

**THE EVOLUTION OF THE BLACK WILDEBEEST, *CONNOCHAETES*
GNOU, AND MODERN LARGE MAMMAL FAUNAS IN CENTRAL
SOUTHERN AFRICA**

by

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DECLARATION

I, the undersigned, hereby declare that the work contained in this dissertation 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: 22 March 2005

ABSTRACT

This study investigates the evolution of modern mammalian faunas in the central interior of southern Africa by testing the hypothesis that the evolution of the black wildebeest, *Connochaetes gnou*, was directly associated with the emergence of Highveld-type open grasslands in the central interior.

Southern Africa can be distinguished from other arid and semi-arid parts of the continent by the presence of an alliance of endemic grazing ungulates. The black wildebeest is characteristic of this alliance. Open habitats are essential for the reproductive behaviour of the black wildebeest, because territorial males require an unobstructed view of their territories in order to breed. The specialised territorial breeding behaviour of the black wildebeest is the reason why the black wildebeest is historically confined to the Highveld and Karoo areas and why it is reproductively isolated from sympatric blue wildebeest, *Connochaetes taurinus*. The finds from a number of fossil-rich localities, dating from the recent past to approximately a million years ago, have been identified. The remains referred to ancestral *C. gnou* have been subjected to detailed qualitative and quantitative osteological comparisons with cranial and post-cranial elements of modern and fossil reference specimens. This material includes extant southern African alcelaphines and fossil materials of *C. gnou*, the extinct giant wildebeest, *Megalotragus priscus*, and North African fossil alcelaphines. The results show that cranial changes in fossil *C. gnou*, particularly the more forward positioning of the horns, basal inflation of the horns and the resultant re-organisation of the posterior part of the skull, preceded other skeletal modifications. These cranial changes indicate a shift towards more specialised territorial breeding behaviour in the earliest ancestral black wildebeest, evident in the specimens of the c. million year old Free State site of Cornelia-Uitzoek. Since the territorial breeding behaviour of the black wildebeest can only function in open habitat and since cranial characters associated with its territorial breeding behaviour preceded other morphological changes, it is deduced that there was a close association between the speciation of *C. gnou* from a *C. taurinus*-like ancestor and the appearance of permanently open Highveld-type grasslands in the central interior of southern Africa. This deduction is supported by the lack of trophic distinction between the modern black and blue wildebeest, suggesting that the evolution of the black wildebeest was not accompanied by an ecological shift. It is concluded that the evolution of a distinct southern endemic wildebeest in the Pleistocene was associated with, and possibly driven by, a shift towards a more specialised kind of territorial breeding behaviour, which can only function in open habitat.

There are significant post-speciation changes in body size and limb proportions of fossil *C. gnou* through time. The tempo of change has not been constant and populations in the central interior underwent marked reduction in body size in the last 5000 years. Vicariance in fossil *C. gnou* is evident in different rates of change that are recorded in the populations of generally smaller body size that became isolated in the Cape Ecozone. These daughter populations, the result of dispersals from the central interior, became extinct at the end of the Pleistocene.

OPSOMMING

Hierdie studie ondersoek die ontstaan van moderne soogdier-faunas in die sentrale binneland van suider-Afrika deur die hipotese te toets dat die evolusie van die swart-wildebees, *Connochaetes gnou*, ge-assosieer en moontlik die gevolg was van die verskyning van Hoëveld-tipe oop grasveld in die sentrale binneland.

Suider-Afrika word onderskei van ander droë en half-droë streke van die kontinent deur 'n alliansie van endemiese grasvretende hoefdiere. Die swart-wildebees is kenmerkend van hierdie alliansie. Oop habitat is noodsaaklik vir die paringsgedrag van die swart-wildebees, aangesien territoriale bulle ononderbroke sig van hul territoria benodig om te kan voortplant. Die gespesialiseerde territoriale paringsgedrag van die swart-wildebees verklaar waarom sy historiese verspreiding tot die Karoo and Hoëveld beperk was en ook sy reprodktiewe isolasie van simpatriese blou-wildebeeste, *Connochaetes taurinus*. Die fossiel-oorblyfsels van 'n reeks lokaliteite, wat in ouderdom strek vanaf die onlangse verlede tot ongeveer een miljoen jaar, is uitgeken. Kraniale sowel as postkraniale elemente van voorouer-*C. gnou* is met elemente van moderne en fossiel eksemplare vergelyk. Hierdie eksemplare sluit materiaal in van moderne suider-Afrikaanse Alcelaphini, fossiel-materiaal van *C. gnou*, die uitgestorwe reuse-wildebees, *Megalotragus priscus*, en Noord-Afrikaanse fossiel-Alcelaphini. Die resultate wys dat sekere anatomiese aspekte van die skedel, soos die vooroor-gebuigde horingvorm, die vergrote horingbasisse en die gepaardgaande herorganisering van die skedelbasis, ander skelet-veranderinge voorafgegaan het in die materiaal van Cornelia-Uitzoek, 'n Vrystaatse lokaliteit van ongeveer 'n miljoen jaar oud. Hierdie kraniale veranderinge wys dat daar 'n gedragsverkuiling na 'n meer gespesialiseerde vorm van territoriale gedrag by die eerste voorouer-swart-wildebeeste was. Aangesien die territoriale gedrag van swart-wildebeeste slegs kan funksioneer in oop habitat en aangesien kraniale aanpassings, wat met territoriale gedrag ge-assosieer word, veranderinge aan ander skelet-dele voorafgegaan het, word dit afgelei dat daar 'n nou verband was tussen die ontstaan van *C. gnou* uit 'n *C. taurinus*-agtige voorouer en die verskyning van Hoëveld-tipe oop grasvelde. Hierdie afleiding word gesteun deur die feit dat moderne swart- en blou-wildebeeste nie trofies onderskeibaar is nie, wat ook impliseer dat die evolusie van die swart-wildebees nie met 'n ekologiese aanpassing gepaardgegaan het nie. Die slotsom is dat die evolusie van 'n suidelike endemiese wildebees-spesie gedurende die Pleistoseen onderhewig was aan die verskyning van 'n gespesialiseerde vorm van territoriale voortplantingsgedrag, wat slegs in oop habitat kan funksioneer.

Daar is ook beduidende post-spesiasie veranderinge in liggaamsgrootte en liggaamsproporsies in fossiel-vorme van *C. gnou*. Die tempo van die veranderinge was nie konstant nie en populasies in die sentrale binneland het merkbaar verklein in die laaste 5000 jaar. Geografiese veranderinge is gedemonstreer in ge-isoleerde populasies met verkleinde liggaamsgrootte in die Kaapse Ekosone. Hierdie dogter-populasies, die produk van vroeëre biogeografiese verspreiding vanuit die sentrale binneland, het uitgesterf teen die einde van die Pleistoseen.

CONTENTS

DECLARATION	ii
ABSTRACT	xi
OPSOMMING	iv
CONTENTS	v
ACKNOWLEDGEMENTS	xii
LIST OF FIGURES	xiv
LIST OF TABLES	xxvii
CONVENTIONS	xxix
CHAPTER 1: INTRODUCTION	1
THE ARID CENTRES OF AFRICA	1
AIM OF THE STUDY	1
DISCOVERY OF A PLEISTOCENE CAPRINE IN SOUTHERN AFRICA	4
CHAPTER 2: HISTORICAL PERSPECTIVE	5
INTRODUCTION	5
THE CENTRAL INTERIOR	5
AREAS NORTH AND WEST OF THE VAAL RIVER	8
THE VAAL RIVER GRAVELS	10
THE CAPE COASTAL ZONE	11
A BIOCHRONOLOGICAL SCHEME	12
A BIOGEOGRAPHIC MODEL	13
DISCUSSION	13
CHAPTER 3. BIOGEOGRAPHY, SPECIATION AND MORPHOLOGY	15
INTRODUCTION	15
BIOGEOGRPAHY	15
Dispersal and vicariance	15
Biogeography and speciation	16
MORPHOLOGY	20
Introduction	20
A morphological blueprint	21
<i>Definition of a morphological blueprint</i>	21
<i>The concept of a morphological blueprint in relation to cladistic terminology</i>	22
Establishing a morphological blueprint	24
<i>Morphological blueprints at the lowest level of taxonomy</i>	24
<i>Morphological blueprints at higher levels of taxonomy</i>	25
MEASUREMENTS, DATA MANAGEMENT AND STATISTICAL METHODS	26
TAXONOMIC SYSTEM UTILISED	27

CHAPTER 4. AFRICAN ARIDITY AND BLACK WILDEBEEST ECOLOGY	30
INTRODUCTION	30
AFRICA SINCE THE MIOCENE.....	30
SOUTHERN AFRICA	32
The landscape	32
Open grasslands and open habitat in southern Africa	33
BLACK WILDEBEEST BEHAVIOUR AND ECOLOGY	35
Feeding behaviour.....	35
Social and reproductive behaviour.....	35
Habitat requirements.....	37
Past and present distribution patterns of wildebeest.....	37
The question of hybridisation between black wildebeest and blue wildebeest.....	39
Parallels between black wildebeest and caprines.....	39
SOUTHERN AFRICA AS A PERIODIC BIOGEOGRAPHIC ISLAND	40
CHAPTER 5. MATERIAL AND FOSSIL LOCALITIES	41
INTRODUCTION	41
MATERIAL	41
Alcelaphini.....	41
<i>Modern material</i>	<i>41</i>
<i>Fossil material.....</i>	<i>43</i>
Caprinae.....	44
<i>Modern material</i>	<i>44</i>
<i>Fossil material.....</i>	<i>44</i>
FOSSIL LOCALITIES FROM THE INTERIOR OF SOUTHERN AFRICA	45
Introduction.....	45
Deelpan.....	45
<i>Introduction</i>	<i>45</i>
<i>Fossil context and radiocarbon age</i>	<i>47</i>
<i>Summary</i>	<i>47</i>
Maselspoort	47
<i>Introduction</i>	<i>47</i>
<i>Fossil context and radiocarbon age</i>	<i>48</i>
<i>Summary</i>	<i>49</i>
Kareepan.....	49
<i>Introduction</i>	<i>49</i>
<i>Fossil context and radiocarbon age</i>	<i>51</i>
<i>Summary</i>	<i>51</i>
Spitskop.....	52
<i>Introduction</i>	<i>52</i>
<i>Fossil context and ESR age</i>	<i>53</i>
<i>Summary</i>	<i>53</i>
Mahemspan	54
<i>Introduction</i>	<i>54</i>
<i>Fossil context.....</i>	<i>54</i>
<i>Geological age.....</i>	<i>56</i>
<i>Summary</i>	<i>56</i>
Sunnyside Pan	57
<i>Introduction</i>	<i>57</i>
<i>Fossil context and ESR age</i>	<i>57</i>
<i>Summary</i>	<i>57</i>

Florisbad spring	58
<i>Introduction</i>	58
<i>Summary of excavations</i>	59
<i>The Florisbad spring mound</i>	60
<i>The fossil fauna</i>	61
<i>The application of the ESR and OSL dating techniques</i>	63
Introduction	63
The third test pit sequence.....	63
Sampling for ESR/OSL analysis	64
Results	65
<i>Discussion</i>	68
Cornelia-Uitzoek	69
<i>Introduction</i>	69
<i>New field work</i>	70
<i>Sedimentary context</i>	70
<i>Mammalian fauna and its geological age</i>	72
FOSSIL LOCALITIES FROM THE CAPE COASTAL ZONE	75
Introduction	75
Elandsfontein	76
Klasies River main site	77
Sea Harvest	77
Swartklip	78
FOSSIL LOCALITIES FROM NORTH AFRICA	79
Introduction	79
Ain Jourdel	79
Ain Boucherit	80
Tighenif (Ternifine)	80
CHAPTER 6. THE CHRONOLOGY AND PALAEO-ECOLOGY OF THE CORNELIAN AND the FLORISIAN LAND MAMMAL AGES	82
INTRODUCTION	82
THE CORNELIAN LMA	83
Taxonomic definition	83
Temporal definition	84
THE FLORISIAN LMA	85
Taxonomic definition	85
Temporal definition	87
The palaeo-ecology of the interior Florisian	88
DISCUSSION	89
The roots of the Florisian ecosystem	89
The demise of the Florisian ecosystem	90
A CHRONOLOGICAL ARRANGEMENT OF FOSSIL ASSEMBLAGES	91
CHAPTER 7: ALCELAPHINE COMPARATIVE OSTEOLOGY	92
INTRODUCTION	92
POTENTIAL CONFUSION IN THE DIAGNOSIS OF ALCELAPHINE FOSSILS	94
HORNCORES AND SKULL	94
Introduction	94
The skulls of <i>C. taurinus</i> and <i>C. gnou</i>	95
Discussion	96

<i>Territoriality</i>	96
<i>Feeding niche</i>	99
The skull of <i>M. priscus</i>	100
<i>Introduction</i>	100
<i>Horns and braincase of <i>M. priscus</i></i>	102
<i>Discussion</i>	105
Sexual dimorphism and geographic variability in the horn cores of <i>M. priscus</i>	105
Sexual selection in <i>M. priscus</i>	106
The lower jaw of <i>M. priscus</i>	107
Discussion	107
<i>Reconstructing the skull of <i>M. priscus</i></i>	107
<i>Phylogenetic relationships in the genus <i>Megalotragus</i></i>	108
<i>Behavioural implications of the skull morphology of <i>M. priscus</i></i>	110
DENTITION	111
Upper dentition	111
<i>Primitive alcelaphines</i>	111
<i>Advanced alcelaphines</i>	111
<i>Discussion</i>	112
Lower dentition	114
<i>Primitive alcelaphines</i>	114
<i>Advanced alcelaphines</i>	114
<i>Discussion</i>	116
Discussion of upper and lower dentitions	116
<i>Morphological groups as reflected by dental characters</i>	116
<i>Dental specialisation in <i>C. gnou</i> as a response to increased territoriality</i>	117
<i>Flexibility in the feeding behaviour of <i>A. buselaphus</i> and <i>D. pygargus</i></i>	119
<i>Parallelism between <i>C. gnou</i> and <i>M. priscus</i> towards a caprine blueprint</i>	119
POSTCRANIUM	120
Introduction	120
Axis	120
<i>Description</i>	120
<i>Discussion</i>	122
Humerus	122
<i>Description</i>	122
<i>Discussion</i>	124
Radius	125
<i>Description</i>	125
<i>Discussion</i>	126
Metacarpal	127
<i>Description</i>	127
<i>Discussion</i>	129
Femur	130
<i>Description</i>	130
<i>Discussion</i>	131
Tibia	132
<i>Description</i>	132
<i>Discussion</i>	134
Metatarsal	135
<i>Description</i>	135
<i>Discussion</i>	136
DISCUSSION	137
Alcelaphine morphological groups	137
Alcelaphine body proportions	137
Caprine-like characteristics of <i>C. gnou</i>	140

Morphological characteristics of <i>M. priscus</i>	142
Morphological relationships in the Alcelaphini	144

CHAPTER 8. THE EVOLUTION OF THE GENUS <i>CONNOCHAETES</i> AND <i>MEGALOTRAGUS</i>-LIKE WILDEBEEST	146
INTRODUCTION	146
FOSSIL HISTORY OF THE GENERA <i>CONNOCHAETES</i> AND <i>MEGALOTRAGUS</i>.....	146
COMPARATIVE OSTEOLOGY OF <i>OREONAGOR TOURNOUERI</i> (THOMAS 1884).....	148
Aïn Jourdel	148
<i>Skull</i>	148
Material	148
Description	149
Discussion	151
Aïn Boucherit	152
<i>Skull</i>	152
Material	152
Description	152
Discussion	154
<i>Upper dentitions</i>	156
Introduction	156
Material	156
Description	156
Discussion	157
<i>Lower dentitions</i>	158
Material	158
Description	158
Discussion	159
<i>Humerus</i>	159
Material	159
Description	160
Discussion	160
<i>Radius</i>	160
Material	160
Description	160
Discussion	161
<i>Metacarpal</i>	161
Material	161
Description	161
Discussion	161
<i>Femur</i>	162
Material	162
Description	162
Discussion	162
<i>Tibia</i>	163
Material	163
Description	163
Discussion	163
<i>Metatarsal</i>	163
Material	163
Comments.....	163
<i>Body proportions of the Aïn Boucherit alcelaphine</i>	164
DISCUSSION.....	164

CONCLUSION	166
CHAPTER 9. THE EVOLUTION OF THE BLACK WILDEBEEST, <i>CONNOCHAETES</i>	
<i>GNOU</i>	167
INTRODUCTION	167
SKULL AND HORNCORES	169
Interior Cornelian	169
<i>Description</i>	169
<i>Discussion</i>	170
Interior Florisian	171
<i>Description</i>	171
<i>Discussion</i>	172
Cape Cornelian	172
<i>Description</i>	172
<i>Discussion</i>	172
Cape Florisian	173
<i>Description</i>	173
LOWER DENTITION	173
Interior	173
Cape coastal zone	174
Discussion	174
POSTCRANIUM	175
Axis	175
Humerus	176
Radius	177
Metacarpal	178
Femur	180
Tibia	180
Metatarsal	181
DISCUSSION	183
Introduction	183
Black wildebeest evolution in geological time	183
<i>Temporal trends</i>	183
<i>The origin of the black wildebeest</i>	185
<i>Evolutionary patterns</i>	186
<i>Territorial behavioural in the earliest black wildebeest</i>	187
<i>The phylogenetic significance of caprine characteristics in black wildebeest</i>	190
Black wildebeest evolution in geographic space	191
<i>Introduction</i>	191
<i>The fossil record of <i>C. gnou</i> in the Cape coastal zone</i>	191
<i>Dispersal and vicariance in black wildebeest evolution</i>	193
General discussion	196
<i>Bergman's 'Rule'</i>	196
<i>The effects of population bottlenecks in the morphology of extant <i>C. gnou</i></i>	196
<i>Genetic evidence for the evolution of the black wildebeest</i>	197
<i>The evolutionary position of <i>C. africanus</i></i>	197
CHAPTER 10. CONCLUSION	199
INTRODUCTION	199
ALCELAPHINE MORPHOLOGICAL GROUPS	199

PARALLELISM IN <i>MEGALOTRAGUS PRISCUS</i> AND <i>CONNOCHAETES GNOU</i>	200
THE EVOLUTIONARY SIGNIFICANCE OF CAPRINE MORPHOLOGIES IN ANCESTRAL BLACK WILDEBEEST	200
THE ORIGIN OF THE GENERA <i>CONNOCHAETES</i> AND <i>MEGALOTRAGUS</i>	201
THE EVOLUTION OF DISTINCTIVE LARGE MAMMAL FAUNAS IN SOUTHERN AFRICA	202
OPEN GRASSLANDS AND TERRITORIAL BEHAVIOUR IN BLACK WILDEBEEST: A MODEL FOR THE EVOLUTION OF THE BLACK WILDEBEEST	205
THE POST-SPECIATION EVOLUTIONARY HISTORY OF THE BLACK WILDEBEEST	206
CONCLUDING STATEMENT	207
REFERENCES	208
APPENDIX A. OSTEOLOGICAL ILLUSTRATIONS AND FIGURES	234
APPENDIX B: TABLES OF MEASUREMENTS	359
APPENDIX C. PRELIMINARY REPORT ON A CAPRINE FROM THE CAPE MOUNTAINS, SOUTH AFRICA (PUBLISHED PAPER)	392
APPENDIX D. SELECTED PUBLICATIONS RELEVANT TO THIS STUDY	408
INDEX TO AUTHOR CITATIONS IN THE TEXT	479

