River. In tandem with this relatively subtle tectonism, it appears that major Plio-Pleistocene diastrophism and volcanism, focussed in the Rungwe highlands and also around the Tanganyika graben, have repeatedly affected biodiversity across a vast portion of Africa including the Katanga-Chambeshi region (Chapters 4 & 5).

8.5.3 Dynamics of Palaeo-Drainage Systems

Tectonism propagating through the southwest extension of the EARS was the ultimate cause of key events, and it has changed key landforms repeatedly with concomitant impacts on biotic habitats and dispersal routes. The latter constitute important, but more proximate, aetiological mechanisms in their own right. These palaeo-drainage dynamics have interfaced so closely with tectonism, that one might question separation of these complementary mechanisms. But it is important to distinguish river impoundments, piracy, and headwater captures as discrete events from the widespread tectonism that modified individual landforms. Discrete bouts of regional tectonism expressed in many of these events, and reconfigured drainage topology. Tectonism acted through focussed impacts at key points across the landscape. Through spatially delimited effects, faulting and folding both created and destroyed palaeo-drainage systems. As expressed across larger spatial realms, these events caused the fusion and fission of aquatic landforms into novel configurations. With the benefit of hindsight, we can see how the majority of these networks had a transient tenure on High Africa. Thus, the tenures of the Trans-Katanga and Palaeo-Chambeshi drainage systems anteceded more recent drainage topologies. Yet, all these networks exhibit a common pattern in how they have inherited and bequeathed many persistent landforms. Consider the Kafue Flats for example. It entered the Pleistocene as part of the Palaeo-Chambeshi River, and was then occupied by a palaeo-lake (maintained by the Palaeo-Kafue River) until it became a floodplain in the modern Kafue River.

Dynamics entailed in the evolution of palaeo-drainage have acted as critical controls over where and when lechwe antelopes have been able to populate portions of High Africa. As importantly, persistence of key wetlands - notably the Kamalondo depression - provided the critical templates where aquatic biota not only persisted but speciated (Chapters 4 & 5). Whilst past climates most likely exercised critical control over hydrological regimes, especially the magnitude and phenology of flooding, these phenomena have hardly been studied. It is reasonable to invoke such inundations as a major control over disturbance regimes of water meadows and dambos. This leads logically to consider how palaeo-climates have influenced lechwe evolution.

8.5.4 Palaeo-Climatic Controls

Vrba (1995a-c) invoked dynamics of palaeo-climates as an ultimate cause of diversification in the African Bovidae (Chapters 2 & 4). Nevertheless, it seems that palaeo-climate has exercised only partial, if not slight, control over evolution of the *K. lechwe* complex. And if it was indeed important, gaps in evidence (especially precise dating of events and landforms) prohibit recognition of such influences. An

interesting example of coupling of drainage evolution with palaeo-climates is revealed in the complex evolution of the Zambezi River. The expansion of Kalahari Sands I (KS I preserved in the VFF) testifies to how arid conditions acted in concert with tectonic controls to modify the Upper Zambezi valley. These dynamics of palaeo-climates likely acted among a complex of causative agencies, as is revealed in how tectonics, palaeo-drainage and palaeo-climate interacted to control peripatric speciation in alcelaphine antelopes. The significance of their combined effects on biotic evolution is exemplified in how mammals dispersed across the former drainage barrier. The aridification of the Upper Zambezi River reveals that tectonics, and not climate, had a far stronger control over lechwes, with floodplains in the Okavango graben isolated from those to the north east in the Katanga-Chambeshi region. Because its timing is constrained against the Batoka Unconformity (in the VFF) this constitutes the singular example, elucidated in this study, of how both geomorphology and palaeo-climate exercised a dual, albeit asymmetrical, control over aspects of biotic evolution. Here, archaeological evidence constrained the geochronology sufficiently tightly to allow this intricate history to be elucidated, and so reveal subtle nuances of landscape changes (Chapter 5, Section 6.4, Fig. 8.1). Without such tight dates on key landforms, it is very difficult to elucidate how palaeo-drainage dynamics has interacted with past climates in an aetiological context.

8.5.5 Organismal Aptations and their Interactions with Higher Level Causes

A macroecological explanation of lechwe speciation would focus on “how” questions of proximate causation. It would focus on neontological phenomena as opposed to the palaeobiological. This would invoke ecophysiological traits with respect to allometric variation of the Bovidae, and place special importance on behavioural and ecological aptations (both adaptations and exaptations, *sensu* Gould 2002) of lechwes to their wetland habitats. Aptations of organisms hold centre stage amongst all mechanisms responsible for evolutionary patterns. This tenet recognizes the organism as the focus of selection and evolution (following Levins & Lewontin 1985, Ghiselin 1997, 2002a, and Rose 2005). Described through Chapters 4-6, and summarized above, water-meadows and thus lechwes have been buffeted in profound ways by dynamics ramifying through the abiotic tiers of the aetiological framework. Judged against the large literature detailing the behaviour and ecology of antelopes in African savannas (Sinclair & Arcese 1995; Du Toit 2003), lechwe antelopes differ clearly from terrestrial antelopes grazing savanna grasslands (Chapter 2). A combination of density dependent (demographic) determinants were invoked to explain how distinct mating systems have evolved amongst three extant lechwe taxa subject to local ecological conditions. These appear to have resulted primarily from male-male competition magnified by female mate choice (Nefdt 1996; Nefdt & Thirgood 1997);

these differences in behaviour have been invoked to explain morphological divergence across the five species (Chapters 6 & 7). An equally important set of causative agents should explain why and how lechwes have remained specialized grazers within floodplains. Their specialized morphological and behavioural adaptations have long been recognized as adaptations to graze muddy floodplains efficiently (Kingdon 1982; Smithers 1983). Pertinently, Williamson (1979, 1994) revealed how Red lechwes selected feeding and resting sites to minimize predation risk. As importantly, antelopes able to exploit this specialized “floodplain grazing-niche” reduce their exposure to cursorial and ambush predators, given that predation by large carnivores can markedly lower recruitment into populations of ungulates (Fitzgibbon & Lazarus 1995; Sinclair 1995; Mills & Funston 2003).

8.5.6 Concluding Remarks

It appears that abiotic controls have dominated evolutionary dynamics across the Katanga-Chambeshi by changing habitats and their attributes, especially vegetation and hydrological regimes via climatic and geological controls (as argued by Cracraft 1992). Within this framework, a complex of behavioural, physiological and morphological adaptations have acted together to constrain habitat selection by lechwes to water meadows. Vrba (1987) demonstrated how such specializations in resource-use among African bovids relate causally to their evolutionary dynamics, as exhibited by patterns of their speciation and extinction. The mosaics of organismal adaptations represented in lechwes render these antelopes sensitive to disturbances of their habitats. Following Vrba (1995a-c), lechwe exemplify stenotopic species whose dependency on specialized ecological resources has heightened their sensitivity to the abiotic agents of evolutionary causation, outlined above.