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LIST OF FIGURES

Figure 1. The three arid centres of Africa with past interconnecting corridors.....	235
Figure 2. A temporal model of black wildebeest evolution, as suggested by Gentry & Gentry (1978). The model illustrates changes in the shape of the horn cores over time. The specimens represented are a modern specimen, NMB-F 84 (A), a Florisbad specimen, FLO 6500 (B), and a specimen from Cornelia-Uitzoek, COR 2838 (C)	236
Figure 3. A map of southern Africa illustrating the different biomes	237
Figure 4. Maps of southern Africa illustrating the historic distribution of the black wildebeest and blue wildebeest (after Skinner & Smithers 1992). The southern limit of the range of the blue wildebeest as inferred from historic records and fossil finds is shown as a line.	238
Figure 5. A map of southern Africa showing the fossil localities as discussed in the text. The insert shows a temporal ordering of the fossil localities (based on data presented in Chapters 5 and 6).	239
Figure 6. A map showing the positions of the Deelpan A & D fossil brown hyaena burrows.	240
Figure 7. Map of the Maselspoort fossil site.	241
Figure 8. Composite views of the Maselspoort mid-Holocene bone occurrence.	242
Figure 9. A map of the Kareepan fossil locality.	243
Figure 10. A map of the Spitskop donga system and fossil localities.	244
Figure 11. A map of Mahemspan showing the approximate position of Van Hoepen's excavation.	245
Figure 12. A map of Sunnyside Pan and the position of the Pleistocene hyaena burrow.....	246
Figure 13. The geographic position and local geology of Florisbad. (After Loock & Grobler 1988).....	247

Figure 14. Plan of the Florisbad spring mound indicating the positions of the excavations, including the three test pits.	248
Figure 15. A model illustrating the depositional history of the Florisbad fossil bearing deposits. It shows the distinction between the two kinds of fossil context; mainly carnivore-accumulated materials from the spring vent structures (B1) and the remains of human habitation on intact land horizons (B2).	249
Figure 16. The distribution of pans in the vicinity of Florisbad, illustrating the Okavango-like aquatic habitat characteristic of the Flosian Land Mammal Age in the interior of southern Africa. (After Grobler & Looek 1988)..	250
Figure 17. Plot of augur drill sections through the Florisbad spring mound (after Brink 1987).	251
Figure 18. Correlation of the profile of the Florisbad spring section (A & C) with the third test pit (B). The third test pit was used as the reference section in the ESR/OSL dating exercise (Grün <i>et al.</i> 1996) The localities of these sections on the Florisbad spring mound are given in Figure 14. The spring section is modified after Kuman & Clarke (1986), while radiocarbon results given in C are from Scott & Nyakale 2002.....	252
Figure 19. ESR and OSL age estimates on fossil teeth and sediments from the third testpit at Florisbad (after Grün <i>et al.</i> 1996)..	253
Figure 20. ESR age estimates on fossil teeth from the Florisbad Spring (after Grün <i>et al.</i> 1996)	254
Figure 21. A north-facing panoramic view of the fossil-bearing deposits of Cornelia-Uitzoek (A). The arrow points from the position of the current excavation (B & C), which was started in 1998.	255
Figure 22. A north-facing diagrammatic section of the fossil-bearing Quaternary deposits of Cornelia-Uitzoek within a basin of Permian Ecca shale (modified after Butzer 1974).....	256
Figure 23. North-facing vertical plot of vertebrate fossils from the new excavations at Cornelia-Uitzoek (A), enlarged and superimposed on an inverted south-facing	

section of the 1998 test excavation (B), illustrating the intrusive nature of the bone occurrence.....	257
Figure 24. A plot of the vertebrate fossils from the new excavations at Cornelia-Uitzoek. The 1998 test cutting is indicated in the north-western corner of the exposure.	258
Figure 25. A large bovid rib and the basal horncores of <i>Megalotragus eucornutus</i>	259
Figure 26. Map indicating the geographic position of fossil localities from North Africa.....	260
Figure 27. An ecological characterisation of ungulate faunas from Cornelia-Uitzoek, from the Florisbad spring and from Kareepan. These assemblages represent respectively the Cornelian LMA, the Florisian LMA and modern faunas of the central interior of southern Africa. The mixed feeder, <i>T. oryx</i> , and the fine feeder, <i>R. campestris</i> , are not included.....	261
Figure 28. A revised biochronology for the last million years in southern Africa. The Cornelian LMA and the Florisian LMA are shown in relation to a geological time scale. The fossil localities from the interior of southern Africa and from the Cape coastal zone are ordered in accord with this temporal frame.....	262
Figure 29. Dorsal and left lateral views of skulls of a male <i>C. gnou</i> (NMB-F 84) (left) and a male <i>C. taurinus</i> (NMB-F 56) (right). The numbers refer to the characters listed in the text, pages 95 – 96.....	263
Figure 30. A comparison of premaxilla width between <i>C. gnou</i> (n = 10) and <i>C. taurinus</i> (n = 10). A t-test shows that there is no statistical difference between the means of the two samples (p=0.98).	264
Figure 31. The skull and horn cores of <i>M. priscus</i> from Erfkroon: frontal view (A), right lateral view (B) and an enlarged right lateral view of the braincase (C).	265
Figure 32. Basal horn core dimensions of <i>M. priscus</i> , illustrating the two palaeopopulations.....	266
Figure 33. Right lateral views of lower jaws of extant Alcelaphini and <i>M. priscus</i> : <i>D. pygargus</i> (A), <i>A. buselaphus</i> (B), <i>M. priscus</i> (C), <i>C. taurinus</i> (D) and <i>C. gnou</i> (E). The lower jaw of <i>M. priscus</i> (C. 2472) is from Mahemspan.....	267

- Figure 34.** An arrangement of the *M. priscus* brain case and horn cores from Erfkroon, an upper jaw from Mahemspan and a complete lower jaw from Mahemspan. This arrangement is the basis for the reconstruction of the skull of *M. priscus*, given in Figure 35..... 268
- Figure 35.** A reconstruction of the skull of *M. priscus*, as would have been found in populations around the Modder River..... 269
- Figure 36.** Occlusal views of the right M² of *Aepyceros melampus* (A), a caprine/early alcelaphine from the Middle Miocene locality of Fort Ternan (B), *Damalacra* sp. from Langebaanweg (C), an advanced alcelaphine from the Shungura Formation Omo (D) and *A. buselaphus* (E). Specimens B to D are after Gentry (1980) and illustrate increasingly derived alcelaphine characteristics, while *A. melampus* (NMB-F 119) is morphologically very similar to the Fort Ternan specimen. The numbers refer to the characters listed in the text, page 111. 270
- Figure 37.** Occlusal views of the left upper dentitions of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 111 – 112. 271
- Figure 38.** Buccal views of the M³ of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). An additional molar of *C. gnou* (F) is included to show the variability in the distally projecting basal part of the metastyle. The numbers refer to the characters listed in the text, pages 111 – 112. 272
- Figure 39.** In A occlusal views are given of the left M₂ of (i) *Aepyceros melampus* (NMB-F 119), (ii) an early alcelaphine from the Middle Miocene site of Fort Ternan (*Kubanotragus tanyceras*), (iii) *Damalacra* sp. from Langebaanweg, (iv) an advanced alcelaphine from the Shungura Formation Omo and (v) *A. buselaphus* (A) (partly after Gentry 1980). Specimens B to F are respectively *D. pygargus*, *A. buselaphus*, *M. priscus*, *C. taurinus* and *C. gnou*. The numbers refer to the characters listed in the text, pages 114 – 115. 273
- Figure 40.** The length of the premolar row against that of the toothrow (A) and a comparison of the means and ranges of toothrow and premolar ratios (B) of extant Alcelaphini and *M. priscus*..... 274

- Figure 41.** Height of mandibular articulation above the occlusal surface in *C. gnou* and in *C. taurinus*. The premolar row (indicated in red) in *C. gnou* is shorter than in *C. taurinus*. This is a function of a distal shift in occlusal pressure, which was caused by a re-arrangement of the major chewing muscles due to the lowered position of the mandibular articulation in relation to the occlusal plane. The lowered mandibular articulation reflects changes to the posterior part of the skull in *C. gnou*. 275
- Figure 42.** Mandibular depth at M₂/M₃ in relation to premolar shortening. The regression line representing *Connochaetes* spp and *M. priscus* (A) suggest that there is no functional relationship between these variables. When *A. buselaphus* and *D. pygargus* are included (B) there is an apparent positive relationship between the variables. This reflects the effect of body size, which masks the absence of a true functional relationship between the two variables. 276
- Figure 43.** Axis: ventral views of male and female extant Alcelaphini and of *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *C. taurinus* (C), *M. priscus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 120 – 121. 277
- Figure 44.** Axis: left lateral views of male and female extant Alcelaphini and of *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *C. taurinus* (C), *M. priscus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 121 – 122. 278
- Figure 45.** Breadth (SBV) against length (LCDe) of the axis of extant Alcelaphini and *M. priscus*. 279
- Figure 46.** Ventral (A) and cranial (B) views of the axis of *M. priscus*. The number refers to the character listed in the text, page 121. 280
- Figure 47.** Cranial articular width (BFcr) against length of the corpus and the dens (LCDe) of the axis in extant Alcelaphini and *M. priscus*. This illustrates the difference between hartebeest-like and wildebeest-like alcelaphines..... 281
- Figure 48.** Dorsal views of the humeri of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 122 – 124. 282

- Figure 49. Lateral views of the humeri of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 122 – 124..... 283**
- Figure 50. Humerus: distal width (Bd) against greatest length (GL) (A), and trochlea width (BT) against the cranio-caudal depth of the medial part of the distal humerus (Dmd) of extant Alcelaphini and *M. priscus*. 284**
- Figure 51. Dorsal views of the radii of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 125 – 126..... 285**
- Figure 52. Lateral views of the radii of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 125 – 126..... 286**
- Figure 53. Radius: proximal views of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D), *C. gnou* (E) and *C. gnou* (F). The numbers refer to the characters listed in the text, pages 125 – 126..... 287**
- Figure 54. Distal views of the radii of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 125 – 126..... 288**
- Figure 55. Proximal width (Bp) against the total length (GL) of the radii of extant Alcelaphini and *M. priscus*. 289**
- Figure 56. Ratios of proximal depth (Dp) over proximal width (Bp) of the radii of extant Alcelaphini and *M. priscus*. This illustrates the greater dorso-volar depth of the radius *A. buselaphus* and *D. pygargus*. 290**
- Figure 57. Dorsal views of the metacarpals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 127 – 129..... 291**
- Figure 58. Proximal views of the metacarpals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 127 – 129..... 292**

- Figure 59. Volar views of the metacarpals of extant Alcelaphini and *M. priscus*. D.**
pygargus (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E).
 The numbers refer to the characters listed in the text, pages 127 – 129..... 293
- Figure 60. Lateral views of the metacarpals of extant Alcelaphini and *M. priscus*: D.**
pygargus (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E).
 The numbers refer to the characters listed in the text, pages 127 – 129..... 294
- Figure 61. Metacarpal shaft width (SD) against length (GL) of extant Alcelaphini and *M. priscus*.** 295
- Figure 62. Proximal depth (Dp) against proximal width (Bp) of the metacarpals of extant Alcelaphini and *M. priscus* (A) and their ratios (B).** 296
- Figure 63. The ratio of distal width (Bd) over distal depth (Dd) of the metacarpals of extant Alcelaphini and *M. priscus*.**..... 297
- Figure 64. The depth of the peripheral part of the medial condyle (Ddp) against the depth of the achsial part of the medial condyle (Dda) of the metacarpals of extant Alcelaphini and *M. priscus*. The regression line represents the combined samples of *C. taurinus* and *C. gnou*.**..... 298
- Figure 65. Dorsal views of the femora of extant Alcelaphini and *M. priscus*: D.**
pygargus (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E).
 The numbers refer to the characters listed in the text, pages 130 – 131..... 299
- Figure 66. Lateral views of the femora of extant Alcelaphini and *M. priscus*: D.**
pygargus (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E).
 The numbers refer to the characters listed in the text, pages 130 – 131..... 300
- Figure 67. Plantar views of the femora of extant Alcelaphini and *M. priscus*: D.**
pygargus (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E).
 The numbers refer to the characters listed in the text, pages 130 – 131..... 301
- Figure 68. Distal views of the femora of extant Alcelaphini and *M. priscus*: D.**
pygargus (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E).
 The numbers refer to the characters listed in the text, pages 130 – 131..... 302
- Figure 69. Femur shaft width (SD) against length (GL) (A) and distal width (Bd) against length (GL) (B) in extant Alcelaphini and *M. priscus*.**..... 303

- Figure 70.** The depth of the lateral condyle (Dld) against the depth of the medial condyle (Dmd) of the metacarpal in extant Alcelaphini and *M. priscus*. The regression line represents the combined samples of *C. taurinus* and *C. gnou*. 304
- Figure 71.** Dorsal views of the tibiae of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 132 – 134. 305
- Figure 72.** Plantar views of the tibiae of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 132 – 134. 306
- Figure 73.** Lateral views of the tibiae of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 132 – 134. 307
- Figure 74.** Distal views of the tibiae of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The dorsal side is towards the top of the page. The numbers refer to the characters listed in the text, pages 132 – 134. 308
- Figure 75.** Distal width (Bd) of the tibia against length (GL) in extant Alcelaphini and *M. priscus*. The regression line represents the *C. gnou* sample. 309
- Figure 76.** The distal depth (Dd) of the tibia against its distal width (Bd) in extant Alcelaphini and *M. priscus*. 310
- Figure 77.** Dorsal views of the metatarsals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 135 – 136. 311
- Figure 78.** Plantar views of the metatarsals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 135 – 136. 312
- Figure 79.** Proximal views of the metatarsals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 135 – 136. 313

- Figure 80. Shaft width (SD) against length (GL) of the metatarsal in extant Alcelaphini and *M. priscus* (A) and the ratios of SD/GL (B). The regression lines in A show the linear relationships of these variable in *C. gnou* and *C. taurinus*..... 314**
- Figure 81. Proximal width (Bp) against proximal depth (Dp) of the metatarsals in extant Alcelaphini and *M. priscus*. The regression lines show the linear relationships of these variables in these taxa 315**
- Figure 82. Distal width (Bd) against greatest length (GL) of the metatarsal in extant Alcelaphini and *M. priscus*. The regression line represents the combined samples of *C. taurinus* and *C. gnou*. 316**
- Figure 83. Depth of the peripheral part of the medial condyle (Ddp) against depth of the achsial part of the medial condyle (Dda) of the metatarsal in extant Alcelaphini and *M. priscus* (A). There is no statistical difference in the ratios of Ddp/Dda among the various taxa (B)..... 317**
- Figure 84. Ratio diagrams of means of limb lengths of Alcelaphini, Antilopini and Caprini. In A the similarity in bodyplans of Antilopini (*Gazella dorcas* & *Antidorcas marsupialis*) and Alcelaphini (*A. melampus*, *A. buselaphus* and *D. pygargus*) is illustrated, but contrasted with the body plan of a primitive sheep, *Ammotragus lervia*. In B the primitive alcelaphine antilopine body plan, as illustrated by *G. dorcas*, is contrasted with the advanced caprine-like bodyplans of *Connochaetes* spp. and *M. priscus*. Data for Antilopini are taken from Peters (1989) and Peters & Brink (1992), while data for *A. melampus* (n = 3) and *O. aries* (n= 4) are from the Florisbad comparative collections of modern mammals. 318**
- Figure 85. A skeletal reconstruction of *M. priscus* (B &C) based on the data presented in this chapter. The body plan of *C. taurinus*, after Kingdon (1982), is given as reference (A). 319**
- Figure 86. A summary of the alcelaphine phylogeny (A), as proposed by Vrba (1997), and a proposed alternative (B), based on the morphological comparisons provided in this chapter..... 320**
- Figure 87. Temporal ranges of fossil members of the wildebeest group, given in the context of the southern African Land Mammal Age scheme and according to a geological time scale. The temporal ranges are based on Gentry & Gentry (1978),**

- Gentry (1978), Geraads (1981), Harris (1988, 1991), Vrba (1997) and data provided in this study. 321
- Figure 88. The original type specimen of "*Antilope*" *ournoueri* from Aïn Jourdel - frontal view (A), enlarged postero-frontal view (B) and a left lateral view (C). The numbers refer to the characters listed in the text, pages 149 – 150. 322
- Figure 89. The neotype of *Oreonagor ournoueri* from Aïn Boucherit; frontal view (A), posterior view (B), forwardly tilted frontal view (C), right lateral view (D) and postero-frontal view (E). Views C to E are enlarged. The numbers refer to the characters listed in the text, pages 152 – 154. 323
- Figure 90. Frontal views of the skulls of *C. taurinus* (A), the type of *Oreonagor ournoueri* (Thomas 1884) (B), the neotype of *O. ournoueri* (C) and of *M. priscus* from Erfkroon (D). 324
- Figure 91. Lateral views of the skulls of *C. taurinus* (A), of the type of *Oreonagor ournoueri* (Thomas 1884) (B), of the neotype of *O. ournoueri* (C) and of the reconstructed skull of *M. priscus* from Erfkroon (D). 325
- Figure 92. Occlusal view of the neosyntype upper jaw 1966-5-37 of *Oreonagor ournoueri* from Aïn Boucherit (A) and occlusal and buccal views an upper jaw fragment 1954-8-17 (B). The numbers refer to the characters listed in the text, pages 156 – 157. 326
- Figure 93. Buccal views of the alcelaphine upper third molars from An Boucherit, referred to *Oreonagor ournoueri*; 1953-22-171 (A), 1953-8-243 (B), 1954-8-7 (C) and an unnumbered specimen (D). The specimens are presented so that they appear to be from the left side of the jaw. The numbers refer to the characters listed in the text, pages 156 – 157. 327
- Figure 94. Lower dentitions assigned to *Oreonagor ournoueri* from Aïn Boucherit; right lateral and occlusal views of the neosyntype lower jaw 1966-5-133 (A), an occlusal view of the neosyntype lower jaw fragment 1954-8-16 (B), an enlargement of the second molar of 1954-8-16 (C) and a line drawing of 1954-8-113 (D). The numbers refer to the characters listed in the text, pages 158 – 159. 328
- Figure 95. Dorsal (A) and lateral (B) views of a right humerus, 19543-8-218, from Aïn Boucherit. The numbers refer to the characters listed in the text, pages 159 – 160. ... 329

- Figure 96. Metacarpals from Ain Boucherit: dorsal views of 1953-22-118 (A) and 1954-8-219 (B) and a proximal view of 1953-8-207 (C). The numbers refer to the characters listed in the text, page 161. 330**
- Figure 97. Ratio diagram (A) of the metacarpals of extant Alcelaphini and those referred to *Oreonagor tournoueri* from Ain Boucherit and a plot (B) of depth of the achsial part of the medial condyle (Dda) against the distal width (Bd) of the metacarpal of extant Alcelaphini and those referred to *O. tournoueri* from Ain Boucherit. The upper regression line indicates *A. buselaphus*, while the lower indicates the combined samples of *C. taurinus* and *C. gnou*. 331**
- Figure 98. Femoral pieces assigned to *Oreonagor tournoueri* from Ain Boucherit: medial (A) and distal views (B) of a distal piece (1953-22-108) and a plantar view of a shaft piece (C). The number refers to the character listed in the text, page 162..... 332**
- Figure 99. Trochlea width (BT) against the dorso-plantar depth of the medial part of the trochlea (Dmd) of the femur, 1953-22-108, from Ain Boucherit..... 333**
- Figure 100. Distal views of tibiae referred to *Oreonagor tournoueri* from Ain Boucherit: 1953-22-113 (A), 1954-15-36 (B) and 1960-5-154 (C). The remarkable *Megalotragus*-like enlargement of the plantar articulation facet for the os malleolare in the Ain Boucherit material is illustrated. Comparative distal views of the tibiae of *A. buselaphus* (D), *M. priscus* (E), *C. taurinus* (F) and *C. gnou* (G) are given. The numbers refer to the characters listed in the text, page 163..... 334**
- Figure 101. Ratio diagram of the limb elements from Ain Boucherit referred to *Oreonagor tournoueri*, showing its primitive body proportions. 335**
- Figure 102. Frontal and lateral views of the horn cores of *C. gnou laticornutus* from Cornelia-Uitzoek (A & B) and *C. gnou antiquus* from Florisbad (C & D). The numbers refer to the characters listed in the text, pages 169 – 171..... 336**
- Figure 103. Dental dimensions of fossil *C. gnou*: length of the molar row against length of the toothrow (A) and ratios of toothrow/premolar row illustrating premolar shortening (B). 337**
- Figure 104. Length and breadth dimensions of the M₂ (A) and a plot illustrating temporal change in the M₂ of fossil *C. gnou* (B)..... 338**