The Mexican Transition Zone (Huidobro *et al.* 2006), Central Highlands of North America (Near & Keck 2005; Kozak *et al.* 2006), and the rich endemism of Madagascar (Wilmé *et al.* 2006) reveal how strongly tectonism has controlled the evolution of biodiversity. Tectonism has exhibited distinct diastrophism in these regions, compared to its more subtle effects across the Katanga-Chambeshi region. In this respect, it is interesting that a recent macroecological review (Jetz *et al.* 2004) expressed surprise at how palaeo-environmental factors primarily explain avian biogeographical patterns across Africa. This study of lechwe evolution reveals how biogeographical explanations that incorporate comprehensive aetiological mechanisms shunt neontological factors into their appropriate, proximate position against deeper earth history. Considering the strong evidence that dynamics of palaeo-environments determined where, when and how lechwes and many other vertebrates evolved, it is not surprising that centres of endemism of Afrotropical birds not only reflect unusually high speciation rates, but correspond to

landscapes buffeted by late Cenozoic tectonism (Fjelds  2003; Cotterill 2006). Representative searches for biogeographical causation are challenged to delve deep into geological time, to consider more encompassing tiers of causation where macroecology is not just lack resolution, but is scarcely applicable (Brooks & McClennan 2002). As they are interpreted in neontological currencies, macroecological patterns obscure the causative agencies, underlying evolutionary patterns and processes we are trying to elucidate. Consideration of deeper controls over the evolutionary history of the *K. leche* complex reveals that, underlying palaeo-drainage dynamics, tectonism ultimately explicates the origins of principal signals in biogeographical patterns.

8.6 TOWARD AN AETIOLOGICAL BIOGEOGRAPHY

"[A]Etiology is so fundamental to scientific classification that is hard to exaggerate its importance. Its neglect has had so many disastrous consequences in the past that the point will be repeated time and again in the present work" M. T. Ghiselin (1997: 74)

This title of an ‘aetiological biogeography’ is indeed something of an oxymoron, because biogeography is a palaeotiological science (sensu Whewell 1837, 1947), at least when pursued along its historical and interpretative trajectories to decipher the origins of biota in space, time and form. Nevertheless, the macroecologists’ endeavours to draw up their strictly nomothetic version of the discipline is weakened by the what awaits to be recognized as a strange neglect of the most informative data available to biogeographers. The myopia of macroecology ignores, at considerable cost, how idiographic narratives detail the individuation of biotic assemblages. The latter are quintessential if we are to succeed in constructing ultimate syntheses in evolutionary biology (Chapter 1). This scientific poverty of macroecology more than justifies belabouring critical issues in these conclusions. As importantly, the principal causes of lechwe evolution are highlighted, because the evidence available points to their far reaching control over the evolution of biodiversity across the Katanga-Chambeshi region. Hence, the closing emphasis, in this section, on how biogeographical classifications should be structured by causative mechanisms.

8.6.1 Spatial and Temporal Foci of Evolutionary Dynamics

The congruence described amongst aquatic molluscs, terrestrial and arundiphyllic (reed-loving) birds, several groups of fishes, reptiles and mammals (Chapter 4) might be described as biogeographic tracks - if we are to apply a contentious panbiogeographical concept (Crisci *et al.* 2003; Huidobro *et al.* 2006). It would stretch speculation too far to attempt to delimit any such tracks across the Katanga-Chambeshi region. The dearth of phylogenies for sufficient surrogate taxa precludes this. It would amount to understanding finer-scaled details in diversification of entire biota across and within regional landforms.

A prerequisite step would be to establish more precisely what the concept of a “biogeographic track” encompasses, beyond “...a sector which connects nodes and affinities” (Heads 2004: 1888). (It appears we are dealing with loaded definitions of concepts as controversial as the species category, which might well decree a review of the scope and complexities of Chapter 3.) The second task would be to reconstruct phylogenies of a diversity of surrogate indicators in sufficient detail, and then identify congruent centres of endemism, and timings and routes of dispersals. This is no small task, as judged just by cichlid fishes and lechwe antelopes!

Nonetheless, these patterns of diversification elucidated among the *K. leche* complex reveal key details in what might be termed a complex jigsaw puzzle of biogeographical history. Many other indicator taxa expand the resolution to understand the natural history of the Katanga-Chambeshi region. Together, they reveal how biotic evolution has been controlled at key points in the landscape (summarized under the Dynamics of Palaeo-drainage Systems, Section 8.5.3). The evolutionary history of these biotic indicators point to key processes and spatial patterns in evolution of aquatic biodiversity across south-central Africa, and reveal how critical processes were focussed around particular landforms. Key speciation events in the *K. leche* complex, which occurred in the Middle Pleistocene, were contained within the Upemba-Lufira and Kafila-Mweru-Bangweulu depressions. These were not only integral to profound rearrangements of the Trans-Katanga and Palaeo-Chambeshi drainage systems, but correspond to a notable episode of tectonism and volcanism focussed in the Rukwa-Rungwe highlands. Complimenting and extending these processes, subsequent events extended to the Okavango-Kafue graben (late Middle to Late Pleistocene). The Batoka Unconformity of the VFF (Chapter 5) is associated with a distinct faunal turnover in the African Pleistocene. Impoundment of the Zambezi River opened the Arid Corridor across the Okavango graben, and its closure coincided with the demise of Palaeo-Lake Bulozzi and Lake Patrick (Figs 8.1 & 8.2). These interrelated events hold special aetiological significance in how they controlled evolution, as revealed in semi-aquatic lechwes and terrestrial mammals. The latter events can be plausibly invoked to explain the origins of the species flock of cichlid fishes, which Joyce *et al.* (2005) naively associated with the tenure of Palaeo-Lake Makgadikgadi (Sections 4.11 & 6.4).

Three pertinent properties stand out in these zones exhibiting focussed biotic and geomorphological dynamics. One, each is delimited by discernable geological boundaries. Two, geodynamics, namely changes in palaeo-drainage, acted on biota intermittently to control dispersals and isolations of populations. Three, they are characterized by young landforms created and modified within ancient geological platforms. Thus, all these zones constitute tectonically active foci, where nascent landforms

have arisen on ancient erosion surfaces in cratonic basins. In the context of the Katanga-Chambeshi region, examples of such young landforms include: the Kamalondo and Lufira depressions; the Bangweulu-Kafila-Mweru rifting zone; and the Rukwa-Rungwe region dividing the Malawi and Tanganyika rifts.

Each landform, around which geobiotic dynamics have been focussed might be termed a node - a concept persistently argued for by panbiogeographers (Crisci *et al.* 2003), as a geographical region across which are focussed discontinuities in biogeographical patterns and processes. Heads (2004: 1889) described a node as “a centre of presence and also absence, as well as being an edge or break of distribution.”. Huidobro *et al.* (2006), for example, described the Mexican Transition Zone as a node; more significantly, they emphasized the congruence of biotic and geological dynamics in time and space across this landscape. Some caution is in order here, because the node appears to be a “catchall concept” applied in panbiogeography to describe a vast arena of biological and geological phenomena (J. Cracraft *pers. comm.*). So I employ the term “contiguity”, alongside “geobiotic”, to describe landforms that can be unequivocally delimited within boundaries that contain the processes that changed both biota and landforms. Their characterization is feasible across the Katanga-Chambeshi region, where such geobiotic contiguities are clearly delimited by folds and/or faults, within ancient drainage basins. I define a contiguity as a landform within, or across, which geobiotic dynamics have been focussed; and so they exhibit a local peak in frequency within encompassing landscapes. As revealed by their historical significance, contiguities stand apart when compared to adjacent landscapes. Close relationships among geological and biological dynamics around, and within, these landforms can be aptly described as geobiotic congruities. These congruent patterns are seen where controls on speciation (vicariant and also peripatric) intersect within, and across, the Rungwe highlands, and the Mweru and Okavango-Kafue graben, respectively. The diastrophism and volcanism of the Rungwe highlands excepted, some geobiotic contiguities have been modified only subtly by Neogene and Quaternary epeirogeny and faulting, especially around the Okavango-Kafue and Buluzi geobiotic-contiguities. An especially interesting history of geobiotic dynamics has been focussed around the Zambezi valley between the Buluzi basin and Batoka Gorge (the Buluzi-Batoka congruity). The Kafue and Upemba rifts are both nascent landforms inherited from more ancient (Triassic) tectonism. Diastrophism around the Mweru and Upemba geobiotic-contiguities manifested in more dramatic changes to topography. Here, the Kundelungu and Upemba horsts and their associated Kamalondo and Lufira depressions constitute a complex of contiguities, where geobiotic dynamics have markedly enriched the biological and geomorphological diversity of Katanga (Chapter 4, Fig. 8.2).

So geobiotic contiguities reflect where geological dynamics, contained within their associated fault structures, have synergistically altered the biodiversity and geomorphology on High Africa. In certain respects, this convergence of evolutionary dynamics around, across, and within geobiotic contiguities parallels analogous patterns exhibited across New Guinea and the Mexican Transition Zone (Huidobro *et al.* 2006), where mobile terranes and their biota have been rearranged around craton margins in a tectonically active region. Albeit, geobiotic contiguities in the Katanga-Chambeshi region are of orders of magnitude smaller area; and constitute nascent landforms on, or bordered by, ancient cratons and their bounding mobile belts. Considered in a broader context, the Katanga-Chambeshi region abuts important theatres of evolutionary activity: pertinently the Eastern Arc and Albertine Rift, and Africa's Great Lakes. Moreover, African landscapes differ fundamentally from New Guinea and the Mexican Transition Zone (see Huidobro *et al.* 2006). The latter's dramatic geodynamics along abutting, active plates contrast against the tectonic behaviour of the African plate, which has exhibited prolonged lateral stability; although its uplift has manifested in widespread epeirogeny, with distinctly local diastrophism and volcanism (Chapter 4).

8.6.2 Biogeographical Classifications Structured by Causative Mechanisms

The complexity of the nested hierarchy of patterns of causation sketched out above (Sections 8.5 & 8.6.1) structures a narrative of fascinating evolutionary history. Framed by a synthesized knowledge of palaeo-environments, this study's scrutiny of a few threads of evolutionary history has described one suite of players across a most complex evolutionary stage. Here, the five taxa comprising the *K. leche* complex are revealed as very young protagonists in a most ancient play on High Africa. Our understanding of such historical phenomena deepens - in fact more precise explanations accrue - where we can tease apart individual causes of associated patterns. Biogeographical patterns not only become much more coherent, but tell us so much more about their origins when structured into classifications contingent on causal mechanisms. Furthermore, lechwes are revealed as surrogate indicators of patterns and processes that have exercised broader controls over a larger evolutionary arena on High Africa. Insights obtained into the evolution of these specialized mammals reveal hitherto under appreciated affinities among aquatic biota across an archipelago of wetlands and Zambezi grasslands. Geobiotic congruities appear to have exercised critical controls over their diversification. A more encompassing view of Quaternary history across the Katanga-Chambeshi region reveals how the complementary palaeontological sciences can unravel links shared in interwoven threads of evolutionary history. As introduced in Section 1.6, patterns derived from extrapolationism and sequencing can be related, with

dissonant signals, into consilient explanations. The central demonstration of this epistemic strategy applies to what we have now to know about the evolution of the *K. leche* complex.

8.7 CONSERVATION PRIORITIES

This section augments previous arguments (Cotterill 2005; Section 1.3) that the conservation of the Katanga-Chambeshi region ranks very high on the global agenda for unprecedented investment. A successful conservation strategy is challenged to combine and balance several objectives, which are focussed on maintaining ecological integrity across large landscapes. Summarized in turn, the following mutually supporting arguments endorse conservation of lechwe populations, and the wetland archipelago across which they have evolved.

8.7.1 Wetland Ecosystems, Wildlife Spectacles and Endangered Phenomena

Dense populations of lechwe antelopes previously dominated the ecology of each floodplain within south-central Africa's wetland archipelago. Black lechwes were estimated to total at least 250 000 on the Bangweulu Flats into the early 20th century, and exemplify how spectacular numbers of lechwe antelopes formed seasonal concentrations in concert with hydrographic cycles. Lechwe hold a keystone role in floodplains, where their herbivory and high biomass dominate trophic pathways. Lechwes are uniquely adapted to exploit water meadow grasslands, the aptly named "lechwe pastures", through the seasonal cycle of floodplains. Foraging activities by large concentrations of Kafue lechwes was shown to benefit flocks of foraging birds attracted to the disturbed substrate, overall enrichment of floodwaters and soils in the lechwe pastures. Allied with substrate disturbance, eutrophication of inundated floodplains sustain zooplankton blooms, so turning these water meadows into important breeding grounds for fishes (Chapter 2). Brower & Malcolm (1991) and Mittermeier *et al.* (2004) have emphasized that such immense concentrations of biota qualify as important conservation targets, where they are still extant. Regrettably, only vestigial fragments of formerly vast populations of lechwes survive, and such concentrations of lechwe are of special conservation significance where they reflect breeding activity. The leks of *K. kafuensis* are the well studied example, whose protection is critical to conservation of this species (Chapter 2). All such concentrations are endangered phenomena.

8.7.2 Biodiversity Values, Vibrant Evolutionary History and Flagship Species

The evolutionary dynamics of lechwes detailed in this thesis bring new context to conservation planning and actions across the wetland archipelago that embraces Katanga. A wealth of evidence emphasizes important conservation values with respect to high endemism and recent evolutionary activity focused

around geobiotic-contiguities across the Katanga-Chambeshi region. Erwin (1991) emphasized that clades comprising recently evolved species should be recognized as prominent targets for conservation strategies. These lechwes exemplify an evolutionary vibrant clade, together with the species-flock of serranochromine cichlid fishes (see Joyce *et al.* 2005), in the Katanga-Chambeshi region. All these taxa, and especially their habitats, deserve priority conservation attention, and all underscore the urgency and importance of conserving hotspots of biotic evolution across the Katanga-Chambeshi region, especially when one acknowledges their evolution has entailed congruent controls across geobiotic-contiguities (Section 8.5).