- Figure 105.** The breadth of the facies cranialis (BFcr) of the axis against the length of the corpus and the dens (LCDe) (A) and the smallest width of the corpus (SBV) against LCDe (B)..... 339
- Figure 106.** Breadth of the trochlea (BT) of the humerus against distal medial depth (Dmd) of interior fossil assemblages (A) and the same plot without *M. priscus*, but including Swartklip 1 (B). The regression line represents the modern sample of *C. gnou*. 340
- Figure 107.** Breadth of the trochlea (BT) of the humerus against distal width (Bd) for interior fossil assemblages (A) and the same plot without *M. priscus*, but including Swartklip (B). The regression line represents the modern sample of *C. gnou*. 341
- Figure 108.** Breadth of the proximal articulation facet (BFp) of the radius against length (GL) (A) and of BFp against proximal breadth (Bp) (B)..... 342
- Figure 109.** Shaft width (SD) of the metacarpal against total length (GL) (A) and distal width (Bd) against GL (B). The upper regression line represents the combined mid-Holocene sample and the lower the modern *C. gnou* sample..... 343
- Figure 110.** Proximal depth (Dp) of the metacarpal against the proximal width (Bp) (A) and the smallest depth of the shaft (DD) against the distal breadth (Bd) (B). The upper regression line represents the combined mid-Holocene samples and the lower the modern *C. gnou* sample. 344
- Figure 111.** Femur: a regression analysis of the total length measurements (GL) and shaft width measurements (SD) of modern *C. gnou* (A) and a comparison of SD measurements among modern and fossil wildebeest (B)..... 345
- Figure 112.** Distal width (Bd) of the tibia against the total length (GL) of fossil and extant wildebeest. 346
- Figure 113.** Distal depth (Dd) of the tibia against its distal width (Bd) for extant and fossil *C. gnou* from the interior of southern Africa (A), and from the Cape coast (B). The regression lines show the linear relationship between the two variables in fossil and modern *C. gnou* and in *C. taurinus*. 347

- Figure 114. Greatest length (GL) of the metatarsal against shaft width (SD) of *C. gnou* from interior (A) and from coastal localities (B). The regression lines show the linear relationship between the two variables in fossil and modern *C. gnou*. 348**
- Figure 115. Proximal width (Bp) of the metatarsal against proximal depth (Dp) (A) and of distal width (Bd) and distal shaft depth (DD) of *C. gnou* from the interior and from coastal localities. The regression lines in A show the relationship between the two variables in fossil and modern *C. gnou*. 349**
- Figure 116. Box and whisker plots (mean, std error and std deviation) illustrating temporal changes in fossil populations of *C. gnou* from the interior of southern Africa: length of the M₂ (A), shortening of the premolar row (B), the axis (C), the distal humerus (D). 350**
- Figure 117. Box and whisker plots (mean, std error and std deviation) illustrating temporal changes in fossil populations of *C. gnou* from the interior of southern Africa: radius length (A), proximal radius (B), metacarpal length (C) and the distal metacarpal (D). 351**
- Figure 118. Box and whisker plots (mean, std error and std deviation) illustrating temporal changes in fossil populations from the interior of southern Africa: femur shaft (A), distal tibia (B) and metatarsal length (C). 352**
- Figure 119. Temporal pattern in wildebeest horn cores, illustrating the evolutionary sequence of the black wildebeest. 353**
- Figure 120. Comparative ratio diagrammes of skeletal elements of fossil *C. gnou*. 354**
- Figure 121. Temporal and spatial patterning in the fossil elements of *C. gnou*: the axis, humerus and radius. 355**
- Figure 122. Temporal and spatial patterning in the fossil elements of *C. gnou*: the metacarpal, tibia and metatarsal. 356**
- Figure 123. Ratio diagrams of limb elements of interior and coastal Florisian black wildebeest. 357**
- Figure 124. A biogeographic model illustrating vicariance in black wildebeest and in other plains-living grazing ungulates. 358**

LIST OF TABLES

Table 1. Chronological scheme of southern African land mammal faunas according to Hendey (1974b).....	13
Table 2. A classification of the family Bovidae adapted from Gentry (1992). Some extinct forms* are added for the sake of reference, while locality information for fossil Alcelaphini is taken from Vrba (1997).	28
Table 3. A selected list of fossil localities and fossil assemblages with black wildebeest materials.....	43
Table 4. Taxonomic list of fossil mammals from the Deelpan A and D brown hyaena burrows according to the number of identified specimens (NISP).	46
Table 5. Taxonomic list of fossil mammals from Maselspoort according to the number of identified specimens (NISP).	48
Table 6. Taxonomic list of fossil mammals from Kareepan according to the number of identified specimens (NISP).	50
Table 7. Taxonomic list of fossil mammals from Spitskop according to the number of identified specimens (NISP). Extinct species are indicated with an asterisk.....	52
Table 8. Taxonomic list of fossil mammals from Mahemspan according to the number of identified specimens (NISP). Extinct species are indicated with an asterisk.	55
Table 9. ESR results from Spitskop A, the Erfkroon overbank deposits, Mahemspan and Sunnyside Pan, given in years before the present (BP) (R. Grün pers. comm.).....	57
Table 10. Taxonomic list of fossil mammals form Sunnyside Pan according to the number of identified specimens (NISP). Extinct species are indicated with an asterisk.	58
Table 11. Taxonomic list of fossil mammals from the Florisbad spring according to the number of identified specimens (NISP), modified afer Brink (1987). Extinct species are indicated with an asterisk.	62

Table 12. ESR age estimates from the third test pit at Florisbad: the results of the early uranium uptake model and the linear uranium uptake model are given as averages (R. Grün pers. comm.)	65
Table 13. Taxonomic list of Cornelia-Uitzoek: a comparison of new material excavated from a slumped hyaena burrow (1998 to 2002), with previously collected material (old collection) Extinct species are indicated with an asterisk.	74
Table 14. Functional interpretation of the skull features of <i>C. gnou</i> in relation to <i>C. taurinus</i>.	98
Table 15. Geological age of fossil assemblages that include specimens of <i>M. priscus</i>.	106
Table 16. External and osteological characters of <i>C. gnou</i> that can be described as caprine or sheep-like.	141
Table 17. The wildebeest-like features of <i>M. priscus</i>.	143
Table 18. The hartebeest-like features of <i>M. priscus</i>.	143
Table 19. Skull measurements of the type specimen of <i>Oreonagor tournoueri</i> (Thomas 1884) from Aïn Jourdel.	150
Table 20. Some diagnostic characters of the skull material referred to <i>O. tournoueri</i> (Thomas 1884) from Aïn Boucherit. The characters are separated into underived characters resembling a generalised wildebeest-like alcelaphine and derived characters resembling <i>Megalotragus</i>.	155
Table 21. Quantification of some of the characters on the lower molars referred to <i>Oreonagor tournoueri</i> from Aïn Boucherit.	159
Table 22. A chronological list of selected fossil assemblages from the interior of southern Africa and from the Cape coastal zone, which have produced fossil materials of black wildebeest.	168
Table 23. Width of the premaxilla in <i>C. taurinus</i> and <i>C. gnou</i>	360
Table 24. Measurements of the lower jaw	361
Table 25. Measurements of the axis	366
Table 26. Measurements of the humerus.	369
Table 27. Measurements of the radius.	373

Table 28. Measurements of the metacarpal..... 377

Table 29. Measurements of the femur..... 382

Table 30. Measurements of the tibia. 384

Table 31. Measurements of the metatarsal..... 388

CONVENTIONS

Binomial names – Latin binomial names of extant species and their English equivalents are used interchangeably.

Cape coastal zone – an area to the west, southwest and south of the Cape Fold Belt.

Cape coastal sites – fossil localities from the Cape coastal zone.

Early Holocene – informal division of 10 000 to 6000 years ago

ESR/OSL - Electron Spin Resonance (ESR) and Optically Stimulated Luminescence (OSL) are two of the newer dating methods used in this study. These methods provide age estimates of previously undated or poorly dated Quaternary fossil materials and deposits in the central interior of southern Africa. The age estimates are the basis for discussing the chronology of large mammal evolution over the last million years. The methods are still undergoing refinement and while the age estimates may lack the precision of established methods, like radiocarbon, they are useful indicators of geological time.

Fossil – The term is used in its original sense, as derived from the Latin verb ‘fodere’, to dig. Any object recovered from below the ground surface could be considered a ‘fossil’. The term is not used in its derived sense, which is to indicate a bone that has become mineralised or partly mineralised.

Interior – an area to the north and east of the Cape Fold Belt, which includes the Karoo, Free State Province and adjacent areas. This area is characterised by an open vegetation structure being virtually treeless, except for river margins, on hills and where artificial disturbance has occurred. Botanically this area equates with the Nama Karoo Biome and the Grassland Biome (Low & Rebelo 1996).

Iziko – modern reference and fossil material were studied in the Iziko South African Museum, which is part of the Iziko museums conglomerate of Cape Town.

Large mammal faunas – The focus of this study is on the large herbivore component of the palaeo-environment, which includes mainly bovids and equids. Bovids and equids constitute the bulk of the large mammal biomass in African environments (Bigalke 1978). In Chapters 5 and 6 the large mammal faunas, consisting mostly of bovids and equids and associated with ancestral black wildebeest, are discussed.

Last Glacial - c. 65 000 to 12 000 years ago. This term is used informally to describe the sites and associated fossil assemblages that date to this time range.

Late Holocene – informal division of geological time from 3000 years ago to the present.

Latin anatomical terms – they are not given in italics, because this would hinder the easy distinction between text and italicised Latin taxonomic names. Latin anatomical terms are used interchangeably with English equivalents.

Mid-Holocene – informal division of geological time from 3000 to 6000 years ago.

Morphological group – the term is used for a group of species that share the same morphological blueprint. In cladistic terminology such a group of species would form a monophyletic group.

Plio-Pleistocene boundary – this is taken at the Gauss-Matuyama geomagnetic boundary around 2.6 million years ago (Van Kolfshoten & Gibbard 1998).

Robusticity – the term is used in the conventional sense, meaning stoutness. It can be expressed by ratios of bone length to transverse dimensions, such as shaft width, shaft depth or distal width. The term is not used in the sense of relative bone strength as reflected by cross-sectional geometry.

Taxonomic names and classification - The taxonomy of Skinner & Smithers (1990) for southern African mammals is followed here. It is preferred over the classification of Bronner *et al.* (2003). For extant and extinct members of the family Bovidae the taxonomy of Gentry (1992), with minor adaptations, is used (Chapter 3).

Terminal Pleistocene - informal division of geological time from 12 000 to 10 000 years ago.

Upper goat fold – a term used here to indicate the lingual ridge on the distal lobe of upper molars in certain bovids, especially members of the Caprinae. It is considered to be the equivalent of the buccal ridge on the mesial lobe of the lower molars, known as a goat fold. Goat folds are usually found in the Caprinae, but also occur in exaggerated form in Hippotragini and Reduncini. Although goat folds are normally absent in extant Alcelaphini, they can occur in underived forms.

CHAPTER 1: INTRODUCTION

THE ARID CENTRES OF AFRICA

Africa can be divided into three centres of aridification - the southwest, the northeast and the north of Africa (Figure 1). These arid areas, which can be traced back to the Miocene, are reflected in the character of the large mammal faunas of the present-day. They have persisted as centres of endemism for arid and semi-arid adapted forms. The evolution and dispersal of the typically African alcelaphine bovids and the dispersal and speciation of taxa of non-African origin, such as the zebras, are linked to these centres (Churcher & Richardson 1978; Gentry 1978; Maglio 1978; Eisenmann 1985, 1992; Vrba 1985, 1997). A group of alcelaphine bovids, the wildebeest, has a fossil record stretching back to more than 2.5 million years ago (Gentry & Gentry 1978; Harris 1991; Vrba 1997). However, the fossil remains of black wildebeest, *Connochaetes gnou*, are only found in southern Africa and in deposits of end-Early Pleistocene and younger age. The focus of this study is on the evolution of wildebeest, and in particular that of the black wildebeest.

The black wildebeest is endemic to the central elevated plateau of southern Africa. This area is a biogeographic island, which includes the Karoo and Highveld. This habitat can be distinguished from the area to the south and west of the Cape Fold Mountains, characterised by the Cape Fynbos vegetation (Taylor 1978). To the northwest and northeast the open plains habitat of the central plateau is bordered by wooded grasslands, such as the Kalahari and Bushveld (Low & Rebelo 1996). Black wildebeest and a number of extant endemic grazing ungulates are associated with this island of open grasslands. These ungulates are the blesbok (*Damaliscus pygargus phillipsi*), the local subspecies of the hartebeest (*Alcelaphus buselaphus caama*) and local forms of the plains zebra (*Equus quagga* subsp.) (Rau 1974, 1978; Skinner & Smithers 1990).

AIM OF THE STUDY

Central to this study is the question of the co-evolution of the black wildebeest and the temperate open grassland habitat in the Pleistocene in southern Africa. The black wildebeest has been selected among the endemic plains species of southern Africa, because of its

demonstrated close association with the modern-day open grasslands (Chapter 4) and because preliminary evidence suggests that it evolved *in loco* (Brink 1993). The black wildebeest has an abundant local fossil record, which stretches back to the end of the Early Pleistocene. The hypothesis, that there is a close relationship between the evolution of the black wildebeest and the appearance of open grasslands in the central plateau of southern Africa, is explored and tested through a set of secondary objectives:

1. A review of the modern environment and behavioural ecology of the black wildebeest
2. The construction of a chronological framework to evaluate the fossil evidence.
3. A detailed osteological comparison of extant southern African alcelaphines and the extinct giant alcelaphine, *Megalotragus priscus* (Broom, 1909).
4. A review of North African fossil alcelaphine material to investigate the origin of the genus *Connochaetes* and to identify the immediate ancestor of the black wildebeest.
5. A survey of black wildebeest fossil materials.

The requirement of placing the fossil samples in a geographic context is relatively easily met by studying fossil samples from known localities. In the course of this study samples were generated by excavating new localities (Chapter 5) and by studying existing museum collections. However, establishing the geological ages of the various fossil samples was initially problematical, because of the temporal limitation of the conventional radiocarbon dating technique and because of the absence of datable volcanic deposits in southern Africa (Klein 1970, 1999). This meant that until the early 1990's Quaternary fossils from the interior of southern Africa were essentially undatable, except by distant comparison with East Africa. In the course of this study the problem was addressed by the application of new methods of dating, such as Optically Stimulated Luminescence (OSL) and Electron Spin Resonance (ESR), which became available in the mid 1980's. These new methods have made it possible to obtain radiometric age estimates for previously undatable southern African Quaternary fossils and deposits. The results of the application of ESR and OSL to Florisbad (Grün *et al.* 1996) and other localities form the temporal framework of this study (Chapters 5 & 6).

A basic requirement before samples of fossil mammal remains can be studied is the need to identify the fossil specimens to the correct taxa. It is now widely accepted that it is beneficial, if not essential, to use modern comparative samples as a frame of reference when studying the

history of an animal species. In this study both postcranial and cranial elements are considered important for taxonomic identification. For this purpose a comparative technique, which has its roots in the conventional veterinary comparative anatomy tradition (*vide* Nickel *et al.* 1992), is employed. In post-World War II central Europe, this technique was developed at the Institute for Palaeoanatomy, Munich University, in the study of the domestication of Old World animals and of archaeological faunal remains from central Europe, the Middle East and Near East (Boessneck 1958, 1985; Von den Driesch 1976, 1983). The aim is to define the morphological essence of a taxon, which is termed here a “morphological blueprint” and approximates the concept of a “Bauplan” (*vide* Ruse 1992; Chapter 3). It refers to a component of morphology that can be taken as characteristic of an organism, or part of it. The concept is used to construct an osteological reference of extant southern African Alcelaphini and *M. priscus* (Chapter 7).

The osteological reference makes it possible to address the questions of the place and time of origin of the wildebeest genus, *Connochaetes*, its separation from the giant alcelaphine genus, *Megalotragus*, and the identity of the immediate ancestor of the first black wildebeest populations (Chapter 8). Alcelaphine materials referred to *Oreonagor tournoueri* (Thomas, 1884) from the North African arid centre were included in the study. This taxon is commonly taken to be the ancestor of the first members of the genus *Connochaetes* (Gentry & Gentry 1978; Vrba 1997).

The osteological reference serves also as the basis for the survey of black wildebeest fossil evidence (Chapter 9). In a study of the Florisbad mammal faunas (Brink 1987), it was noted that the horn cores of Florisian black wildebeest are different in shape from modern specimens and considerably more robust. Broom (1913), Cooke (1974), Vrba (1976) and Gentry & Gentry (1978) also noted these differences. The latter proposed that the horn shape of the Florisbad black wildebeest is a transitional form in an evolutionary series, intermediate between earlier Cornelian specimens and the living form (Figure 2). In the exploratory phase of the present study this hypothesis was tested and essentially supported (Brink 1993). In this study the survey of the fossil materials of the black wildebeest is aimed at addressing the question of its co-evolution with open grasslands.

DISCOVERY OF A PLEISTOCENE CAPRINE IN SOUTHERN AFRICA

An unexpected development from the survey of fossil wildebeest samples was the identification of Pleistocene caprine material in sites in montane areas of southern Africa. This material had previously been referred to a small black wildebeest form (Klein 1978; Brink 1984), because only dentitions and cranial elements were used for identification. This practice was and still is common in the study of Quaternary fossils in southern Africa. The caprine remains have been discussed in this dissertation (Appendix C), because they show the power of the approach in resolving the palaeontological record and because of their palaeo-ecological importance in illustrating parallel evolution with the wildebeest lineage

In the initial stages of this project the comparative approach was also tested in a study of postcranial equid materials from Florisbad originally described as *Equus lylei* Dreyer 1931 (Brink 1994). This study provided evidence in support of the existence of an extinct small zebra with ass-like body proportions and osteomorphology. Contrary to the view of Cooke (1950), this equid was distinct from the plains zebra. When it emerged that Eisenmann was using a similar comparative approach in the study of equid remains (Eisenmann *et al.* 1988), a collaborative programme for the study of the Pleistocene equids of southern Africa was initiated and is continuing (*e.g.* Eisenmann & Brink 2000; Eisenmann 2000). Although equids are associated with the centres of aridity a fuller discussion of their position in the evolution of southern African mammalian faunas lies outside the scope of this dissertation (*vide* Eisenmann 2004).

CHAPTER 2: HISTORICAL PERSPECTIVE

INTRODUCTION

Quaternary palaeontology as a field of study is not formally taught at any South African university and the few practitioners in this field of study have been trained informally and in other disciplines. However, in spite of this there is a rich local tradition in mammalian palaeontology that has had impact beyond the borders of the country and disproportionate to the numbers of practitioners in the field. A brief overview is given of the growth of the discipline in South Africa and the origin of some of the issues addressed in this study. Although broadly chronological this overview follows a geographic structure.

THE CENTRAL INTERIOR

The first recorded discovery of fossil mammalian material in southern Africa was in 1839. In that year the skull of a giant long horned buffalo from Pleistocene deposits of the Modder River, Free State Province, was reported to the Geological Society in London by Andrew Geddes Bain. The specimen was not formally named at this time, but it was described and named much later in 1891 by Seeley as “*Bubalus Bainii*” (Gautier & Muzzolini 1991). However, in 1851 fossil long horned buffaloes had been described from North Africa by Duvernoy (1851) as “*Bubalus antiquus*”. Thus, the name “*antiquus*” has priority over “*bainii*”. It is ironic that the first recorded find of a Quaternary fossil from southern Africa bears the name referred to a north African specimen, which was discovered at a later date.

After the turn of the 20th century, Robert Broom, who was then professor in zoology and geology at the Victoria College, now the University of Stellenbosch, described new material and created a number of new species, such as *Equus capensis* (Broom 1909a), based on a lower jaw fragment from the Cape Flats, and “*Bubalis priscus*” (Broom 1909b) on a cranial fragment from the Modder River. The focus on the central interior of southern Africa, and the Free State Province in particular, was maintained in the pioneering stage of Quaternary palaeontology with Broom’s initial description of the Florisbad spring fossils (Broom 1913). For the first time in southern Africa Broom was able to show the co-existence of prehistoric people and extinct mammals. This research stimulated Thomas F. Dreyer, professor of

geology and zoology at the Grey University College in Bloemfontein, now the University of the Free State, to continue with fieldwork at Florisbad. He also undertook systematic descriptions of the fossil material from Florisbad and other sites, such as Matjes River (Dreyer & Lyle 1931). In 1932 Dreyer obtained sufficient research funding to allow him to excavate an extensive area around the Florisbad spring. In the process he recovered large samples of fossil mammal material, Middle Stone Age artefacts and the now famous Florisbad human skull fragment (Dreyer 1935). This find was historically important, because it was only the third discovery of a pre-modern human fossil in sub-Saharan Africa. Only the discovery in 1921 by miners of the archaic human skull from Kabwe, Zambia (Mennell 1929), and Raymond Dart's description of the type specimen of *Australopithecus africanus* from Taung (Dart 1925) preceded the Florisbad discovery. The discovery of the Florisbad hominid underscored the importance of the central interior in the study of human and mammalian evolution and it encouraged Dreyer to extend his work to Vlakakraal, a spring site near Florisbad, and to other localities in the central interior (unpublished manuscripts in the library of the National Museum). Wells, Cooke and Malan (1942) later described the fossils from Vlakakraal.

Dreyer's influence on the discipline was somewhat diminished by his disagreements with his contemporaries from both Cape Town and Johannesburg on both palaeontological and archaeological issues (unpublished correspondence in the library of the National Museum, Bloemfontein). An example is Dreyer's insistence that the Florisbad human skull does not represent an African Neanderthal, but a locally evolved lineage, which eventually led to indigenous Khoisan-speaking populations (Dreyer 1935, 1947). This was the cause of disagreement with Drennan, a leading human anatomist of the time, who maintained that the Florisbad skull represents an "African Neanderthal" (Drennan 1935, 1937; unpublished manuscript in the library of the National Museum). At a much later stage Wells (1969) held the view that the Florisbad hominid together with the Border Cave specimen represented a "proto Negro-proto Bushman" stage of evolution. Wells's view of the evolutionary position of the Florisbad human skull was much closer to Dreyer's original interpretation. Dreyer's view was also surprisingly close to the present-day consensus view on the position of the Florisbad skull, that it represents an ancestral population of pre-modern humans in sub-Saharan Africa that led to the first fully modern humans (*vide* Bräuer 1984; Stringer 1992; McBrearty & Brooks 2000). However, because of the significance given at the time to

Eurasian human fossils, such as the Neanderthals from Europe and *Homo erectus* from East Asia, such an interpretation was untenable in Dreyer's lifetime. In spite of these differences in opinion, which at times became personal, Dreyer was presented with an honorary doctorate by the University of the Witwatersrand for his pioneering work on fossil human origins and mammalian evolution (P.V. Tobias pers. comm.).

In 1922 the appointment of E.C.N. van Hoepen as director and palaeontologist at the National Museum in Bloemfontein gave further impetus to palaeontological research in central southern Africa. The well-known Cornelia-Uitzoek site was discovered and investigated by Van Hoepen (1930, 1932a,b, 1947). During the late 1930s and early 1940s Van Hoepen excavated a major fossil occurrence at Mahemspan, a pan site in the Wesselsbron district, Free State (unpublished records in the library of the National Museum, Bloemfontein). Although this material was never fully published, it is extensive and forms an important part of the present study. As a pioneer Quaternary palaeontologist Van Hoepen's contribution can be seen in his work on fossil equids and on fossil suids from Cornelia. He identified some of the dental characters that allow distinction between the Cape quagga (*E. quagga quagga*) and the plains zebra (*E. quagga* subsp.). His work on this topic was translated from the Afrikaans into Russian by Gromova, a prominent Russian palaeontologist of the first half of the previous century, and so became known to V. Eisenmann, a specialist on equid evolution, who is presently at Muséum national d'Histoire naturelle in Paris (V. Eisenmann pers. comm.). Eisenmann incorporated this information in establishing the range of criteria that are currently in use for the distinction between the two species of equid (Eisenmann & De Giuli 1974; Eisenmann & Brink 2000). Besides being influenced by Van Hoepen's work on equids Gromova was instrumental in developing the osteological distinction between wild forms of sheep and goats, which made it possible for Boessneck *et al.* (1964) to develop the osteological distinction for the domestic forms of the two species.

Van Hoepen's pioneering work on the suids from Cornelia-Uitzoek has proved useful in establishing a suid biochronology, as initially applied in East Africa (Cooke & Wilkinson 1978; Harris & White 1979).

The creation of large numbers of new species on cranial elements, and sometimes on individual teeth, was common in the pioneering phase in Quaternary palaeontology in South

Africa. Perhaps the best known of these pioneers was Robert Broom. Sidney H. Haughton (1932a & b) was another influential figure of this generation. Many of the taxa created later became synonymised by the next generation of researchers represented by H.B.S. Cooke, L.H. Wells, R.F. Ewer, Singer and C.S. Churcher (Churcher & Richardson 1978; Cooke 1950; Cooke & Wilkinson 1978; Ewer 1957, 1962; Ewer & Cooke 1964; Singer & Boné 1960; Wells 1959a & b, 1964b).

In the 1950s A.C. Hoffman (1953, 1955) and A.J.D. Meiring (1956) provided some continuity in Quaternary palaeozoology and archaeology in the central interior. By the late 1960s, with the death of Hoffman, and with Meiring taking up a teaching position at the University of Fort Hare, the momentum of Quaternary palaeontological fieldwork in the interior was diminished. The lack of interest in Quaternary palaeontology at what was then the University of the Orange Free State and at the National Museum, which was understaffed at that stage (Van der Bank 1998), were the reasons for this decline. After the 1960's only the summary volume on the Cornelia-Uitzoek locality, with discussions on the sediments (Butzer 1974), fossil mammals (Cooke 1974) and stone artefacts (Clark 1974), appeared in print. In the early 1980s the acquisition of the Florisbad fossil site as a research station of the National Museum provided a new impetus. The acquisition was due mainly to the efforts of J.J. Oberholzer, then director of the National Museum. New research followed at Florisbad and at other Quaternary fossil localities in the interior (Clarke 1985; Rubidge & Brink 1985; Kuman & Clarke 1986; Brink 1987, 1988, Scott & Brink 1992; Brink *et al.* 1995, 1999). The present study forms part of this renewed phase of work in the interior of southern Africa.

AREAS NORTH AND WEST OF THE VAAL RIVER

In areas to the north of the Vaal River gold mining activities and the need for lime, were indirectly responsible for the advancement of Quaternary palaeontology. The first australopithecine was discovered at Taung and described by Dart (1925). This was followed by the discovery of more early hominid fossil localities at Sterkfontein, Swartkrans, Kromdraai and Makapansgat. Lime miners exposed these fossil-bearing deposits (Dart & Craig 1959; Tobias 1997, 2001). The scientific study of these fossil deposits and their contents was largely due to the efforts of Dart and Broom and this in turn stimulated younger scientists of the time, such as Tobias (1997). Tobias initiated the systematic investigation of

the Makapansgat localities, when he conducted student expeditions to the Makapan Valley in the mid-1940's. These expeditions rekindled Dart's interest in the australopithecines. In 1947 James Kitching working under Dart's direction discovered the first hominid from the Limeworks site. This was soon followed by more hominid discoveries by James Kitching and his brothers Ben and Scheepers. James Kitching was largely responsible for producing the impressive fossil collections from the Limeworks, which are now housed in the Bernard Price Institute for Palaeontology, University of the Witwatersrand (Kitching 1951, 1953, 1965, pers. comm.). Although he made a significant contribution to Quaternary palaeontology Kitching is better known for his contribution in his primary research interest, Karoo-aged mammal-like reptiles.

Dart's osteodontoceric theory was an attempt to provide a taphonomic interpretation for the fossil bone assemblages from the Makapansgat Limeworks (Dart 1949, 1957). At that time C. K. Brain was already involved in the study of the geological formation of hominid-bearing cave breccias (Brain 1958), and Dart's osteodontoceric theory stimulated him to develop the field of bone taphonomy, aimed at understanding the fossil assemblages from cave deposits. Brain's taphonomic research program started in the mid-1960's, was focussed on Swartkrans and continued until recently (Brain 1967, 1974, 1976, 1980, 1981, 1993). After the initial work at Sterkfontein by Dart, his students and Broom, P. V. Tobias continued to direct the research at this locality. Initially A.L. Hughes and latterly R.J. Clarke have been responsible for the fieldwork there. Clarke recently discovered a virtually complete australopithecine skeleton in the Member 2 of Sterkfontein (Clarke 1998). Sterkfontein has produced one of the largest fossil hominid collections known.

The study of the hominid-bearing cave breccias and the Swartkrans project of C.K. Brain led to two schools in palaeo-zoology being established at the Transvaal Museum in Pretoria. These are the departments of Palaeontology and Archaeozoology. The research activities of E.S. Vrba, a fossil bovid specialist, and others, such as A. Turner, a carnivore specialist (Turner 1984, 1985, 1986, 1987), were directly stimulated by Brain's work on the hominid-bearing cave breccias. Vrba's initial work on fossil bovids from the Plio-Pleistocene sites of Sterkfontein, Swartkrans and Kromdraai was important in providing a relative faunal chronology for these localities (Vrba 1974, 1975, 1976). Latterly she has become known for theoretical work on evolutionary processes involving cladistic analyses and for her

contributions in drawing palaeoclimatic inferences from the fossil bovid record (Vrba 1979, 1988, 1995; 2000; Vrba *et al.* 1989). Recently she has studied the fossil bovid material from the Middle Awash, Ethiopia (Vrba 1997). Currently J.F. Thackeray is continuing palaeontological research at the Transvaal Museum (Thackeray 1995; Thackeray *et al.* 1996).

In the late 1970's a research program to study animal remains from archaeological sites was established at the Transvaal Museum. The archaeozoological work of Voigt and Plug has been aimed at the study of mostly Holocene and Late Pleistocene material (Voigt 1979, 1986; Voigt & Plug 1984; Plug 1989, 1990, 1992, 1993a, 1996a, 1996b; Plug & Roodt 1990; Plug & Skelton 1991; Plug & Engela 1992; Plug *et al.* 1997; Plug *et al.* 2003). Recently Plug & Badenhorst (2001) summarised a large body of data from such sites and their survey provides an insight into temporal and spatial patterns of prehistoric faunal distribution in southern Africa.

R.F. Ewer, C.S. Churcher and A.W. Gentry made substantial contributions to the study of southern African fossil mammals. Ewer studied carnivores and suids (Ewer 1955a, 1955b, 1956a, 1956b, 1956c, 1956d, 1958, 1962), while Churcher focussed on fossil hyracoids, equids and giraffids (Churcher 1956, 1978, 1982, 1986, 1993; Churcher & Richardson 1978). Churcher maintained a strong interest in southern African, East African and North African fossil mammals and is still active (Churcher 2000; Churcher *et al.* 1999). Gentry, who is a specialist in ruminant evolution and based at the Natural History Museum in London, is known in particular for his work on Miocene to Pleistocene bovids from East Africa, but he also contributed to the study of southern African fossil bovids. (Gentry 1978, 1980; Gentry & Gentry 1978). His current interests are in early ruminant evolution (Gentry 1990, 1995).

THE VAAL RIVER GRAVELS

Mining activities resulted not only in the discovery of the hominid-bearing cave breccia sites, but also the discovery of fossil deposits along the Vaal River, a by-product of alluvial diamond mining. The first studies of fossil mammals from the Vaal River date to the 1920's (Haughton 1922; Broom 1925; Dart 1928). In 1928 a fossil assemblage from the Vaal River gravels near Barkley West was donated to the Natal Museum (Wells 1959a). In addition to

their contributions to research on the fossil material from the hominid cave breccia sites, H.B.S. Cooke and L.H. Wells also studied the fossils from the Vaal River gravels (*vide* Cooke 1939, 1949; Cooke & Wells 1946; Wells 1959a, 1964a, 1964b). This work aided in the correlation of the old terraces of the Vaal River (Cooke 1949; Butzer 1984).

THE CAPE COASTAL ZONE

Apart from the early work of Broom, the 1950's discovery of the Elandsfontein fossil site on the Cape west coast near Saldanha Bay, and a human skull fragment (Singer 1958; Singer & Wymer 1968), marked the beginning of Quaternary palaeontology in the Cape coastal zone. Singer had a pioneering role in stimulating palaeontological research in the Cape (Singer 1961, Singer & Hooijer 1958; Singer & Boné 1960; Singer & Fuller 1963; Hendeby & Singer 1980). The growth of palaeontological research in the Cape coastal zone postdates similar developments in other parts of South Africa.

In 1963 Singer commissioned H.J. Deacon to initiate systematic excavations at Elandsfontein (Deacon 1998). This work was followed by further excavations by Wymer, who also carried out the first excavations at Klasies River on the Tsitsikamma coast (Singer & Wymer 1968, 1982). The work at Elandsfontein and at Klasies River gave increased momentum to palaeontological research in the Western Cape. Q.B. Hendeby, who worked under R. Singer, and investigated some of the same sites (Singer & Fuller 1963), initially focused on Middle and Late Pleistocene fossil assemblages from the Cape coastal zone. These included Melkbos and Swartklip 1 & 2 (Hendeby 1968; Hendeby & Hendeby 1968). Later he directed his attention to the early Pliocene site of Langebaanweg and its carnivore fossils (Hendeby 1974a), and his research there is acknowledged as a major contribution.

The link between Quaternary palaeontology and archaeology, which developed during the 1960's and 1970's in the Western Cape, was largely driven by shared interests in palaeoecology and archaeology in the community of researchers (Deacon 1976; Hendeby & Deacon 1977; Klein 1972, 1976, 1980, 1984, 1986; Klein & Cruz-Urbe 1991). R.G. Klein is a North American based archaeologist, who developed his interests in palaeontology and faunal analyses through collaboration with Hendeby at Iziko South African Museum. His work on southern Africa Quaternary mammalian faunas from the Cape coastal zone has provided a

valuable bridge between Quaternary palaeontology and Stone Age archaeology and contributed much to the continuing interest in Quaternary palaeontology in this area. The work of D.M. Avery on micromammals (D.M. Avery 1982, 1987, 2002) and G. Avery on fossil birds and the taphonomy of carnivore accumulated bone assemblages can also be seen as a product of this trend (G. Avery 1988; G. Avery *et al.* 1984, 1998).

A BIOCHRONOLOGICAL SCHEME

H.B.S. Cooke, L.H. Wells and R.F. Ewer were instrumental in drawing up the first biochronological scheme based on fossil mammals for southern Africa. Such schemes, in which a local site name is used to refer to other faunas of similar character, are commonly used in other parts of the world (Savage & Russel 1983). Cooke (1952) made the first informal attempt to create such a scheme and suggested three groupings of southern Africa Quaternary sites. This was followed in 1955 by recommendations at the Third Pan African Congress on Prehistory (*vide* Clark 1957: xxxi, xxxii), which proposed that East African terms should be used as a basis for the development of a general African terminology, contrary to Cooke's earlier suggestion. However, Wells (1962) pointed out that faunal stages are best identified by local site names and in subsequent works the recommendation concerning the use of an East African based terminology was not followed. In 1960 Ewer and Cooke (Ewer & Cooke 1964) established a four-stage scheme in which locality terms were used to indicate four biochronological phases in the southern African mammalian sequence. This scheme remained unchanged except for some minor modifications (Wells 1962, 1967, 1969; Cooke 1967), until Hendey (1974a, b) revised it by contracting the previous Swartkrans and Sterkfontein Faunal Spans into the Makapanian Land Mammal Age and by adding the Namibian and Langebaanian Land Mammal Ages (Table 1). Later McKee (1993) attempted mammal seriation schemes for Plio-Pleistocene southern African mammals, which are based on the presence and absence of time-sensitive taxa. These seriation schemes are essentially refinements of the Land Mammal Age scheme and are potentially useful, but their reliability is dependant on the quality of primary identifications in published reports (see Chapter 6 for further discussion).

Table 1. Chronological scheme of southern African land mammal faunas according to Hendeby (1974b).

Land Mammal Ages	Approximate geological age
Namibian	Miocene
Langebaanian	Early Pliocene
Makapanian	Late Pliocene/Early Pleistocene
Cornelian	Middle Pleistocene
Florisian	Late Pleistocene

A BIOGEOGRAPHIC MODEL

When the first biochronological schemes for southern African land mammals were proposed there was a developing awareness of the importance of geographic distribution patterns of large mammals. Wells (1957,1962) and Cooke (1957) had attempted the first explicit palaeo-biogeographic interpretation of Pliocene and Quaternary fossil mammals, but the existence of a southwest-northeast arid corridor in Africa had been anticipated by the zoologist, Austin Roberts, in 1937, when he addressed the South African Association for the Advancement of Science in Windhoek (Wells 1962). Roberts relied solely on the modern distribution patterns of arid-adapted taxa. The idea of an arid corridor linking the faunas of southwest Africa and northeast Africa was pursued further by Balinsky (1962) and Wells (1962). This insightful idea is of great importance in understanding modern and past distribution patterns of large mammals, but it has not been given the prominence it deserves in studies of southern African Quaternary mammals.

DISCUSSION

There are three salient points emerging from this brief historical overview:

- The first is the importance of fossil hominid discoveries as the driving force in the study of fossil mammals.

- The second is the emergence of attempts to provide both temporal and geographical perspectives on Plio-Pleistocene large mammal evolution.
- A third point of interest is that in identifying fossil materials there has been an almost complete focus on cranial material. Postcranials have largely been ignored in taxonomic studies. In taphonomic work only the size categories of large mammal families, such as in bovids, are recognised.

The latter two points are of primary interest in this study and receive considerable discussion. The application of new dating techniques provides a temporal framework for Early/Middle Pleistocene mammal evolution in the central interior of southern Africa. This temporal framework serves as the basis for redefining the Cornelian and Florisian Land Mammal Ages and for assessing alcelaphine and wildebeest evolution. The biogeographic approach applied to the fossil record adds a spatial component to this study. The morphological technique gives access to the postcrania of fossil bovids, which previously were thought to be undiagnostic.