Extirpated by the mid-20th century, and so passing away unacknowledged, the extinction of Roberts' lechwe is revealed as an unrecognized pruning of the *K. leche* species complex by anthropogenic agencies. The biogeographical significance of the Pambayshe Swamps are attested to by at least three extant endemic fishes (Section 4.11, Appendix 2), additional to the extinct Roberts' lechwe. Weaknesses in taxonomy and thus conservation planning and action stand out in this respect. Extinction of *K. robertsi* enforces vigilance against allowing any other such taxa to slide to extinction because of errors in biological knowledge and inadequate conservation attention.

Charismatic vertebrates also constitute umbrella and flagship species. They focus concern and support toward conservation of biodiverse landscapes. Alongside Wattled crane, *Grus carunculatus*, and Shoebill, *Balineiceps rex* (both birds attract considerable conservation attention in their own right) all lechwe species highlight the conservation importance of vast wetlands across the Katanga-Chambeshi region. Analogous to *K. smithemani* and Bangweulu tsessebe, *Damaliscus superstes*, in the Bangweulu depression, *K. anselli* can be singled out as the charismatic antelope endemic to Upemba Swamps (Cotterill 2005).

8.7.2 Regional Conservation Strategies

Recent biogeographical reviews of Afrotropical biodiversity (e.g. Mutke *et al.* 2000; Fjeldså 2003; De Klerk *et al.* 2002a, 2002b, 2004) revealed that high topographic heterogeneity is an important determinant of high species richness and endemism. This is expressed in the high heterogeneity of Katanga's landscapes (rich in biotic habitats) on nascent landforms created in ancient landscapes by Plio-Pleistocene tectonics and palaeo-climates (Broadley & Cotterill, 2004; Cotterill 2004, 2006). Katanga's wetlands exhibit a complementary high endemism (Malaisse 1997, Chapter 4, Appendix 3). High values for species richness and endemism equate the Katanga-Chambeshi region with the forests of the Eastern

Arc and East African Coast, and west African Guinean forests (Broadley & Cotterill 2004; Cotterill 2006). More subtle aspects of Katanga's geophysical history reveal that its wetlands were previously connected across a larger archipelago, and encompassed within the Katanga-Chambeshi region. Cognisance of this history brings otherwise fragmentary data into context. Conservation plans and activities cannot ignore ecological and evolutionary linkages across the landscapes of the Katanga-Chambeshi region preserved in biogeographical patterns and extant hydrological links.

A credible conservation strategy cannot ignore larger spatial patterns and processes across ecological complexes. Water flux contained within river catchments is a critical ecosystem process across the landscape mosaic. Centred around principal drainage channels, as exemplified by the Florida Everglades Ecosystem, water flow across the Florida Peninsula drives longitudinal, vertical and lateral fluxes of matter and energy. Persistence of all these interlinked ecological and geomorphological processes is essential to the integrity of all habitats and biodiversity embedded in the larger landscape (Steinman & Denning 2005). With respect to south-central Africa, conservation plans and actions cannot be confined to only maintaining principal wetlands (Bangweulu, Kamalondo, Lufira, and Okavango). Such challenges are exemplified across the Upemba and Kundelungu Complex (UKC) of Katanga's protected areas, where the combined richness of ecological patterns and processes ramify from local habitats through to entire catchments covering the Zambian-Congo drainage systems. The importance of maintaining the integrity of hydrological processes cannot be overemphasized, if a protected area network is to maintain biodiversity over the longer term within and among these wetlands (Cotterill, 2004, 2005, 2006). Evolutionary and ecological options are more likely to persist where landscape mosaics are managed on sound ecological principles.

The case of the Katanga-Chambeshi region parallels the detailed argument by Cowling *et al.* (1999) for a regional conservation strategy to encompass biodiverse regions across southwest Africa. Besides Lake Mweru and the Luapula Flats, astride the common border of DRC and Zambia, notable protected areas and biodiversity hotspots in Zambia extend from the Ikelenge Pedicle in the west (Cotterill, 2002a,b), embrace the UKC, Bangweulu Flats and Kasanka National Park, and extend across the Luongo and Kalungwishi Rivers (including Lusenga Plain) to Mweru-Wantipa and Sumbu (see Leonard 2005 for site descriptions). This region is situated between the two pedicles of Katanga and Ikelenge, and extends eastward to the Tanganyika rift and Rungwe-Rukwa highlands, and constitutes an arena of ecosystem management. It encompasses the Kamalondo, Lufira, Luapula-Mweru, and the Bangweulu-Chambeshi drainage systems. Conservation values of all these extant freshwater ecoregions were detailed by Thieme

et al. (2005). The logical mechanism is a strategy developing a Trans-Frontier Conservation Area (TFCA) borrowing on strengths pioneered in southern Africa (Hanks 2001), as developed for the Four Corners area centred on the Victoria Falls and Kazungula (Timberlake & Childes 2003). Maintenance of ecological integrity is a prime objective for such international conservation projects, challenged to acknowledge how interlinked mosaics of drainage systems share significant evolutionary history. This especially applies to Katanga. A sound future for sustainable socio-economic development in this mineral and agriculturally rich region hinges on maintaining both ecological integrity and biodiversity across Katanga and northern Zambia.

8.8 NEW PERSPECTIVES, OPPORTUNITIES AND CHALLENGES

This study has sketched out an evolutionary history of lechwe antelopes, consolidated by reviews of other indicator taxa. Construction and elaboration of a narrative of landscape evolution proved quintessential to frame and refine an understanding of key evolutionary events. It is interesting to acknowledge how signatures of genetic evolution dovetail with facets of Plio-Pleistocene landscape evolution, such that this knowledge combines as a natural history of the Katanga-Chambeshi region. These insights into speciation and dispersals of selected indicator taxa reveal an evolutionary theatre, whose biota has been enriched by both endemic and dispersant species. The narrative of their evolution incorporated only some pertinent details (where known) of Plio-Pleistocene palaeo-environments. Yet, we are challenged to understand a vast canvas of history across immense, ancient landscapes. Considerable opportunities exist for future studies to flesh out how the biodiversity of south-central Africa has evolved with respect to the geodynamics compiled through Chapters 4 and 5 (Fig. 8.3). Here, geobiotic-contiguities highlighted above (Section 8.5.5, Fig. 8.2) constitute landforms whose evolutionary dynamics have exercised far reaching influences on the region's biodiversity (aquatic and terrestrial). More such undiscovered geobiotic-contiguities quite likely exist across High Africa.