CHAPTER 3. BIOGEOGRAPHY, SPECIATION AND MORPHOLOGY

INTRODUCTION

Chronology is a basic requirement in palaeontology, given the concern with constructing phylogenies and the need to arrange fossils according to geological age. However, any attempt at understanding evolutionary processes, as seen in the fossil record, should take into account both the chronology of morphological change and the way it is expressed in geographic space (Nelson & Platnick 1981). In this chapter the biogeographic and morphological approach to the fossil record is outlined.

BIOGEOGRAPHY

Dispersal and vicariance

The distribution patterns of organisms in geographic space and in time concern the field of biogeography, while zoogeography is the branch concerned with animal distribution in particular (Udvardy 1969; Cox & Moore 1980). An animal species can be defined as a grouping of organisms, which share certain distinctive characteristics, such as social and breeding behaviour, morphology, feeding behaviour, and habitat requirements. These aspects can be seen as components of a system, which interact with the natural environment (Leuthold 1977). This interaction produces a distinctive pattern of distribution of the species (Cox & Moore 1980). Therefore, the characteristics of a species predict the habitat in which it can live (Udvardy 1969), and will determine its distribution in geographic space.

When environmental conditions become favourable through climatic or habitat change, they allow species to disperse (Cox & Moore 1980). They are able to expand their ranges and occupy a previously inaccessible geographic space. Inherent in the concept of dispersal is the “move away from a point of origin” (Udvardy 1981), but it also includes the idea of crossing a previously existing barrier (Cox & Moore 1980). A common view is that when dispersal occurs it may cause the reproductive isolation of daughter populations from the ancestral population. In biogeographical terms the two processes, range expansion and the reproductive isolation of daughter populations, are known respectively as dispersal, or mobilism, and as vicariance, or immobilism (Nelson & Platnick 1981; Croizat 1981; Udvardy 1981; Cox 2001).

There have been extensive debates in the field of historical biogeography on whether vicariance or dispersal best accounts for distributional patterns in taxa (*e.g.* Wallis & Trewick 2001). To address this question in the context of this study it is instructive to review the historic background. Ball (1976) has distinguished three phases of development in the field: a descriptive or empirical phase, a narrative phase and an analytical phase. The narrative phase is considered to reflect more traditional ways of creating scenarios and is typified by a view that considers fossils as the “ultimate key to understanding historical relationships” (Ball 1976: 506). The analytical phase, which is thought to start with the phylogenetic systematics, or cladistics of Hennig (1966), is essentially the combination of the cladistic method with a vicariance approach developed by Croizat (1958, as quoted in Croizat 1981; Humphreys & Parenti 1986). In this phase cladistic methods are applied to biogeography and it is described by the term “cladistic biogeography” (Humphreys & Parenti 1986). In cladistic biogeography areas of endemism are ranked according their presumed relatedness to each other, similar to the way organisms are ranked in a cladistic study. This method makes cladograms of areas, which are tested by cladograms of individual taxa occupying those areas. Although Croizat stated that sedentism, or immobilism, is the more important process and without it “vicariant distributions would be impossible” (Croizat 1981: 509), it appears that some consensus has been reached in this field of study. It is commonly accepted now that for vicariance to occur a preceding dispersal event is necessary and that both processes must be considered important for understanding patterns in the geographic distribution of animals. This was recognised by Brundin (1981) and Short (1981), but also by Humphreys and Parenti (1986).

Biogeography and speciation

If the characteristics of a species determine the kind of habitat in which it can live, the question arises of how these characteristics evolve and of the role of vicariance in the process of evolution. To address these questions one needs to return to the definition of a species. Under natural conditions reproductive isolation of populations of organisms from other similar organisms can be taken as grounds for considering the former a distinct species from the latter (Odum 1971; Paterson 1985; Dietrich 1992; Schwartz 1999; Mayr 2001). Inherent in this definition is the concept of mate recognition, as explained by Paterson (1985). This involves members of a species recognising other members as potential mates. According to

this view closely related, but sympatric organisms can maintain specific distinction on the basis of mate choice.

In contrast, the Neo-Darwinian view is that biogeographic isolation is the primary mechanism for reproductive isolation (Mayr 1942, 2001). It is assumed that when a species of large mammal expands its range, or disperses, from a centre of origin, it may result in genetic changes to the daughter populations due to reproductive isolation, which may lead to the formation of a new species. This agrees with the biogeographic view that reproductive isolation can result when a formerly more-or-less uniform habitat becomes fragmented (vicariance) or when a dispersal event occurs across a pre-existing barrier (dispersal) (Nelson & Platnick 1981). This process, where morphological distinctiveness appears in daughter populations that are reproductively isolated due to biogeographic isolation, has also been termed allopatric “speciation” (Mayr 1942, 2001; Vrba 1985). In the Neo-Darwinian view it is also accepted that reproductive isolation and speciation can occur through “mere distance”, if the geographic area occupied by a species is too large to allow gene flow between the daughter populations (Ford 1955: 99). In this case reproductive isolation between daughter populations may occur even without the presence of a biogeographic barrier, but simply due to genetic drift expressed in geographic space. The result is a cline (Huxley 1939, as quoted in Ford 1955), which in time may give rise to reproductively distinct populations and can lead to the formation of a new species. Therefore, the biogeographic concept of vicariance can be defined in evolutionary terms as genetic changes occurring in populations that became reproductively isolated from other similar populations due to their separation in geographic space. The Neo-Darwinian view is to define such spatially separated and reproductively isolated populations as either separate species or incipient species (Mayr 2001). The assumption is that in the time after a dispersal natural selection is the agent responsible for the genetic changes that occur in reproductively isolated daughter populations.

However, this view has been challenged and it has been suggested that biogeographic isolation need not be invoked to explain the process of speciation. Goldschmidt (1940) suggested that certain kinds of mutations have a large effect on developmental processes that lead at once to new and stable forms. Goldschmidt referred to such changes as macromutations, which could be distinguished from micromutations. The former is seen as the basis for speciation, while the latter is thought to reflect the effects of natural selection that

do not necessarily lead to a new species, such as when daughter populations are biogeographically isolated from each other. This view is a departure from the Neo-Darwinian view in that natural selection is not seen as the sole mechanism that governs speciation. The shortcoming of Goldschmidt's argument was that he could not satisfactorily define the genetic mechanism that causes macromutation (Dietrich 1992). Recently, a genetic mechanism has been found that can explain macromutations. It was noted that mutations affecting regulatory genes, known as "homeobox genes", can spread sufficiently in the recessive state among individuals of a population to become manifest abruptly in the form of "morphological, physiological or behavioural novelties" (Schwartz 1999: 28). These morphological and other kinds of changes appearing abruptly can effect reproductive isolation in sympatric populations. Mate recognition among individuals from such a population will differentiate them from sympatric populations in which the changes had not occurred. The discovery of the effect of homeobox genes in evolution is significant for understanding the process of speciation in that it provides a genetic basis for the commonly observed phenomenon in palaeontology that evolutionary novelties in the fossil record appear suddenly, as punctuations (*vide* Eldredge & Gould 1972). Goldschmidt (1940, 1952) anticipated this discovery when he referred to these fundamental genetic shifts as macromutations.

Heterochrony is an evolutionary phenomenon that probably can be linked to the sudden appearance of novelties. The term "heterochrony" has undergone marked shifts in meaning since the time that it was used to describe exceptions to the "rule" of universal recapitulation (Gould 1992). Recapitulation predicts that ancestral adult stages will appear earlier and earlier in the ontogeny of the descendants through the accelerated development. In this way the descendant forms will show all the ancestral stages in the process of its development. Heterochrony was thought to reflect exceptions to universal recapitulation, until it was shown that this "law" does not apply in all cases. Today the term is taken to mean phylogenetic change in development timing (Gould 1992: 164). Thus, heterochrony can result in either a speeding up or a slowing down of development timing, resulting in either peramorphosis or paedomorphosis. Heterochrony may be a side effect of mutations to homeobox genes (Schwartz 1999), which may trigger either acceleration or the slowing down of development. Such minor changes can cause large-scale phynetic re-organisation. Heterochrony can be linked to the processes of punctuated equilibria and macromutations in the sense that they

refer to major re-organisations in organisms leading to new and stable forms (Goldschmidt 1940, 1952; Dietrich 1992; Gould 1977, 1992).

Another factor that can drive large-scale phenetic re-organisation is known as Baldwinian co-evolution (Oppenheimer 2004), where behavioural innovations drive evolution. Co-evolution may be another manifestation of the effects of mutations to homeobox genes. It has been proposed as an important factor in human evolution in that behaviour can generate genetic responses. In this sense co-evolution implies a positive relationship between behaviour and a genetic response, which is not compatible with the concept of natural selection.

Reproductive isolation through geographical isolation can lead to genetically distinct daughter populations (vicariance), but it is not necessarily a prerequisite for speciation. However, the view adopted here is that where it can be demonstrated, biogeographic isolation should be recognised for its potential in causing vicariance. Both in the living large mammal faunas of Africa (Kingdon 1997) and the fossil record (Vrba 1976, 1997; Gentry & Gentry 1978) the effects of vicariance are evident. This applies particularly in the bovid and equid faunas. In cases where biogeographic isolation can be demonstrated, this can usually be linked to physical aspects of the environment, such as ecological complexity or the size of the area occupied by a population of organisms (*vide* Ford 1955; MacArthur & Wilson 1967). In alcelaphine bovids a good example of vicariance due to genetic drift is the local forms, or subspecies, of the hartebeest, *A. buselaphus*, which occur throughout Africa and formerly in Arabia (Uerpman 1987; Kingdon 1997). The process of dispersal and subsequent genetic drift resulted in regional populations, or subspecies, which can be seen as an example of a cline. Another example is the sub-Saharan distribution of the subspecies of the plains zebra, *E. quagga* (Rau 1974; Eisenmann 1997). The subspecies of hartebeest and of the plains zebra represent populations that are very closely related. This probably reflects a relatively recent date of their dispersal and genetic drift (micromutation), which did not lead to speciation. Evidently the time since their respective dispersal events was sufficient to have allowed sufficient morphological differentiation in the daughter populations of the hartebeest and the plains zebra to have allowed speciation.

In summary, given enough time a dispersal event can be followed by reproductive isolation and this can lead to vicariance and genetically distinct daughter populations. Biogeographic

isolation may lead to the appearance of a new species, but it is not a prerequisite for speciation. Contrary to the Neo-Darwinian view, speciation can occur rapidly through a major genetic re-arrangement (*vide* Goldschmidt 1952; Schwartz 1999), which may be visible in the fossil record as punctuations. This can occur in sympatric populations.

MORPHOLOGY

Introduction

It has been noted that biogeography is subordinate to systematics and that “biogeography can be no better than the taxonomy it must use to describe distributions.” (Patterson 1981: 447). This highlights the obvious need to be able to identify a fossil specimen to the correct taxon. Although the process of taxonomic identification, or diagnosis, is partly subjective and depends on the skill of the researcher, its objectivity can be enhanced by systematic and reproducible methods. The comparative morphological technique employed here has its roots in the comparative anatomy tradition of the 19th and early 20th century as developed in veterinary research (Nickel *et al.* 1992). It has been adapted by archaeozoologists, or osteo-archaeologists to archaeological problems, such as the osteological distinction between domestic sheep and goats and the process of domestication (Boessneck 1985; Boessneck *et al.* 1964; Boessneck & Von den Driesch 1978; Von den Driesch 1983). This application of comparative anatomy to the Holocene fossil record has had major impact on the study of domestication, since it enabled the tracing of the history of domesticated animals in greater confidence and detail than was previously possible. In southern Africa this methodology has found application in archaeozoology (*vide* Plug & Badenhorst 2001 with included references), but only to a limited extent in the field Quaternary palaeontology (Brink 1993, 1994; Watson & Plug 1995; Brink *et al.* 1999).

In studies of Quaternary palaeontology this morphological technique provides access to information from osteological materials, which were previously assumed to be “undiagnostic”, such as large ungulate postcranial elements in fossil collections (Plug & Peters 1991; Peters & Brink 1992; Brink 1993, 1994; Watson & Plug 1995; Peters *et al.* 1997 – see also Peters *et al.* 1994 and Klein 1994 for discussion). Whereas this technique was first

applied to the study of domestication, *i.e.* genetic modification to animals due to human intervention (Boessneck 1985; Benecke 1994; Clutton-Brock 1987), it is applied here to record morphological changes, which reflect genetic shifts due to natural processes. The basis of this technique is the concept of a morphological blueprint, also known as a “Bauplan” (Ruse 1992; Mayr 2001),

A morphological blueprint

Definition of a morphological blueprint

The morphology of an organism is a constituent element of its phenotype and can be defined as the observable physical manifestation of the organism, which includes its physiology and behaviour. The phenotype of an organism at any given time is the consequence of its genotype and the environment in which it is developing at that moment (Lewontin 1992), and can be observed as morphology. Morphology consists of two inter-dependant components, size and shape. Since dimensions (size) contribute to proportions and since proportions contribute to shape, both size and shape combine to produce the characteristic morphology of a given organism, or parts of it. The general morphology of an animal and the morphology of its constituent skeletal elements reflect the suitability of the animal to a specific ecological niche. This suitability, also known as adaptation, includes not only morphology, but also physiology and behaviour (Moen 1973; Leuthold 1977; Mayr 2001).

In evolutionary biology the term “adaptation” is commonly taken to mean “the evolutionary modification of a character under selection for efficient or advantageous (fitness-enhancing) functioning in a particular context or set of contexts” (West-Eberhard 1992: 13). Since the morphology of an organism, or those of its constituent parts, can be observed as discrete characters and since all characters evolved, one may deduce from the above statement that all morphologies are adaptations and, therefore, are functional. On the contrary, morphology is seen here as a totality of characters, some more easily observed than others (and only in relation to other similar characters), which defines the phenotype of the organism. It is accepted that there is a component in morphology that reflects function, but that morphology cannot be explained entirely by function (*vide* Lauder 1995; Padian 1995). Certain aspects of morphology tend to be less amenable to change in spite of functional needs and can be described as tending towards being genetically entrenched. The phylogenetic entrenched

nature of certain morphologies has been noted before in a study of uinatheres, where plesiomorphic dental characters related to the ancestry of the animals are retained without any apparent function (Turnbull 2002). Such morphologies, which cannot be explained by function, have been described as “vestigial form” being the product of “selective forces” no longer in operation (West-Eberhard 1992). Therefore, certain components of morphology may be explained by function, but the balance cannot be, but tends to be genetically entrenched and to be less prone to change. Morphology may be driven by functional needs or other “selective forces”, but is governed by the constraints of phylogeny.

In practice all the morphological traits of a species, which make it unique and distinguish it from other species, are its morphological blueprint. The blueprint consists of a combination of features inherited from a string of ancestors, from the very distant to the very recent past. It includes the concept of a body plan. The blueprint of species is reflected mainly in the morphological characters that refer to major genetic re-organisation in ancestral forms (*vide* Schwartz 1999). When these characters become fixed, they can be considered to be ‘constrained by phylogeny’. Such genetically fixed morphology can be latent, or recessive, but may re-emerge under certain conditions. Morphological blueprint morphology may reflect both the processes of macromutation and micromutation.

A morphological blueprint is relative to the taxonomic level at which it is applied. At lower orders of taxonomy it will tend to reflect more recently acquired characteristics, such as produced by genetic drift. At higher levels of taxonomy genetically entrenched characters that reflect major re-organisations in morphology (macromutations) will tend to be more important. Therefore, a morphological blueprint can be defined as a relative term reflecting morphologies that tend towards being genetically entrenched, but which is complemented by morphologies that reflect more recently acquired characters, which often can be related to function.

The concept of a morphological blueprint in relation to cladistic terminology

In general terms the goal of phylogenetic systematics, or cladistics, is to establish phylogenetic relationships between taxa and to order them hierarchically into monophyletic groups on the basis of synapomorphies (Wiley *et al.* 1991). However, in the process of

establishing a morphological blueprint morphological characters are not given polarities as being either ancestral or derived. Rather, the aim is that all available morphology should be considered without bias as far as is possible. In establishing a morphological blueprint the immediate aim is not to construct a phylogeny, but rather to diagnose to the correct taxon. This is in contrast to the working method in phylogenetic systematics (Wiley *et al.* 1991).

Even if it is not their primary purpose, morphological blueprint characters can be useful for indicating relatedness and can eventually be applied in a phylogenetic analysis. For example, it is possible to diagnose morphological ‘overprinting’ in the process of establishing a morphological blueprint, which refers to more recently acquired characteristics, such as functional adaptations. This can be illustrated by convergence of form in animals with very different phylogenies (Mayr 2001). Such convergence in form can be due to similarity in behaviour and therefore function, but the origin of the animal can be deduced from characters that are conservative and not prone to change. There are numerous examples of this phenomenon, but an example from sub-Saharan Africa is the resemblance of the body shape of the bovid tribe Tragelaphini to deer, the family Cervidae. The role of deer, as specialised, large-bodied browsers, is assumed to some extent in sub-Saharan Africa by animals such as kudu (*Tragelaphus strepsiceros*) and bushbuck (*T. scriptus*). Kudu in particular is very deer-like in its overall body shape and in some details of its skeleton. Nonetheless, the bovid origins of the tribe Tragelaphini are not in doubt, as is evident in genetically fixed characters, such as, for example, horns instead of antlers and the shape of the metatarsals (*vide* Bosold 1966). Therefore, although the convergent deerlike characteristics of kudu and bushbuck are real, their blueprints are those of tragelaphine bovids.

It may be argued that morphological overprint characters may equally be named “shared derived characters”, or “synapomorphies”, which define the node of the monophyletic group (= the tribe Tragelaphini in the above example) and that those characters that tend to be genetically fixed are identical to the concept of “plesiomorphy” (Wiley *et al.* 1991). This may be valid, but the difference in the two approaches is that the total morphology of the organism is taken into account in establishing blueprint characters, while in phylogenetic systematics only synapomorphies are considered useful for morphological analysis. In this sense it may be advisable that a morphological analysis, in which blueprint characters are first defined, precede a cladistic analysis.

To summarise, the process of establishing a morphological blueprint requires the consideration of the totality of diagnostic features, as is explained in Boessneck *et al.* (1964), but these characters are not given a polarity. In contrast, in cladistic terminology these characters can be either plesiomorphic or synapomorphic for a given clade. In the application of the concept of a morphological blueprint, both recently evolved characters and more ancestrally inherited characters may be used to define the morphological blueprint. The morphological blueprint approach to the identification of a fossil specimen is top down. The identity of a fossil specimen is established by first noting those features which place it in a higher taxonomic position. Identification is continued to progressively lower taxonomic levels, with the goal to identify the specimen at the lowest possible taxonomic level, *i.e.* at the species, subspecies or population level.

Establishing a morphological blueprint

Morphological blueprints at the lowest level of taxonomy

Since there is a need for the process of identification to be independently reproducible, the criteria used for identification need to be clearly defined. Such criteria, or diagnostic characters, are established by means of multiple comparisons of modern specimens of known identity. It is a process of morphological distillation and is dependent on the availability of sufficiently large samples of modern reference material. Large samples are necessary to distinguish natural individual variation from those characters that are diagnostic for the taxon (*vide* Boessneck *et al.* 1964; Peters *et al.* 1997). Therefore, although the application of a morphological blueprint is a hierarchical process, where a fossil specimen is first included in higher orders of taxonomy, the generation of such blueprint data starts at the lowest level of taxonomy, *i.e.* ideally at the population, sub-species or species level.

Usually the species that are selected for comparison are from the same taxonomic grouping, but at the lowest functional level above the species. In the family Bovidae this level is usually the tribe, which would be an example of a monophyletic group in cladistic terminology. In practical terms the process of comparison starts with two individuals per species, one male and one female. All observable differences between the two species seen in the original sample are noted. Characters relating to sexual dimorphism are noted in addition to general

characters. At the same time standard measurements are taken. In this study the standard work of Von den Driesch (1976), with modifications by Peters (1986) and by Brink (Brink *et al.* 1999), is followed. The next step in the process involves testing the reliability of these characters by repeating the comparison with additional comparative specimens. In this way it is possible to factor out individual variation from diagnostic characters that are meaningful for identification at the required level of taxonomy. Occasionally there are single characters that are “infallible” for identification at a particular taxonomic level, but usually all diagnostic characters, whether plesiomorphic or apomorphic in a given context, are used to provide a consensus of identity.

Because of normal variation in populations not all characters defined as diagnostic may be equally expressed in all individuals. Some characters may only be useful as an indication of a morphological trend and this may vary in expression between individuals (Boessneck *et al.* 1964). The morphological blueprint at the species level, or at lower levels of taxonomy, will tend to have characters related to more recent morphological changes, which may have functional meaning and, therefore, may tend to be apomorphic in a given context. Furthermore, not all skeletal elements are equally diagnostic. In ungulates, as specialised runners, it is usual that the more distally situated a limb element is, the more diagnostic it is.

Morphological blueprints at higher levels of taxonomy

At levels above the species the morphological blueprint will reflect morphologies of increasingly genetic depth. As it is possible to define a morphological blueprint of a given skeletal element for a species, so it is possible to distil from such characters higher order characters, which define the next level of taxonomy. For example, by using those characters, or combination of characters, which are uniquely shared by black wildebeest and blue wildebeest it is possible to establish a morphological blueprint for the genus *Connochaetes*.

An example of how this method can complement a cladistic analysis concerns a skull feature of the fossil taxon *Megalotragus priscus*. The fused condition of the horn pedicels of *M. priscus* was in the past diagnosed as a synapomorphy, shared by the extant hartebeest (Vrba 1979). However, through the application of this method of comparison, the blueprint of *M. priscus* is clearly that of a large wildebeest and it is not closely related to the modern hartebeest (*vide* Chapter 7). For this reason, the fused condition of the horn pedicels in both

M. priscus and the hartebeest must have evolved independently and, therefore, represents parallel evolution. This can be termed a homoplasy due to parallelism (Mayr 2001). Thus, although the present study is not explicitly cladistic, blueprint characters may be useful for such an analysis.

To summarise, the process of establishing a morphological blueprint starts at the lowest taxonomic level, which is usually the species, and proceeds towards higher taxonomic levels. The process of identification, and classification, where the morphological blueprint is applied, is the reverse. It utilises the morphological blueprint by applying such knowledge initially at higher taxonomic levels and then at progressively lower levels. The aim of taxonomic identification is to reach at least the level of the species.

MEASUREMENTS, DATA MANAGEMENT AND STATISTICAL METHODS

Since dimensions are components of morphology, measurements need to be included in the process of morphological description. Measurements may occasionally reveal morphology that is not immediately visible to the eye (*vide* Brink *et al.* 1999), but more usually they are used to support an observed morphology (Eisenmann & Brink 2000). Another application of measurements in palaeobiology is to trace temporal changes in body size of organisms, as in the well-known cases of size reduction and proportional changes in domesticated mammals (Boessneck & Von den Driesch 1978). In the present study measurements on the various skeletal elements of fossil black wildebeest have been treated in a similar way, by ordering them in geological time. This allows the documentation of morphological and size changes in a similar way as changes in domesticated animals have been traced.

For data management, graphic projections and statistical testing the StatSoft package, CSS Statistica version 5.1, is used. All measurements were entered in the spreadsheet facility of this package and from this database graphic projections and statistical testing were done.

Bivariate graphic projections were used to explore the metric data, to illustrate size and proportional differences between taxa and to indicate temporal patterns in size changes in fossil material of *C. gnou*. Where sample sizes are sufficiently large the variation within a

given population or species is illustrated by means of ellipses indicating 95% confidence limits.

Simple linear correlations (Pearson r) are used to determine the extent to which two dimensions of a skeletal element are proportional to each other. The correlation coefficient (r) represents the linear relationship between the two variables.

To evaluate the difference in means between two groups a t-test is can be used. However, to test for significant differences between the means of multiple samples, such as for the different temporal samples of fossil *C. gnou*, analyses of variance (ANOVA) were applied. Tukey's Honest Significant Difference test for unequal sample sizes was used as a post-hoc test. In these tests F is the variance ratio. In all tests the statistical difference is considered significant at $p < 0.05$.

Ratio diagrams are multivariate graphic projections that take into account both size and morphology, with the advantage that close 'contact' with the original data is maintained. These projections are used to illustrate the comparative morphology of individual skeletal elements, the body proportions of alcelaphines and the temporal trends in fossil *C. gnou*. This method, also known as Simpson diagrams, allows the simultaneous graphic projection of a number of discrete measurements on specimens, which can be of greatly varying sizes (Simpson 1941; Eisenmann 1979). Logarithmically transformed (\log_{10}) means of measurements are plotted against the transformed means of measurements of an arbitrary species, which is used as reference, or baseline, and is presented as the zero values in the diagrams. In the case of the tribe Alcelaphini the blue wildebeest, *C. taurinus*, is used throughout as the reference, while in the case of the Caprini the barbary sheep, *Ammotragus lervia*, is used as the reference.

TAXONOMIC SYSTEM UTILISED

The taxonomy of southern African Bovidae at the subfamily and tribal levels used in this study follows that of Gentry (1992; Table 2). For the Alcelaphini all extant forms and some of the extinct fossil taxa are indicated, but for the other tribes only a selection of living and extinct species is included. At the generic and species levels there are some minor

modifications to Gentry's system, such as the generic name for the giant long horned buffaloes. The name *Homoiceras* Bate is preferred to *Pelorovis* Reck. The latter is considered inappropriate, because there is doubt concerning the ancestor-descendant relationship of *P. olduvaiensis* and the geologically younger long horned buffaloes (Gautier & Muzzolini 1991; Geraads 1992; Peters *et al.* 1994; Klein 1994).

Asterisks indicate extinct forms in Table 2. In this study the genera *Connochaetes*, *Megalotragus**, *Oreonagor**, *Numidocapra**, *Beatragus*, *Parmularius**, *Alcelaphus* and *Damaliscus*, of the tribe Alcelaphini, and the genera *Ovibos*, *Budorcas*, *Makapania**, *Ovis*, *Capra*, *Hemitragus* and *Ammotragus*, of the subfamily Caprinae, are of primary interest.

Table 2. A classification of the family Bovidae adapted from Gentry (1992). Some extinct forms* are added for the sake of reference, while locality information for fossil Alcelaphini is taken from Vrba (1997).

Subfamily	Tribe	Genus	Species	Common name
Bovinae	Tragelaphini	<i>Tragelaphus</i> <i>Taurotragus</i>	many spp. <i>oryx</i>	<i>e.g.</i> bushbuck, kudu, nyala eland
	Boselaphini (non-African)			
	Bovini	<i>Syncerus</i> <i>Pelorovis</i> <i>Homoiceras</i>	<i>caffer</i> <i>olduvaiensis</i> * <i>antiquus</i> *	Cape buffalo Fossil form (North & East Afr.) Fossil form (North, East & S. Afr.)
	Cephalophini	<i>Cephalophus</i> <i>Philantomba</i> <i>Sylvicapra</i>	<i>natalensis</i> <i>monticola</i> <i>grimmia</i>	red duiker blue duiker grey duiker
Antilopinae	Neotragini	<i>Raphicerus</i>	<i>campestris</i> <i>melanotis</i> <i>sharpei</i>	steenbok grysbok Sharp's grysbok
	Antilopini	<i>Madoqua</i> <i>Oreotragus</i> <i>Antidorcas</i>	spp. <i>oreotragus</i> <i>marsupialis</i> <i>recki</i> * <i>bondi</i> *	dik dik klipspringer springbok Fossil form (S. & East Afr.) Fossil form (S. Africa)
		<i>Gazella</i> <i>Antilope</i>	spp. <i>cervicapra</i>	gazelles Black buck (Indian)
Hippotraginae	Reduncini	<i>Kobus</i>	<i>leche</i> <i>ellipsiprymnus</i>	lechwe waterbuck
		<i>Redunca</i>	<i>fulvorufula</i> <i>arundinum</i>	mountain reedbuck southern reedbuck
	Hippotragini	<i>Hippotragus</i>	<i>equinus</i> <i>niger</i>	roan sable

		<i>Oryx</i>	<i>leucophaeus</i> <i>gazella</i>	blue antelope - recently extinct gemsbok	
Alcelaphinae	Aepycerotini	<i>Aepyceros</i>	<i>melampus</i>	impala	
		Alcelaphini	<i>Connochaetes</i>	<i>taurinus</i> <i>gnou</i>	blue wildebeest black wildebeest
			<i>Megalotragus</i>	<i>kattwinkeli</i> *	Fossil form (East & ?S. Afr.)
				<i>euicornutus</i> *	Fossil form (S. Afr.)
				<i>priscus</i> *	Fossil form (S. Afr.)
			<i>Oreonagor</i>	<i>tournoueri</i> *	Fossil form (North Afr.)
			<i>Numidocapra</i>	<i>crassicornis</i> *	Fossil form (North & East Afr.)
			<i>Rabaticeras</i>	<i>arambourgi</i> *	Fossil form (North, East & S.Afr.)
			<i>Beatragus</i>	<i>hunteri</i> <i>antiquus</i> *	Hunter's hartebeest (East Afr.) Fossil form (East Afr.)
			<i>Alcelaphus</i>	<i>buselaphus</i> subspp.	hartebeest/kongoni
			<i>Damaliscus</i>	<i>pygargus</i> subspp. <i>niro</i> *	blesbok/bontebok Fossil form (East & S. Afr.)
				<i>lunatus</i>	tsessebe/topi
			<i>Parmularius</i>	spp.	Fossil forms (North, East & S. Africa)
Caprinae	Ovibovini	<i>Ovibos</i>	<i>moschatus</i>	muskox (northern hemisphere)	
		<i>Budorcas</i>	<i>taxicolor</i> <i>churcheri</i> *	takin (East Asia) Fossil form (East Africa)	
		<i>Makapania</i>	<i>broomi</i> *	Fossil form (South and ?East Africa)	
	Caprini	<i>Ovis</i>	spp.	sheep (Eurasia)	
		<i>Capra</i>	spp.	goats (Eurasia)	
		<i>Capra</i>	<i>ibex</i>	ibex (North Africa/Europe)	
		<i>Ammotragus</i>	<i>lervia</i>	Barbary sheep (North Africa)	
		<i>Hemitragus</i>	<i>jemlaicus</i>	Himalayan thar (Asia)	
	Indet. caprine	<i>Oreamnos, Rupicapra, Nemorhaedus</i> etc. – northern hemisphere			

CHAPTER 4. AFRICAN ARIDITY AND BLACK WILDEBEEST ECOLOGY

INTRODUCTION

The separate post-Oligocene geological and geomorphological histories of the three parts of Africa resulted in similar semi-arid to arid climatic conditions in these areas. Arid-adapted faunas evolved in these evolutionary centres, which functioned as areas of endemism from where dispersal of such forms occurred by way of interconnecting corridors. These processes, which are evident in the Miocene to recent faunal record of the continent (Maglio & Cooke 1978), produced the distinct Aethiopian character of African faunas (Bigalke 1978). However, through time the biogeographic continuity in the semi-arid to arid parts of Africa was repeatedly interrupted by the evolution of endemic faunas. The endemic character of these centres often became weakened by subsequent extinctions and renewed dispersals. In southern Africa the most recent example of such endemism concerns the appearance of the black wildebeest and the associated grazing ungulate fauna. This fauna is adapted to the open-structured highveld-type temperate grasslands, which differentiate southern Africa from East Africa and North Africa.

The link between open-structured temperate grasslands, winter cold and fire has been postulated as the cause for the expansion of open-structured highveld grasslands in southern Africa (Brain 1985). These grasslands are essentially treeless and receive frost at night on an average of around 100 days per year. In southern Africa aridity and cold winter temperatures combine to produce the characteristic grasslands, to which the black wildebeest is adapted. In this chapter background is given on the appearance of aridity as a characteristic of the palaeoclimates of Africa, but in particular of southern Africa, and on the close relationship between open habitat and black wildebeest reproductive behaviour and ecology.

AFRICA SINCE THE MIOCENE

The appearance of aridity in the palaeo-climates of North, East and southern Africa primarily reflects changes to the palaeo-geography of the continent. The transformation of African

palaeoclimates to aridity or semi-aridity appears to start first in the south-western parts of southern Africa at the end of the Oligocene or Early Miocene, as reflected in the fossil record of the coastal area of Namibia (Axelrod & Raven 1978; Deacon 1983; Partridge *et al.* 1995; Pickford & Senut 1999, 2003). The early aridification of the southwestern parts of Africa was initiated with the formation of the proto-Benguela Current at the end of the Oligocene. This current conveys cold polar water to the west coast of southern Africa and is the main reason for aridity along the southwest coast of Africa (Axelrod & Raven 1978).

The aridification effect of the cold north-flowing Benguela Current was enhanced by tectonic uplift, which affected the interior of southern Africa in the Early Miocene and later at the end of the Miocene/early Pliocene. Tectonic uplift also affected East Africa in the Early Miocene, and was caused by geological buoyancy deep within the earth's mantle, known as the African Superswell. In East Africa the formation of the East African Rift System further associated with the elevation of the landscape (Partridge *et al.* 1995). In both East Africa and in southern Africa tectonic uplift had the effect of preventing the free circulation of rain bearing weather systems from coastal areas and caused aridification. Thus, central southern Africa and East Africa share semi-arid to arid climates due to their elevated landscapes, but they are differentiated by the presence to the southwest of Africa of the cold Benguela current, which caused an earlier onset of arid climates in the southwest of Africa (Axelrod & Raven 1978).

In East Africa tectonic uplift and the formation of the East African Rift System resulted in the dynamic landscapes conducive to the preservation of fossils. Volcanic deposits, associated with the tectonic instability of the area, are useful for the purpose of radiometric dating. For this reason East Africa has the best dated and the most abundant and continuous Miocene to Pleistocene fossil record in Africa (Hill 1995; Pickford 2001). Southern Africa, although experiencing Miocene to early Pliocene tectonic uplift, has a more stable Plio-Pleistocene landscape and consequently less favourable sedimentary conditions existed for the preservation of fossils. Also, the lack of volcanic deposits suitable for radiometric dating hampers the process of age determination so that most of the southern African Cainozoic fossil record, with the exception of the Middle and Late Pleistocene, is dated mainly by means of faunal correlation with East Africa.

North African climates dried out with the closure of the Tethys Sea, when Africa-Arabia was joined to Asia during the mid-Miocene resulting in the termination of a major latitudinal system of climatic circulation (Axelrod & Raven 1978). Therefore, although North Africa did not experience tectonic uplift, unlike southern and East Africa, it also underwent Miocene to Pliocene cooling and aridification due to changes in circulation patterns resulting from the closure of the Tethys Sea and the formation of the proto-Mediterranean Sea (Dupont & Leroy 1995). Consequently, the North African arid belt and its associated arid-adapted large mammal faunas can be traced beyond Africa into the Middle East and Arabia (*vide* Uerpmann 1987). However, due to landscape stability the quality of the Neogene fossil record in North Africa resembles southern Africa in that it is less abundant than East Africa and in the absence of volcanic deposits suitable for dating purposes (Geraads *et al.* 2004).

Thus, in spite of the differential quality and datability of the fossil record in the three arid centres, it appears that Africa as a whole, with the possible exclusion of the core areas of the modern equatorial rainforest, have undergone palaeoclimatic change over the last c. 20 million years that tended towards producing grasslands and savannahs in semi-arid to arid conditions. These changes were modulated by the steady cooling trend in the earth's atmosphere (Brain 1985) and by the global glacial-interglacial cycles (Shackleton 1995), in which colder periods are generally associated with more arid conditions in Africa (Deacon & Lancaster 1988).

SOUTHERN AFRICA

The landscape

Southern Africa can be divided into two main physiographic zones, a coastal zone and an uplifted central plateau zone. The central plateau consists essentially of the Karoo geographical region and the Highveld and is bound to the south by the Cape Fold mountain ranges. It is an elevated and planed landscape, the product of processes initiated at the end of the Jurassic when rift faulting fragmented the Gondwana super continent (Du Toit 1954; King 1978; Partridge & Maud 2000). The Cape coastal zone is situated beyond the Cape Fold Mountains. It is characterised by sandstones and clay stones of the Cape Supergroup, which predate the Karoo sequence (Du Toit 1954). The Cape soils, which are derived from such rocks, are not generally fossiliferous, except where phosphatic and younger calcareous rocks

produce sedimentary conditions that allow the preservation of Quaternary fossils. The narrow coastal plain around southern Africa extends below the sea to form a continental margin, which was exposed as dry land during glacials when the sea level regressed (Van Andel 1989).

In Africa a long period of stability and planation followed the fragmentation of Gondwana, which resulted in the “African” land surface. This land surface survives today as the central part of the Highveld and as relict landforms in other localities in southern Africa (Partridge & Maud 2000). The period of stability was terminated in the Early Miocene through tectonic uplift along a number of axes. Large scale uplift at the end of the Miocene further elevated the interior plateau by approximately 1000 m and tilted the marginal regions outwards (King 1978; Axelrod & Raven 1978). This undulating and planed landscape exposes rocks of the Karoo Supergroup, consisting mostly of the Dwyka, Ecca and Beaufort Groups, but is broken by small inselbergs (“koppies”) of dolerite. Igneous intrusion during the Jurassic caused the dolerite hills and ridges to remain prominent as the landscape became planed down. Dolerite intrusions are also the origin of numerous springs by acting as impervious barriers within aquifers of the Karoo geological sequence. Towards the end of the Cainozoic the Karoo deposits have become eroded and infilled, leaving remnant, isolated sedimentary pockets of mostly mid- to late Quaternary age. In more western parts small internal drainage basins are formed, which are semi-arid features, known as pans. Virtually the whole landscape was recently covered by a thin drape of Holocene aeolian deposits (Loock & Grobler 1988). Generally the sediments and soils of the interior are rich in calcium-carbonate, which often allows good preservation of Quaternary fossils in sedimentary deposits, such as those found at springs, pans and around river drainages.

Open grasslands and open habitat in southern Africa

Botanically the central plateau encompasses the Nama Karoo and the Grassland Biomes (Low & Rebelo 1996; Figure 3). The Cape coastal zone includes the Succulent Karoo Biome in the west, the Fynbos Biome in the southwest and south, the Thicket Biome in the southeast and Savanna Biome outliers to the northeast.

The Nama Karoo Biome (Low & Rebelo 1996) is on the western half of the central plateau and its elevation is between 1000 and 14000 meters above sea level. It is mainly a summer

rainfall area, with precipitation varying between 100 and 520 mm per year. The lime-rich shallow soils produce a dominant vegetation of grassy dwarf shrub land. Under certain conditions, such as where soils are deeper, grasses can be more dominant. The Nama Karoo grades into the drier Succulent Karoo to the west as winter rainfall becomes more predominant. The Grassland Biome adjoins the Nama Karoo to the northeast on the central plateau at elevations of between 1350 and 2150 meters above sea level. It receives summer rainfall and equates approximately with the term “Highveld”. The highest parts are in the east in the highlands of Lesotho and the Drakensberg. Grasslands are characterised by a single layer of grasses with the degree of cover dependent on rainfall. Rainfall varies between 450 and 800 mm. Rainfall decreases from northeast to southwest in accordance with the topography and synoptic climatic patterns. Soils vary from duplex soils, with clay underlying aeolian sand, to clay soils, which are derived from the rocks of the underlying Karoo Super Group. Open grasslands occur on these soil types and also marginally to the east of the Drakensberg escarpment in Kwazulu-Natal (Low & Rebelo 1996).