The Katanga-Chambeshi region frames a wetland archipelago encompassed within the Zambezian phytochorion of high plant endemism. It is most pertinent to acknowledge the diversity of the flora in these wetlands is poorly known (Chapter 2). Comparisons of what is known about patterns of endemism and speciation across these overlapping bioregions leads to five inferences about their shared evolutionary histories. One, patterns of aquatic and botanical evolution across High Africa reveal a segregation in their evolutionary dynamics, with respect to how biota evolved across the wetland archipelago in relation to vegetated landscapes (as understood by forest-savanna expansions and contractions driven by palaeo-climates). Two, diversification of aquatic vertebrates in the Katanga-

Chambeshi region has been focussed across particular landforms as a function of their stenotopy (exemplified by lechwes). Three, conceptualized as geobiotic-contiguities of biogeographical significance, geodynamics and biotic processes have been focussed within and across particular landforms to forge congruent patterns. Although evolution of aquatic (and some terrestrial) species exhibit marked control around geobiotic-congruities, such patterns are not apparent in the Zambebian flora. Four, overall congruence in endemism of aquatic vertebrates and terrestrial plants in both bioregions points to ultimate control by High Africa's ancient topography (of basins and swells) on biodiversity evolution. Five, there is considerable scope to compare evolutionary dynamics of their respective biota, especially their wealth of endemics.

Through a process of consilient illumination, this multidisciplinary study combined colligated facts to reveal intricate patterns in how drainage systems have evolved. For any such study in African biogeography stands to benefit from reconstructing the evolutionary dynamics of their habitats. Where feasible, the scope of such explorations can extend from genomics to geology, seeking out interrelated signatures preserved in organisms, fossils and landforms, from which can be deciphered shared evolutionary histories. The consilient resolution obtained from colligations of interlinked patterns can extend to decipher causes of historical phenomena. This is demonstrated, for example, in the research needed to understand the origins of biota endemic to the sandy dilungu of Katanga's plateau (see Broadley & Cotterill 2004; Cotterill 2006) stands to gain powerful insights from exhaustive consideration of all interlinked historical evidence. Close scrutiny of all available data can be expected to reveal unsuspected links between colligations of historical patterns that manifest in consilient insights. These opportunities motivate explorations to extend beyond a platform of knowledge built by taxonomic and ecological studies of dilungu and their biota. Expansion of such studies, along evolutionary scales, can begin by recognizing these dilungu as surviving outliers in the Mega-Kalahari sand sea, whose evolution reflects intimate control by palaeo-climatic dynamics. Analogously, study of the evolutionary dynamics of the mavunda (*Cryptocephalum*) and mushitu (Guineo-Congolian) forests in the Zambebian region will obviously benefit from examining how palaeo-dynamics of these forest islands have interfaced with grasslands, and the vaster expanses of miombo dry forests. Further explication of their shared history stands to benefit especially where common causes (in their ramifying effects) can be discerned within an aetiological framework, analogous to that sketched above with its focus on lechwe evolution (Sections 8.4-5). It is here that studies of biodiversity and landforms associated with dilungu, mushitu, mavunda, and equally miombo, stand to benefit from evidence gleaned about how key events in landscape evolution interacted with palaeo-climates (Chapters 4 & 5, Fig. 5.7). To date, explanations of

these dynamics have only considered palaeo-climate alone as the primary determinant (Benson & Irwin 1965a-c, 1966; Barham 2000, 2002).

Currently, the incompleteness of historical data weaken such cross-disciplinary explorations of the origins of biota and landforms. For example, the archaeological record provided much needed temporal resolution on aspects of biogeographical patterns. The availability of such evidence is distinctly patchy, whilst a widespread lack of geochronological precision is a general problem that weakens interpretations. Moreover, it cannot be denied there are vagaries in the archaeological dataset, applied to the VFF and Okavango-Kafue graben. Greater precision in our understanding stands to improve on three fronts. Firstly, sequencing and analysing more genetic loci of sufficient indicator taxa will go far to remedy our vast ignorance of phylogenetic and phylogeographic patterns. Secondly, a far more critical weakness is that the biodiversity in much of south-central Africa has barely been explored. Existing museum collections are decades old, with a high proportion of taxa represented by very few specimens. There is no substitute to building comprehensive natural science collections, which can only accrue through thorough inventories that target poorly known taxa and regions. Multi-disciplinary research on Madagascar's biodiversity by Yoder *et al.* (2005) exemplifies the great benefits that flow to science, society and conservation when structured inventories synthesize vouchered facts. (This is an apt epistemic example of how specimens preserve tentelic information (Cotterill 2002a).) Thirdly, and as critically, unprecedented resolution will follow from precise dating of landforms across High Africa. Quantifications of cosmogenic isotopes provide a powerful technology to unravel these facets of earth history (see Cockburn & Summerfield 2004; Von Blanckenburg 2005). Obtaining such empirical data for key taxa and landforms is critical to resolve core puzzles highlighted in this study. In particular, we will be better positioned to understand how Zambezian grasslands have evolved with respect to palaeo-environmental dynamics across High Africa, and especially palaeo-drainage dynamics. Current uncertainties are exemplified in our presently sketchy understanding of only a few species and proximate patterns in the biogeography of water meadows and dambo grasslands (Chapters 2 & 4).

Hominids populated Plio-Pleistocene landscapes across High Africa, where a wealth of archaeological evidence documents the transition from the Early to Middle Stone Age. The richness of the archaeological record preserved around the Victoria Falls, Kafue Flats and elsewhere across graben and river valleys of the Katanga-Chambeshi region testifies to how hominids exploited wetland margins along rivers as vast as the Palaeo-Chambeshi. Living sites preserved on lacustrine sediments suggest these hominids tracked expansions and contractions of palaeo-lakes closely. It is remarkable that we can

only guess at which species of *Homo* knapped such an abundance of ESA and MSA tools! In part at least, the Katanga-Chambeshi region, especially its wetland archipelago, constituted a template that framed critical episodes in hominid evolution. So this is yet another argument to study and manage these landscapes with due seriousness; and this study of lechwe antelopes has pointed to alluvial and lacustrine sediments to search for hominid fossils. Hopefully, future researches will yield new evidence to better understand our own species' origins on High Africa. To conclude, the evidence synthesized in this study points to a wealth of intricate evolutionary case studies, awaiting elucidation, preserved across the Katanga-Chambeshi region. This juxtapositioning of a wetland archipelago amongst terrestrial landscapes across High Africa makes for a unique evolutionary theatre, across which respective patterns of speciation can be explored. Its rich evolutionary history parallels and might well become known to exceed that of the Gálapagos and Africa's mountains and Great lakes.

“The inland waters of Africa remain an unexplored frontier, another unknown in a continent whose darkest secret is human ignorance of its rich natural history” J. Kingdon (1990: 232)

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Appendix 1. List of museum specimens examined of the *Kobus leche* complex, which vouch for many of the localities plotted in Fig. 2.1. Pelage and mensural data obtained from selected specimens are analysed in Chapter 7. Names of African countries updated to follow Broadley & Minshull (1988).