The Nama Karoo Biome and the Grassland Biome cut across a substantial rainfall gradient from east to west. Although their boundary is thought to be dynamic (Acocks 1975), they share an essentially open and treeless vegetation structure. The open vegetation structure is interrupted only by some tree and bush development along drainages and on koppies. Bush encroachment in this area seems to be stimulated by artificial disturbance, such as overgrazing. These biomes accommodate almost identical ungulate faunas, characterised by springbok, blesbok, black wildebeest and plains zebra or Cape quagga (Skead 1980), suggesting that the distinction between the two biomes, which is based on botanical considerations, does not apply to the distribution patterns of large mammal populations. This is suggested by Holocene and Late Pleistocene fossil evidence from the Karoo (Brink et al. 1995; Bousman et al. 1988; Plug & Badenhorst 2001) and by the reports of early travellers in the Karoo area (Skead 1980; Cullinan 1992). Thus, in terms of vegetation structure and the character of the ungulate faunas one may consider the central interior plateau of southern Africa to be one biogeographic entity, even though in phytogeographic terms it is divided into two biomes.

BLACK WILDEBEEST BEHAVIOUR AND ECOLOGY

Feeding behaviour

The black wildebeest are predominantly grazers, preferring short grass leaf material. They can modify their feeding behaviour to include up to 37 % dicotyledonous material in Karoo environments (Van Zyl 1965; Von Richter 1974; Vrahimis in press). In grasslands the proportion of grass selected increases and can be around 90 %. It is essentially non-selective, but has preference for certain species of grass when available (Vrahimis in press). Bulk feeders, *sensu* Hofmann & Stewart (1972), have the ability to shift their feeding behaviour to include a proportion of dicotyledonous material. This is because their digestive physiology, which is adapted to cope with low quality grass material, can quite easily process material of higher protein and carbohydrate content (Moen 1973; McDonald *et al.* 1973; Sinclair 1983; W. Hylander pers. comm.). However, the opposite is not possible, where selective browsers of high quality dicotyledonous plant material shift to grazing. The black wildebeest is a specialised grazer of short grass, similar to its close relative, the blue wildebeest (Hofmann & Stewart 1972; R.C. Bigalke pers. comm.). However, it can feed on smaller items of nutrient-rich material, such as freshly grown grass or even occasionally dicotyledonous material.

Social and reproductive behaviour

Social and reproductive behaviour in bovids are closely linked to their ecology. The behavioural systems can be classified according to the degree or kind of territoriality (Jarman 1974). Leuthold distinguishes between territorial behaviour systems in which territories are either resource-based and those in which they are not, but have primarily social significance (Leuthold 1977). Examples of the former include bovids, such as kudu, nyala, reedbuck, grey rhebok, oribi, duikers and many species of the Neotragini, that are more sedentary, where the territories coincide with the entire home range. Examples of the second category are bovid species, such as all Alcelaphini, waterbuck, lechwe, puku, Grant's gazelle, Thomson's gazelle and springbok. These animals are gregarious and their territories are primarily of social significance. In this category non-territorial males form bachelor herds, while dominant males occupy territories, which are used for mating purposes. Females visit such mating areas, but non-territorial males are excluded.

An extreme form of territorial social behaviour in animals is known as the lek or arena system, where mating territories are very small and locally aggregated in dense clusters that are maintained over long periods of time. Among the bovids this system of territorial behaviour is known only in the Uganda kob. However, under conditions of high population density certain bovids can develop this behaviour temporarily (Estes 1991; Leuthold 1977).

Alcelaphines are typical examples of gregarious bovids with non-extreme or “normal” territorial behaviour. However, there is a subtle, but distinct, difference in the degree of territoriality in mating behaviour of the two living species of wildebeest. The black wildebeest tends to have more specialised territorial behaviour than the blue wildebeest, to the extent that its mating behaviour resembles the lek system of the Uganda kob. Black wildebeest dominant males form territorial networks and receptive females will approach territorial males (Vrahimis in press). In black wildebeest territoriality is obligate, with the maintenance of territories a prerequisite for reproduction. In blue wildebeest the degree of territoriality can be flexible and is dependent on external factors. In the situation of a confined environment where there is a dense aggregation of animals, such as in the Ngorongoro crater, blue wildebeest may become territorial (Estes 1969). On the other hand, blue wildebeest males have been observed to herd groups of females for mating purposes (Attwell 1977). This is observed when blue wildebeest aggregate in large numbers in unconfined space, as also happens in the yearly migrations in the Serengeti (Leuthold 1977; Estes 1991). When blue wildebeest males become territorial it is usually only for the time of the rut (Attwell 1977), while dominant black wildebeest males tend to maintain territories throughout the year (Von Richter 1972, 1974). The maintenance of fixed territories in the black wildebeest is a prerequisite for reproduction, but it is not so for the blue wildebeest. The breeding behaviour of the blue wildebeest can be described as variable and the maintenance of fixed breeding territories in geographic space only occurs in the breeding season and when suitable habitat is available. Black wildebeest territorial behaviour may be described as derived in representing the extreme of the spectrum of the breeding behaviour observed in the blue wildebeest. Black wildebeest territories are fixed localities, while blue wildebeest territories need not be tied to a specific locality, but can be social space (Attwell 1977).

Habitat requirements

The territorial reproductive behaviour of black wildebeest is reflected in its habitat selection. Breeding males require unobstructed vision to survey the territories that they control. On some game reserves in the Free State, where black wildebeest have been kept in marginal habitat with insufficient open space, territorial males have been observed to remove obstructing branches and bushes to gain the necessary visual control over their breeding territories (Kok & Vrahimis 1995). Another example of this extreme form of behaviour is from the Soetdoring Nature Reserve, close to the Florisbad Research Station, where a territorial male black wildebeest was observed to target an acacia tree in its territory over a number of years, eventually destroying it. Under natural conditions, where there are no restrictions on movement, black wildebeest will not occupy breeding territories in marginal habitats. The territorial breeding behaviour of black wildebeest demands open habitat, which can be visually surveyed and controlled.

Past and present distribution patterns of wildebeest

The requirement of an open habitat has been the main factor restricting the natural distribution of black wildebeest. The historically recorded distribution of black wildebeest coincides closely with the extent of the Grassland and the Nama Karoo biomes (Figure 4). The present geographic limits of these two biomes would be a very close approximation of the historical distribution of the black wildebeest before they were virtually exterminated by hunting, by drought and by the disruption of farming in the interior of southern Africa. Although the Nama Karoo and Grassland biomes are affected by fluctuating summer rainfall patterns the primary production of grass over the whole area provided sufficient food for migrating large grazing ruminants. They share an open habitat necessary for black wildebeest reproduction.

Black wildebeest was historically recorded in open grassland habitats to the east of the escarpment in areas of Kwazulu-Natal and Swaziland (Von Richter 1974; Skead 1980; Vrahimis in press). It is possible that these distribution records from peripheral areas reflect the mobility of black wildebeest herds in response to seasonal changes in food quality and availability. The disturbance caused by the rapid expansion of the agricultural and hunting frontier during the second half of the 19th century did not allow first hand research records of seasonal movements of black wildebeest. However, one can assume that plains-adapted game

species followed patterns of seasonal movement. It is likely that black wildebeest would have migrated seasonally, in spite of its more fixed territorial behaviour.

During the Last Glacial, and earlier in the Middle Pleistocene, ancestral populations of black wildebeest were able to extend their range onto the glacially exposed continental platform to south of the Cape Fold Mountains (Brink 1993). This provides further proof of the flexibility of the black wildebeest as a grazer, but more specifically of its need for open habitat. One may envisage the glacially exposed continental shelf on the southern margin of South Africa, to the south of Cape Agulhas, as temperate grasslands (Klein 1975, 1983; Chapter 9). In character and in structure these habitats would have resembled the grasslands of the interior, although probably impoverished in terms of soil nutrient availability (Chapter 9).

The territorial mating behaviour of black wildebeest is also the basis for its spatial differentiation from the blue wildebeest. Blue wildebeest is at home in savannah and wooded grasslands, which are in the northwestern and northeastern parts of southern Africa extending into East Africa (Skinner & Smithers 1990). The natural distribution of the black wildebeest was focussed on the central plateau of southern Africa. However, historical records and the fossil record indicate that blue wildebeest periodically overlapped in range with black wildebeest in the southern open grasslands, which are peripheral to the core areas of its distribution (Skead 1980; Plug & Engela 1992; Brink et al. 1999; Plug & Badenhorst 2001; Chapter 5). Occasionally blue wildebeest even occurred to the south of the Orange River (Skead 1980; Cullinan 1992). Although the southern open grasslands are peripheral to its main distribution area, blue wildebeest can overlap with black wildebeest, because of similar feeding requirements and because blue wildebeest is more flexible in breeding behaviour. However, black wildebeest cannot occur in wooded grasslands, because of its specialised territorial breeding behaviour. For this reason blue wildebeest can overlap in distribution with black wildebeest, but not *vice versa*. Fossil evidence suggests that in the past blue wildebeest had a virtually pan-African distribution (Vrba 1976, 1997; Gentry & Gentry 1978; Geraads 1981; Harris 1991; Harris *et al.* 1988), occurring in all three arid centres, but excluding the equatorial forests.

The question of hybridisation between black wildebeest and blue wildebeest

In spite of differences in body size, horn and skull shape, body proportions and coloration black wildebeest is closely related to the blue wildebeest. The modern blue wildebeest appears to be the virtually unchanged descendants of the ancestral populations from which black wildebeest evolved (Gentry & Gentry 1978; Brink 1993). This close genetic relationship allows the two species to interbreed with fertile offspring (Fabricius *et al.* 1988; S. Vrahimis pers. comm.; I. Rushworth pers. comm.; personal observation). The author became aware of the problem of hybrids when collecting black wildebeest material from game reserves and game farms in the Free State Province to augment the comparative collections at the Florisbad Research Station. Although several hybrid individuals have been added to the Florisbad collections, these specimens are not included in the present study.

Although in the past there was a natural overlap in the distribution of the two species, no interbreeding was recorded historically and none is evident in the fossil record. The disruption of the social behaviour of black wildebeest through their confinement and restriction on farms and reserves, often in sub-optimal habitat, is the likely cause of the interbreeding. The differences in breeding behaviour and in mate recognition of the two extant species of wildebeest are the reasons why there is no past record or indication of interbreeding under natural conditions.

The fact that the hybrid offspring are fertile may prove disastrous for the survival of the black wildebeest. The species is under threat and a black wildebeest conservation plan is being formulated to ensure the survival of the species (S. Vrahimis pers. comm.).

Parallels between black wildebeest and caprines

There are very obvious parallel adaptations in black wildebeest and advanced forms of sheep, such as North American thin horn sheep, *Ovis dalli*, and bighorn sheep, *O. canadensis* (Geist 1971). Parallels include the enlarged horns, which are forwardly pointed, and the pneumatisation of the basal parts of the horns, which extends into the frontal bones of the skull. These structures are adaptations associated with increased aggressiveness and frequency in horn contact between competing males and are designed to absorb the impact of frequent horn-to-horn and head-to-head contact. Large horns and displays of aggressive behaviour

influence mate selection in females and are related to breeding success in dominant males. The observations of Geist on the morphology of the horns and how this is related to social and breeding behaviour have relevance to the black wildebeest. The salient characteristic of black wildebeest behaviour is its general aggressiveness, which in the breeding season is focussed on the maintenance of breeding territories by dominant males. Aggressive behaviour is expressed in the frequency of head contact (Vrahimis pers. comm.). To accommodate this behaviour there are structural adaptations in the frontal parts of skull, such as the enlargement of the basal bosses and the forward horn curvature. These and other soft tissue characters are caprine-like adaptations (*vide* Chapter 7).

SOUTHERN AFRICA AS A PERIODIC BIOGEOGRAPHIC ISLAND

Southern Africa can be seen as an ecological island (Cox & Moore 1980), in that the open, treeless habitat of the Karoo and the Highveld is structurally different from the area from neighbouring areas with wooded grasslands. The open habitat of central southern Africa acts as an isolating mechanism by restraining the movement of specialised ungulates, such as black wildebeest and blesbok that are dependant on open vegetation for reproduction. The “island effect” of the open habitat of the South African interior is reflected in the convention to refer to southern Africa as a “sub-region” distinct from the rest of Africa (Skinner & Smithers 1990).

CHAPTER 5. MATERIAL AND FOSSIL LOCALITIES

INTRODUCTION

The modern and fossil materials used in this study are outlined in the first section of this chapter. In the second section a description of fossil localities from the interior of southern Africa that were investigated in the course of this study is given. Summaries are provided of fossil localities from the Cape coastal zone and from North Africa.

MATERIAL

Alcelaphini

Modern material

Modern material of *C. gnou*, *C. taurinus*, *A. buselaphus caama* and *D. pygargus* from the Iziko South African Museum, the National Museum and the Transvaal Museum was used as the basis for the osteological comparison (Chapter 6). Because of the anthropogenic disruption of the mammal populations of southern Africa, a large proportion of modern specimens used in this study derive from *ex-situ* populations. This raises the question of whether these samples reliably reflect the original populations of the central interior.

The black wildebeest was on the verge of extinction at the turn of the 20th century and again in the 1930's, so that the species has experienced two genetic bottlenecks (Vrahimis pers. comm.). Thus, the largest proportion of the Florisbad black wildebeest reference specimens, which is housed in the collections at the Florisbad Research Station and is from Free State game reserves and game farms, may be expected to show the effects of the two population bottlenecks. However, due to the foresight of Van Hoepen, who made a black wildebeest collection in the 1930's, a small sample of black wildebeest, which predates the second bottleneck, is available for study in the Florisbad large mammal collections. This collection, as well as samples of very late Holocene fossil material, demonstrates that the modern black wildebeest populations from the Free State show no discernable effects of the two bottlenecks. Thus, even if the genetic variability of modern Free State black wildebeest was

reduced, it seems not to be expressed in the morphology of the animals. For the present purpose the black wildebeest reference samples used in this study can be considered to be a reliable representation of pre-20th century black wildebeest populations of the interior of southern Africa. The Florisbad black wildebeest study collection is complemented by a sample from the Iziko South African Museum. This sample represents a culled population from the Cape Point Nature Reserve, which was experimentally introduced in the 1960's. Although this sample derives from outside of the natural distribution area of black wildebeest, the specimens were measured and found not to fall outside of the variation of specimens from Free State game reserves and for this reason the Cape Point sample is included in the reference sample.

The blue wildebeest study sample consists of a mix of animals from intact populations, from game reserves and from zoological gardens. Surprisingly few blue wildebeest skeletons are available in the main South African institutions with large mammal skeletal collections, the Iziko South African Museum, the Florisbad Research Station and the Transvaal Museum.

Because the southern subspecies of the hartebeest, *A. buselaphus caama*, was effectively extinct in the central interior by the mid-20th century, all specimens from Free State game reserves are the result of translocation from nearby areas (S. Vrahimis pers. comm.). However, these specimens also represent the local subspecies. In addition to game reserve specimens, a few individuals of the southern subspecies from the Bloemfontein zoological gardens are included in this study. Measurements from Peters *et al.* (1997) were included to increase the sample.

Modern populations of the blesbok have been under similar stress to the hartebeest and black wildebeest. However, there is the added complication that since the 1960's the large-scale translocation of bontebok into the Free State has disrupted the genetic integrity of the blesbok considerably. The problem has been addressed and apparently rectified in nature reserves of the Free State provincial government, but on private game farms in the Free State and neighbouring areas bontebok are still kept and bred. There is, therefore, some possibility that the blesbok sample used in this study may contain hybrid blesbok X bontebok individuals. For the purpose of this study, hybrids are not considered a problem, as the bontebok and blesbok are two subspecies of *D. pygargus* and resolution to subspecific level is not needed

here. However, this problem will have to be addressed when a systematic comparison of the two subspecies is undertaken.

In addition, a few specimens of the tsessebe, *D. lunatus*, from the Florisbad collections were used for informal comparison. Due to the rarity of the Hunter's hartebeest, *Beatragus hunteri*, only one incomplete specimen from the osteological collections in the Muséum national d'Histoire naturelle, Paris, was examined.

Fossil material

In tracing the fossil history of the black wildebeest certain skeletal elements were selected for study. These include the skull, lower dentition, axis, humerus, radius metacarpal, femur, tibia and metatarsal. It was decided not to include the upper dentition, since this would potentially duplicate the patterns evident in the lower dentitions. Table 3 gives a list of fossil localities and assemblages, which have produced fossil material of black wildebeest referred to in this study.

Table 3. A selected list of fossil localities and fossil assemblages with black wildebeest materials.

LAND MAMMAL AGE	Interior of southern Africa	Cape coastal zone
Recent	Deelpan Maselspoort Kareepan	
Florisian	Spitskop Mahemspan Sunnyside Pan Florisbad Spring Gladysvale	Elandsfontein (Bone Circle) Swartklip Sea Harvest Klasies River Elandsfontein (in part)
Cornelian	Cornelia-Mara Cornelia-Uitzoek	Duinefontein 2 Elandsfontein (in part)

For addressing the question of the origins of the genera *Connochaetes* and *Megalotragus*, all the available alcelaphine materials from Aïn Jourdel, Aïn Boucherit and Aïn Hanech were examined. These specimens were compared with the large collection of *M. priscus* from Mahemspan. This material included the type material *Oreonagor tournoueri*, “Gorgon” *mediterraneus*, *Numidocapra crassicornis* *Connochaetes taurinus progna* and material referred to these taxa. For comparison with East African material, published accounts were used, including Gentry & Gentry (1978) and Harris (1991).

Caprinae

Modern material

The comparative specimens of *O. moschatus*, *B. taxicolor*, *A. lervia*, *C. ibex ibex*, *C. hircus* and *O. aries* examined are from collections of the Institut für Palaeoanatomie, University of Munich, Munich, Natural History Museum, London and the Florisbad Quaternary Research Department, National Museum, Bloemfontein (Brink 1999; Appendix C).

Fossil material

The new caprine species occurs in the Nooitgedacht no. 1 and Nooitgedacht no. 3 carnivore lairs, in Boomplaas Cave, Rachelsrivier Cave in the Baviaanskloof and Colwinton in the north-eastern Cape foothills of the Drakensberg (Deacon *et al.* 1984; Brink 1984; Brink 1999; Appendix C). New material of this species has been identified from the Middle Pleistocene sequence of Gladysvale Cave (Lacruz *et al.* 2002), but is not included in the descriptions.

Makapania broomi from the Limeworks deposits, Makapansgat, is the only southern African fossil caprine available for comparison with the new species (Gentry 1970a). ‘*Bos*’ *makapaani* from Buffalo Cave, Makapan Valley, is too poorly known to be of use in the osteological comparisons (Gentry 1996).