***Kobus anselli*: 35 specimens**

DEMOCRATIC REPUBLIC OF CONGO (DRC): Kadia 8°22'S, 26°37'E (MRAC 17692, 17958-17962, 18274-92). Katobwe, Lualaba River, 8° 51'S, 26°5'E (FMNH 27571-7). Kiabo Kaleka, 8°44' S, 26°02'E (MRAC 18565). Moleka, Lac Kabele, N of Bukama, 8°52'S, 25°57'E (MRAC 19161). Region du Lac Kabamba, 7°55'S, 27°0'E (MRAC 19162-3, 19168).

***Kobus kafuensis*: 121 specimens**

ZAMBIA: Basanga, Namwala, Kafue Flats 15°7'S, 26°52'E (NMZB 18713). Blue Lagoon Ranch (NMZB11599). Chinsali, 1527d1 (BM 1969.1147). Kafue Flats (BM 1921.5.7.4, FMNH 57675, NMZB 4904, 10302-4). Mazabuka (NMZB 8830-1). Lochinvar Ranch, Kafue Flats (BM 61.727 Lectotype of *kafuensis*, NMZB 5001 Holotype of *grandicornis*, NMZB 4613, 5002-8, 5010-2, 9849-50, 10583-5, 10587-8, 11039, 11042-54, 11512-7, 11855-8, 11856-8, 11862-3, 11888-90, 11894-6, 11899-11901, 11905, 11907, 11954, 11956-7, 11960-4, 11975, 11982-5, 11988-91, 17639-40, 17645, 17647, 17651-3, 17655-6, 18631-4, 18637-8, 18650, 18657, 18662-4, 18666-7, 18725-6, 28248-9, 33305, 50585, BM 1966.435-9). Luwato, Kafue River, Chinsali 1527d1, (BM 1932.9.1.229, 1932.9.1.320.). Masofu, N of, (MRAC 3057). Mafungu, N of (MRAC 3065). Namwala, Kafue Flats, 1526c4 (BM, 1921.7.18.34).

***Kobus leche*: 65 specimens**

ANGOLA: No precise locality (BM, 1937.2.18.1), Luena tributary to Zambezi (NMZB 8359). Galangwe Region, 120km N of Villa da Posste, Bord du Rio Cubango, 13°50'S, 16°18'E (MRAC 18924).

BOTSWANA: No precise locality (BM 1997.268, NMZB 56412-3). Chiefs Island, Okavango Swamps (NMZB 56370). Chobe Game Reserve (NMZB 56410-1, 56414-6, 56418, 56420). Chobe Game Reserve, Ihaha (NMZB 50588). Chobe GR, Kasane (NMZB 50587), Chobe GR, Sidudu (NMZB 56407). Chobe GR, Nanyanga (NMZB 50586). Chobe River near Dinyanta (BM 1881.7.27.2). Gomoti (NMZB 56372-3). Kabulubula, 15 m W of Kasane (NMZB 56417). Khwaai River (NMZB 18635-6, 22518). Kochikou (AMNH 161024). Kwaai, Mochaba River (AMNH 83543-4, 83546, FMNH, 34468-9, 34471). Linyanti River (FMNH 135330-1). Maun, 1923c4 (NMZB 5491-4). Nokaneng (USNM 470191-2). Pontoon, Okavango, 1922d2 (NMZB 59200). Botletle River (formerly Zoaga River), Lake Ngami 20°7'S (BM 1850.7.4.2 Holotype of *leche*, CUMZ H22.682 Topotype).

NAMIBIA: Caprivi (NMZB 4434), Sambio-Mbunga, Grootfontein (BM 1935.9.1.350).

ZAMBIA: Barotseland (BM 1899.3.21.1-2). Busanga Plain 14°11'S, 25°52'E (NMZB 34076-8, 34198). Kaboshya, Lukanga Swamp, 1428d1 (NMZB 7527). Kabwe Stream, Sichifulo, Kalomo (NMZB 10591). Kasempa District, E of Sefpa Rd, 13°28' S, 25°50' E (NMZB 10166-7). Kawambwa District, Chisenga Island, Luapula Flats, Lake Mweru, 9°52' S 29°7' E (NMZB 2751, 2753). Mambova 17°37' S, 25°7' E (NMZB 11967). Masozhi, Kasempa District (BM 1961.728). Minginga-Luswishi Confluence, Ndola District, 13°20'S, 27°43'E (NMZB 5066-7). Ngimbu, 14°45'S, 24° 1.6'E (AMNH 118473-4). Sekute Fishing Camp, 17°37'S, 24°7'E (NMZB 11933). Simarama Flats, 1725c1 (NMZB 11934).

***Kobus robertsi*: 4 specimens**

ZAMBIA: Kalungwishi River (RMAC 8211). Luena River (BM 13.11.26.1). Luongo River (BM

13.11.27.1 Neotype, BM 14.1.7.11).

***Kobus smithemani*: 68 specimens**

DEMOCRATIC REPUBLIC OF CONGO (DRC): Katanga Pedicle (MRAC 2924).

ZAMBIA: Bangweulu Flats (BM 1916.7.16.2, MRAC 2687, 7364-6, 7923-5, 7939). Bwela Flats, Chinsali, 1031b4 (BM 1933.3.6.46). Chilorle Flats, Chambeshi River, 1031d2 (BM 1907.11.15.1, 3).

Chitambo, N of, Bangweulu Depression, 1230a1 (BM 99.2.22.1 Holotype). Imbo Jumo, Luapula River (BM 1921.7.18.36). Itiri Plain, SE Lake Bangweulu, 12°7'S, 30°37'E (NMZB 11114-22).

Kasama, S Bangweulu Flats (MRAC 8209). Kasheshe, Chambeshi River (BM 1912.3.16.1). Lake Bangweulu (BM 2000.715, 1904.2.15.2). Lake Bangweulu, Mpika Area, 1131b4 (NMZB 1771, 4, 2750, 2756, 5222, 17594-8, 17600-6, 20153-5). Lake Chiyaya, Bangweulu Flats (AMNH 161159-60). Lake Tshale, S Bangweulu Flats (MRAC 8210). Luapula, Bangweulu Flats (MRAC 8213).

Lukanga Plain, SE Bangweulu (BM 1961.729, NMZB 1772, 1776-7). Nashinga Dambo, Chilorle Flats, Chambeshi River, 1031d2 (BM 1907.11.15.2). Panta, S Bangweulu Flats (MRAC 8212).

Mukamba, 1229b2 (BM 1912.12.21.1). SE Lake Bangweulu (NMZB 2757, 5213, 5224, 11141-5, 11372, 11374).

Appendix 2.1 Details of 140 haplotypes of CRHV1 discovered in the *Kobus leche* complex, under which are listed all individuals sequenced, as described in Chapter 6. Sequence variation classified using Collapse (Posada 1999). 121 sequences represent skin snips obtained from trophy males for *K. kafuensis* (Kafue Flats, designated Kk), *K. leche* (Busanga Swamps, designated Bu, and Okavango Delta, designated Kl) and *K. smithemani* (Bangweulu Flats, designated Ks). As detailed below (Appendix 2.3) and described in Chapter 7, sequences of Cytochrome b and the nuclear intron SPTBN were obtained for a subsample of these fresh and museum specimens.

- | | |
|----------------|---------------|
| 1. Bu1 [1] | 31. KaQ1 [1] |
| 2. Bu2 [1] | 32. KaQ2 [1] |
| 4. Bu11 [1] | 33. KaQ3 [3] |
| 5. Bu12 [1] | KaQ5 |
| 6. Bu13 [6] | KaQ6 |
| Kk20 | 34. KaQ4 [1] |
| Kk64 | 35. KaQ7 [1] |
| Kk69 | 36. Kk1 [1] |
| Kk87 | 37. Ks12a [6] |
| Kk90 | Ks10 |
| 7. Bu5 [2] | Ks1am |
| Kl31 | Ks21a |
| 8. Bu6 [2] | Ks3 |
| Kl31a | Ks41a |
| 9. Bu7 [1] | 38. Kk17 [3] |
| 10. Bu8 [1] | Kk58 |
| 11. Bu9 [1] | Kk92 |
| 12. Ka10 [1] | 39. Kk18 [1] |
| 13. Ka11 [1] | 40. Kk32 [1] |
| 14. Ka12 [1] | 41. Ks35a [4] |
| 16. Ka16 [1] | Ks13a |
| 17. Ka17 [1] | Ks22a |
| 18. Ka2 [1] | Ks37a |
| 19. Ka24 [1] | 42. Kk39 [1] |
| 20. Ka26 [1] | 43. Kk44 [1] |
| 21. Ka27 [1] | 44. Kk51 [1] |
| 22. Ka28 [1] | 45. Kk53 [1] |
| 23. Kk100 [17] | 46. Kk54 [2] |
| Kk19 | Kk55 |
| Kk2 | 47. Kk59 [1] |
| Kk2a | 48. Kk6 [1] |
| Kk3 | 49. Kk60 [1] |
| Kk4 | 50. Kk61 [2] |
| Kk5 | Kk88 |
| Kk52 | 51. Kk62 [1] |
| Kk56 | 52. Kk74 [1] |
| Kk57 | 53. Kk76 [1] |
| Kk66 | 54. Kk80 [1] |
| Kk7 | 55. Kk82 [1] |
| Kk77 | 56. Kk85 [1] |
| Kk8 | 57. Kk86 [1] |
| Kk89 | 58. Kk9 [1] |
| Kk95 | 59. Kk91 [1] |
| Kk98 | 60. Kk93 [1] |
| 24. Ka30 [1] | 61. Kk94 [1] |
| 25. Ka3 [1] | 62. Kk96 [1] |
| 26. Ka4 [1] | 63. Kk97 [2] |
| 27. Ka6 [1] | Ks16 |
| 28. Ka7 [1] | 64. Kk99 [1] |
| 29. Ka8 [1] | 65. Kl1 [8] |
| 30. Ka9 [1] | Kl18 |

K119	Ks41
K135	Ks5
K141	105. Ks12 [1]
K16	106. Ks14 [1]
K18	107. Ks15 [1]
K19	108. Ks15a [1]
66. K110 [2]	109. Ks17 [2]
K139	Ks19
67. K111 [5]	110. Ks2 [1]
K117	111. Ks20 [3]
K124	Ks39
K132	Ks9
K155	112. Ks21 [1]
68. K113 [1]	113. Ks23 [1]
69. K114 [1]	114. Ks24 [1]
70. K115 [1]	115. Ks25 [1]
71. K116 [2]	116. Ks26 [1]
K12	117. Ks27 [1]
72. K120 [1]	118. Ks28 [1]
73. K125 [2]	119. Ks28a [1]
K133	120. Ks29 [1]
74. K126 [4]	121. Ks30 [1]
K14	122. Ks32 [1]
K147	123. Ks33 [1]
K15	124. Ks34 [1]
75. K127 [2]	125. Ks35 [1]
K136	126. Ks36 [1]
76. K128 [1]	127. Ks36a [1]
77. K129 [2]	128. Ks37 [1]
K137	129. Ks38 [1]
78. K13 [1]	130. Ks4 [3]
79. K130a [1]	Ks42
80. K133a [1]	Ks45
81. K134 [3]	131. Ks40 [1]
K156	132. Ks43 [1]
K17	133. Ks43a [1]
82. K134a [1]	134. Ks44 [2]
83. K135a [1]	Ks46
84. K136a [1]	135. Ks47 [1]
85. K137a [1]	136. Ks48 [1]
86. K140 [1]	137. Ks49 [1]
87. K142 [1]	138. Ks6 [1]
88. K143 [1]	139. Ks7 [1]
89. K144 [1]	140. Ks8 [1]
90. K145 [1]	
91. K146 [1]	
92. K148 [1]	
93. K149 [1]	
94. K150 [1]	
95. K151 [1]	
96. K152 [1]	
97. K153 [1]	
98. K154 [1]	
99. Kr2 [1]	
100. Kr3 [1]	
101. Kr4 [1]	
102. Ks1 [1]	
103. Ks10a [1]	
104. Ks11 [3]	

Appendix 2.2 Details of the total of 105 Museum Specimens (see Appendix 1 for provenance) from which DNA was successfully extracted and sequenced for mtDNA Control Region (561bp) as described in Chapter 6. This includes partial CRHV1 sequences (incomplete) not listed under the haplotype list, and not analysed in Chapter 6.

Bu5 NMZB FWC4970	Kk83 NMZB 11899 no sequence used
Bu6 NMZB FWC 4969	Kk84 NMZB 11894 no sequence used
Ka10 RMAC 17959	Kk85 NMZB 11907
Ka11 RMAC 18286	Kk86 NMZB 5001
Ka12 RMAC 17958	Kk101 BM 1921.7.18.34 no sequence used
Ka13 RMAC 18279	KI30a NMZB 10166
Ka16 RMAC 19163	KI31 NMZB 11934
Ka17, RMAC	KI31a NMZB 11933
Ka2, RMAC 18290	KI33a NMZB 5067
Ka24 RMAC 18275	KI34a NMZB 10591
Ka25 RMAC 18277 no sequence used	KI35a NMZB 7527
Ka26 RMAC 19162	KI36a NMZB 2751
Ka27 RMAC 18276	KI38 NMZB 11967
Ka28 RMAC 19161	KI43 NMZB 50586
Ka29 RMAC 2924 no sequence used	KI44 NMZB 56413
Ka3 RMAC 7913	KI45 NMZB 56416
Ka30 RMAC 18291	KI46 RMAC 18924
Ka31 RMAC 18288	KI47 NMZB 59200
Ka4 RMAC 17960	KI48 NMZB 56373
Ka6 RMAC 18292	KI49 NMZB 56372
Ka7 RMAC 18287	KI50 NMZB 18635
Ka8 RMAC 17692	KI51 NMZB 56370
Ka9 RMAC 17961	KI52 NMZB 22518
KaQ1 FMNH 27571 Holotype of <i>Kobus anselli</i>	KI53 NMZB 10167
KaQ2 FMNH 27572	KI54 NMZB 2753
KaQ3 FMNH 27573	KI55 NMZB 18636
KaQ4 FMNH 27574	KI56 BM 35.9.1.350
KaQ5 FMNH 27575	Kr2 BM 1914.1.7.11 Neotype of <i>Kobus robertsi</i>
KaQ6 FMNH 27576	Kr3 BM 1913.11.27.1
KaQ7 FMNH 27577	Kr4 BM 1913.11.26.1
Kk59 NMZB 10584	Ks1a BM 1927.8.16.12
Kk60 NMZB 11051	Ks21 NMZB 2750
Kk61 NMZB 10303	Ks22 NMZB 11116 no sequence used
Kk62 NMZB 18666	Ks23 NMZB 1774
Kk63 NMZB 18713 no sequence used	Ks24 NMZB 1771
Kk64 NMZB 17640	Ks25 NMZB 1772
Kk65 NMZB 17645 no sequence used	Ks26 NMZB 20155
Kk66 NMZB 11964	Ks27 NMZB 11120
Kk67 NMZB 11962 no sequence used	Ks28 NMZB 2757
Kk68 NMZB 11954 no sequence used	Ks29 NMZB 5222
Kk69 NMZB 11963	Ks30 NMZB 1777
Kk70 NMZB 5010 no sequence used	Ks31 NMZB 1776 no sequence used
Kk71 NMZB 5003 no sequence used	Ks32 NMZB 5213
Kk72 NMZB 17647 no sequence used	Ks33 NMZB 5224 no sequence used
Kk73 NMZB 11043 no sequence used	Ks34 NMZB 11115
Kk74 NMZB 11900	Ks35 NMZB 2756
Kk75 NMZB 18663 no sequence used	Ks36 RMAC 13351
Kk76 NMZB 11981	Ks48 BM 1907.11.15.1
Kk77 NMZB 11990	Ks49 BM 1907.11.15.2
Kk78 NMZB 11862 no sequence used	Ks50 BM 1907.11.15.3 no sequence used
Kk79 NMZB 11888 no sequence used	Ks51 BM 1933.3.6.46 no sequence used
Kk80 NMZB 11896	
Kk81 NMZB 11895 no sequence used	
Kk82 NMZB 11983	

Appendix 2.3. Museum Specimens and Skin Snips Sequenced for Cytochrome b and Intron 1 of SPTBN

Cytochrome b

Bu1
 Bu2
 Bu5
 Bu6
 Kk20
 K131
 K131a
 K12
 K15
 K134
 K156
 K134a
 K135a
 K136a
 K137a
 Kk101
 Kk2
 Kk4
 Ka3
 Ka4
 Ka6
 Ka7
 Ka9
 KaQ1
 KaQ2
 KaQ3
 KaQ5
 Ks1
 Ks14
 Ks16
 Ks6
 Ks7
 Ks8
 Ks48
 Ks49

SPTBN

KaQ3
 Ka4
 Kr2
 Kr2a
 Kr3
 Kr4
 Kk1
 Kk4
 Kk9
 Kk51
 Kk52
 Kk54
 Kk87
 Kk93
 K17
 K126
 K127
 K134
 K135
 Ks3
 Ks5
 Ks7
 Ks12
 Ks16
 Ks18
 Ks38
 Ks40

Appendix 3. Distributions of selected endemic organisms confined to drainage systems of Katanga, southern Democratic Republic of Congo and principal components of the Palaeo-Chambeshi Archipelago. This includes Kunene, Okavango-Upper Zambezi and Upper Kafue drainage systems. Endemic lechwe antelopes of the *Kobus lechwe* complex are tabulated for comparison. In addition to Fishbase (www.fishbase.com) the following sources were consulted for distributional data and taxonomic authorities: *Kneria* and *Parakneria*, *Notobranchius*, *Oreochromis*, *Synodontis*, and *Varicorhinus* (Banister 1973; Banister & Bailey (1979); Bell-Cross 1982; Bell-Cross & Minshull 1988; Malaisse 1997; Skelton 2001); *Chiloglanis* and *Tilapia* (Balon & Stewart 1983 and Malaisse 1997); and *Tylochromis* (Stiassny 1989). *Orthochromis*, although reported as *Schwetzochromis* by Greenwood & Kullander (1994) follows Salzburger *et al* (2005).

Kunene and/or Cuanza	Okavango and Upper Zambezi	Upper Kafue	Bangweulu - Chambeshi	Lower Luapula Lake Mweru	Kalungwishi	Luongo	Lufira	Upemba (Kamalondo depression)
Red Lechwe? <i>K. cf. lechwe</i> Kunene † Upper Cuanza	Red lechwe <i>Kobus lechwe</i>	Local endemic Kafue Lechwe <i>Kobus kafuensis</i> Busanga Red lechwe <i>Kobus lechwe</i>	Black lechwe <i>Kobus smithemani</i>	Luapula Red lechwe <i>Kobus lechwe</i>	Roberts lechwe † <i>Kobus robertsi</i>			Upemba lechwe <i>Kobus anselli</i>
<i>Barbus breviceps</i>	<i>Barbus breviceps</i> <i>B. bellcrossi</i> <i>B. thamalakanensis</i>		<i>Barbus owenae</i>	<i>Barbus pseudognathodon</i> <i>B. myersi</i>				
<i>Labeo ansorgii</i> Boulenger 1907	<i>Labeo lunatus</i> Jubb 1963			<i>Labeo simpsoni</i>			<i>Labeo simpsoni</i>	
<i>Kneria maydelli</i>	<i>Labeobarbus codringtoni</i> <i>Kneria polli</i>	<i>Kneria cf. auriculata</i>		<i>Labeobarbus stappersi</i> <i>Kneria stappersi</i>		<i>Kneria paucisquamata</i>	<i>Labeobarbus stappersi</i> <i>Kneria katangae</i>	<i>Kneria wittei</i>
	<i>Parakneria fortuita</i>			<i>Parakneria malaissei</i>			<i>Parakneria kissi</i> and <i>P. lufirae</i>	
				<i>Chiloglanis macropterus</i> and <i>C. elisabethianus</i>		<i>Chiloglanis macropterus</i>	<i>Varicorhinus altipinnis</i> , <i>V. iphithimostoma</i> , <i>V. wittei</i>	<i>Varicorhinus lupuensis</i> and <i>V. upembensis</i>