FOSSIL LOCALITIES FROM THE INTERIOR OF SOUTHERN AFRICA

Introduction

Fossil localities from the interior (Table 3) and their fossil contents are briefly described and discussed in this section. The order is of increasing geological age from youngest to oldest. Black wildebeest materials from these assemblages are used for the analysis and discussion in Chapter 9. With the exception of Florisbad and Cornelia-Uitzoek, these localities are largely unpublished, as they were investigated in the fieldwork phase of this study. Florisbad and Cornelia-Uitzoek are part of the continuing research programme of the Florisbad Quaternary Research Dept. of the National Museum and are more extensively published (see below). The materials from Deelpan, Kareepan, and Sunnyside Pan represent carnivore accumulated bone assemblages, while Mahemspan is likely to represent natural deaths or carnivore kills. In the early 1940's Van Hoepen excavated Mahemspan. This locality was re-investigated on a limited scale as part of this study. The Maselspoort and Spitskop materials are from colluvial and fluvial contexts. The Florisbad fossil site is associated with a dolerite-controlled spring and much of its fossil-bearing deposits are either caused by spring activity or by the reworking of external material by spring action. The spring fossil assemblage represents carnivore kills and scavenging around the ancient spring (Brink 1987, 1988). The Cornelia-Uitzoek material is a mix of carnivore-accumulated materials from intrusive burrows into valley fill sediments and material derived from old land surfaces (Brink in press). Figure 5 shows the position of the fossil localities in the interior of southern Africa.

Deelpan

Introduction

Deelpan is situated about 30 km west of Bloemfontein on the farm Meriba. The site consists of a pan, lunette and springs (29° 11' S; 25° 45' E; Figure 6). The long axis of the pan is aligned north-northeast, the lunette is situated on its southeastern margin and the springs are on the southern edge of the pan. The spring deposits have produced a late Holocene palinological record (Scott & Klein 1981; Scott & Brink 1992). Butzer (1984) described the lunette sediments.

L. Scott collected vertebrate remains from a west-facing section in the lunette from a fossil locality, Deelpan A, which was described by Scott and Klein (1981) as a brown hyaena burrow. In 1987 further samples were collected and a report was published on all the materials from the site (Scott & Brink 1992). In 1993 the fossil occurrence, Deelpan D, was discovered a few meters to the south of Deelpan A and was excavated in its entirety. The material from Deelpan D is unpublished, but a combined faunal list of both the A and D occurrences is given in Table 4. A considerable portion of the original Deelpan A burrow has not been excavated. Deelpan B and C are palaeo-botanical localities.

Table 4. Taxonomic list of fossil mammals from the Deelpan A and D brown hyaena burrows according to the number of identified specimens (NISP).

	NISP
Rodentia	
<i>Pedetes capensis</i>	2
Carnivora	
<i>Lycaon pictus.</i>	9
<i>Canis mesomelas</i>	46
<i>Aonyx capensis</i>	2
<i>Calogale pulverulenta</i>	3
Perissodactyla	
<i>Equus quagga burchellii</i>	5
Artiodactyla	
<i>Damaliscus pygargus</i>	22
<i>Connochaetes gnou</i>	75
<i>Antidorcas marsupialis</i>	137

Fossil context and radiocarbon age

Both Deelpan A and D are fossil brown hyaena lairs. Material submitted for radiocarbon analysis produced very recent dates for both accumulations. Deelpan A has a date of 150 ± 20 BP (Pta-6346), while Deelpan D is dated to 120 ± 45 BP (Pta- 6348). These age estimates indicate that the sites are penecontemporaneous.

Summary

Deelpan A and D can be treated as single sample. The radiocarbon ages from both localities show that the vertebrate material represents a time immediately prior to or coeval with the initiation of the early- to mid-19th century disruption of the interior, with the beginning of large-scale agriculture and the extermination of large game. This is the significance of these two fossil samples. Apart from the records of early travellers in central southern Africa, fossil material, such as from Deelpan A and D, is the only direct evidence that can provide some understanding of the ecology of the central interior before its disruption by modern intensive farming. Even though large mammal communities of the central interior were affected by the activities of Iron Age and pastoralist peoples, there is no evidence of domesticated animals in the Deelpan assemblage. In this respect the Deelpan vertebrate remains reflect a relatively undisturbed ecosystem.

Maselspoort

Introduction

In the spring of 1991 a schoolboy Francois Henning, discovered sub-fossil bones eroding out of the bank of the Modder River about 500 m below the dam wall of the Maselspoort resort ($29^{\circ} 01' 50''$ S; $26^{\circ} 24' 50''$ E; Figure 7). This was reported to the National Museum and further investigation revealed *in situ* black wildebeest limb bones in overbank deposits. Heavy rains and flooding prompted a rescue excavation, which revealed a large number of wildebeest limb elements, mostly in articulated positions, together with the articulated upper portion of a human skeleton, including the skull and mandible.

Fossil context and radiocarbon age

The first objective was to recover the specimens visible in the vertical face of the riverbank on the assumption that the occurrence was a remnant that had escaped erosion. This proved not to have been the case, as fossil specimens, including the partial human skeleton, extended into the deposit. An area of approximately 3 X 2 m² was cleared to create a horizontal platform for a controlled excavation (Figure 8). The deposit was systematically excavated and all specimens were plotted in three dimensions.

The excavation yielded a series of articulated black wildebeest limbs and the upper portion of a human skeleton. As the elements of the human and animal remains were still articulated it is assumed that at the time of deposition soft tissue, such as tendons, were still present. These materials were deposited on the west bank of the Modder River on a sub-horizontal bedding plane in overbank deposits under conditions of low depositional energy. The uniform nature of the occurrence and the articulated condition of the skeletal elements suggest that deposition was a single event. Post-mortem damage to specimens, including the human remains, indicates minor carnivore interference, which probably occurred before transportation by water. The fossil sample from Maselspoort yielded a very restricted taxonomic list (Table 5).

Table 5. Taxonomic list of fossil mammals from Maselspoort according to the number of identified specimens (NISP).

	NISP
Primates	
<i>Homo sapiens</i>	7
Carnivora	
<i>Felis sp.</i>	1
Artiodactyla	
<i>Connochaetes gnou</i>	74

The cause of death of the various components cannot be established with certainty on the available evidence. The remains were transported by water, probably under flood conditions and one may assume that the components may have had very similar post-mortem histories. One possible interpretation is that the bone remains were eroded out from hyaena burrows on the banks of the river. An alternative hypothesis is that these fossils accumulated as a result of animals drowning and being transported by a flood. Slackwater situations during floods in rivers can account for this kind of deposition (*vide* Zawada 2000). Burial appears to have been rapid, and probably happened soon after deposition. The radiocarbon age of a bone sample is 3770 ± 50 BP (Pta 5879).

Summary

The Maselspoort fossil occurrence provides a valuable sample of black wildebeest limb elements. This population of black wildebeest long predates the historic bottlenecks in the black wildebeest gene pool in historic times and complements the sample from Kareepan in being mid-Holocene in age.

Kareepan

Introduction

In 1995 fossil material was discovered on the farm Kareepan, near Bloemhof, North West Province ($27^{\circ} 30' 30''$ S; $25^{\circ} 36' 30''$ E; Figure 9), in the process of mining for alluvial diamonds in the gravels of the Vaal River. The miner and owner of the farm, Mr. Cobus Roos, informed the National Museum of this discovery. During a two-week field season at the end of 1995 members of the Florisbad Quaternary Research Department, National Museum, excavated a sample of fossil material from a series of fossil hyaena burrows. Following this, in continuing their work the miners collected further fossil material from the same context as the mechanical excavators removed the overburden. In this way the fossil assemblage from Kareepan was considerably enlarged and it provides an excellent study sample of mostly plains-living ungulates, including black wildebeest, and small carnivores (Table 6).

Table 6. Taxonomic list of fossil mammals from Kareepan according to the number of identified specimens (NISP).

	NISP
Tubulidentata	
<i>Orycteropus afer</i>	2
Lagomorpha	
<i>Lepus</i> sp.	1
Rodentia	
<i>Hystrix africae-australis</i>	8
Carnivora	
<i>Vulpes chama</i>	95
<i>Canis mesomelas</i>	41
<i>Lycaon pictus</i>	2
<i>Crocuta crocuta</i>	1
<i>Parahyaena brunnea</i>	28
<i>Proteles cristatus</i>	15
<i>Felis lybica</i>	1
<i>F. caracal</i>	1
Perissodactyla	
<i>Equus</i> sp. cf. <i>E. quagga</i>	65
Artiodactyla	
<i>Phacochoerus africanus/aethiopicus</i>	58
<i>Taurotragus oryx</i>	19
<i>Damaliscus pygargus</i>	195
<i>Alcelaphus buselaphus</i>	110
<i>Connochaetes gnou</i>	611
<i>A. marsupialis</i>	475
<i>Raphicerus campestris</i>	3

Fossil context and radiocarbon age

The fossil vertebrates occur in pockets of sandy loam soil, which is capped by a thick layer of calcrete that is variably consolidated. The method of excavation was to remove the calcrete capping by a mechanical excavator in order to expose the pockets of unconsolidated fossiliferous sediment. The pockets of fossil-bearing sediment were then excavated in the conventional way. Although the larger part of the fossil assemblage from Kareepan was recovered during subsequent mining, the smaller excavated sample serves as a taphonomic control.

A detailed taphonomic analysis of this sample has not been undertaken, but observations point to the assemblage being predominantly the result of brown hyaena denning activities. As in other cases where hyaenas have accumulated bone material in their dens, there is evidence for multiple primary sampling agents. It appears that porcupines and possibly spotted hyaenas may have contributed to the assemblage.

A radiocarbon assay of a bone sample gave a date of 2770 ± 40 BP (Pta-7070). This makes the material broadly contemporaneous, but somewhat younger than, the sample from Maselspoort and important for the same reasons.

Summary

The location of the Kareepan is on the western edge of the open grassland area and close by there is an island of Kalahari Plains Thorn Bushveld immediately east of the Vaal River (Low & Rebelo 1996), which largely corresponds with the Sandveld Nature Reserve. In spite of the proximity of a Kalahari-type habitat in the present there is almost no indication of this in the faunal composition of the Kareepan fossil assemblage. The mid-Holocene palaeo-environment was evidently open, semi-arid grassland and comparable to what would have been found in the western Free State before disruption by farming.

Spitskop

Introduction

A series of dongas on the farm Spitskop 789, adjacent to a hill known as Spitskop (28° 26' 50" S; 27° 47' 50" E), have produced a rich vertebrate fauna of Florisian character (Appendix A). Father Michael Klein of the Roman Catholic Mission in Senekal discovered this locality in the late 1980s. Father Klein and the author collected at Spitskop from 1989 until 1996. In spite of attempts to manage the erosion, the unconsolidated sediments of low clay content are eroding rapidly (Figure 10). There are three discrete fossil occurrences, named Spitskop A, B and C. Spitskop B is a Holocene hyaena burrow and has produced a remarkably complete black wildebeest skull, while Spitskop C appears to be taphonomically similar, but older than the Holocene, because of the presence of the giant buffalo, *H. antiquus*. Only the fossil sample from Spitskop A is considered here (Table 7). Due to the rapid rate of erosion the Spitskop dongas have become less productive latterly, and the site may be exhausted.

Table 7. Taxonomic list of fossil mammals from Spitskop according to the number of identified specimens (NISP). Extinct species are indicated with an asterisk.

	NISP
Perissodactyla	
* <i>Equus capensis</i>	21
<i>Equus</i> sp. cf. <i>E. quagga</i>	1
Artiodactyla	
<i>Phacochoerus africanus/aethiopicus</i>	15
<i>Taurotragus oryx</i>	4
* <i>Homoioceras antiquus</i>	1
<i>Hippotragus</i> sp.	2
* <i>Damaliscus niro</i>	10
<i>D. pygargus</i>	4
<i>Alcelaphus buselaphus</i>	2
<i>Connochaetes taurinus</i>	19
<i>Connochaetes gnou</i>	25

* <i>Megalotragus priscus</i>	11
* <i>Antidorcas bondi</i>	2
<i>A. marsupialis</i>	1

Fossil context and ESR age

Although most of the material was collected out of context, occasional pieces were recovered *in situ*. From the positions of these specimens it appears that the fossils may have derived from the same sedimentary horizon as Later Stone Age artefacts, which also occur in these dongas. The sedimentary matrix is a reddish brown silty sand and the fossil specimens are often calcretised. Calcrete infillings and adhesions have damaged the outer surface of many specimens. The assemblage is highly fragmented, more so than would be expected in carnivore accumulations. It is possible that this assemblage was the primarily the product of human subsistence activities.

Stone artefacts were not collected systematically. Field observations show them to be made on crypto-crystalline rocks in the main and to be typologically Later Stone Age, younger than *c.* 22 000 (Deacon & Deacon 1999).

ESR samples were collected and analysed by R. Grün and readings for the background radiation of the sediment were made where fossil specimens were found *in situ*. An ESR date of 15 000 BP was provided by R. Grün (pers. com.). This date corresponds to the end of the Last Glacial, a time when world temperatures were starting to recover to Holocene levels, and accords with the presence of Later Stone Age artefacts. The bone material contains insufficient collagen for radiocarbon assay (A. Fuls pers. comm.).

Summary

Although the faunal sample from Spitskop has a Florisian character, it lacks the lechwe, *K. leche*, and has only a few specimens of Bond's springbok, *A. bondi* (Table 7). The fact that these taxa are consistently under-represented in Last Glacial deposits from the interior, such as Sunnyside Pan, Mahemspan (see below) and the overbank deposits of Erfkroon (Churchill *et al.* 2000), suggests that this may be due to the relatively young age of the deposits and the

effects of aridification during and after the Last Glacial in the interior of southern Africa. However, *A. bondi* is present in the Last Glacial deposits of Rose Cottage Cave (Plug & Engela 1992), which lies towards the east and along a gradient of increasing rainfall.

Mahemspan

Introduction

In the late 1930s and early 1940s Van Hoepen and Hoffman excavated a large faunal sample from the lunette of Mahemspan (27° 45' 50" S; 26° 08' 50" E), situated between Hoopstad and Wesselsbron, Free State Province (Unpublished reports in library of the National Museum). In 1994 the site was revisited and the approximate position of the excavation was relocated through the help of Mrs. De Villiers, the owner of the farm. She was present when Van Hoepen conducted his excavation (Figure 11). Fossil material in the same state of preservation as in the collections at Florisbad was found on the surface. Unfortunately a trial pit did not reveal *in situ* material.

Fossil context

The *in situ* fossil material collected by Van Hoepen and Hoffman is positioned at the base of the modern lunette and the original death assemblage appears to have been deposited in a marsh-like area. This can be deduced from the extensive presence of calcium carbonate deposits in and on the fossils. The fossil matrix, which is still attached to many specimens in the old collection at Florisbad, is a pale-brown, partly calcretised sand. The site is now covered by aeolian sand, as was the case before the material was exposed by wind action during the intense droughts of the 1930's (Unpublished reports in library of the National Museum), but is now part of a ploughed land (Figure 11).

The Mahemspan fossil material is unusually complete. The giant alcelaphine, *M. priscus*, is the predominant element in the collection and is represented by virtually all skeletal elements. The Mahemspan collection of *M. priscus* represents probably the largest and most complete sample of this species in southern Africa (Table 8; *vide* Chapter 6). The completeness of the material and the predominance of large-bodied taxa raise the question of selective recovery of the material. However, from the care that was taken in the preparation of the fossils before excavation and the meticulous accessioning of the material it is evident that the excavators

took considerable trouble to recover the material as completely as possible. It is, therefore, unlikely that the taxonomic pattern and skeletal part representation are due to selective recovery. The presence of suncracks and porcupine gnawing on specimens, the absence of hyaena coprolites and the paucity of carnivores in the fossil assemblage argue against the likelihood that it represents the contents of ancient hyaena burrows. This and the fact the bones were originally deposited in marshy conditions, may point to the possibility that the Mahemspan assemblage represents natural deaths or carnivore kills on the edge of a pan. This is analogous to the Florisbad Spring assemblage, which is considered to represent the remains of carnivore hunting and scavenging around the ancient springs (Brink 1987, 1988; see below).

Table 8. Taxonomic list of fossil mammals from Mahemspan according to the number of identified specimens (NISP). Extinct species are indicated with an asterisk.

	NISP
Rodentia	
<i>Hystrix africae-australis</i>	1
Carnivora	
<i>Crocuta crocuta</i>	7
<i>Panthera leo</i>	1
Perissodactyla	
* <i>Equus capensis</i>	80
<i>Equus</i> sp. cf. <i>E. quagga</i> subsp.	48
Artiodactyla	
<i>Hippopotamus amphibius</i>	4
<i>Phacochoerus africanus/ aethiopicus.</i>	17
<i>Taurotragus oryx</i>	21
* <i>Homoioceras antiquus</i>	28
<i>Kobus leche</i>	21
<i>Hippotragus</i> sp.	2
* <i>Damaliscus niro</i>	11
<i>D. pygargus</i>	19
<i>Alcelaphus buselaphus</i>	10
<i>Connochaetes taurinus</i>	9
<i>C. gnou</i>	24
* <i>Megalotragus priscus</i>	241
* <i>Antidorcas bondi</i>	1
<i>A. marsupialis marsupialis</i>	6

Geological age

Although the assemblage has not been fully published, various authors made use of the material and formed opinions on its geological age (*vide* Cooke 1974; Gentry and Gentry 1978). Van Hoepen (1947) and Hoffman (1953) used cranial elements from this assemblage for taxonomic descriptions. Cooke (1974) considers Mahemspan material to be Florisian in age, but somewhat older than the Florisbad spring material. However, based on the shape of the black wildebeest horn cores Gentry & Gentry (1978) suggested an age younger than the Florisbad spring material. Recently, dental specimens and attached matrix were submitted for ESR analysis and the results for an early uranium uptake model are around 12 000 years BP and for a linear uranium uptake model are around 13 – 17 000 years BP (Table 8). These dates support the suggestion of Gentry & Gentry (1978) that the Mahemspan assemblage postdates that of the Florisbad Spring. It is noteworthy that the aquatic indicators, such as *H. amphibius*, *K. leche* and *A. bondi*, are underrepresented compared to the Florisbad spring assemblages (Brink 1987). This taxonomic pattern is also seen in the Spitskop A assemblage and it probably reflects the intense aridification of the interior in this time.

Summary

The Mahemspan assemblage is useful for the purposes of this study in providing a fossil sample of a mix of black wildebeest and blue wildebeest that is probably younger than Florisbad. However, it is particularly significant in including by far the largest and most complete set of *M. priscus* cranial and postcranial elements known from southern Africa. The Mahemspan *M. priscus* sample is used as if it were a modern sample for establishing the morphological background to evaluate black wildebeest evolution. The morphological description of the cranial and postcranial elements of *M. priscus* given in Chapter 7 refutes the contention that the animal was hartebeest-like (Hoffman 1953; Klein 1994).

Sunnyside Pan

Introduction

In 1987 J.C. Loock of the Dept of Geology, University of the Free State, discovered a cluster of fossil bones eroding out of base of the lunette of Sunnyside Pan (28° 39' S; 26° 09' 30" E; Figure 7)Figure 12), which is situated some distance north of Florisbad. Loock and the author excavated these specimens.

Fossil context and ESR age

This fossil assemblage came from an eroded Pleistocene hyaena burrow. From the reconstructed position of the original burrow in relation to the palaeo-landsurface and from damage to the fossil specimens it seems that the assemblage was buried in stable soils for a considerable period of time. ESR samples were collected and the results are given in Table 9, which suggests an age equivalent to Marine Isotope Stage 3 (MIS 3) of the Last Glacial.

Table 9. ESR results from Spitskop A, the Erfkroon overbank deposits, Mahemspan and Sunnyside Pan, given in years before the present (BP) (R. Grün pers. comm.).

	Early uptake model	Linear uptake model
Spitskop A	15 000	- *
Erfkroon overbank	15 – 20 000	18 – 28 000
Mahemspan	12 000	13 – 17 000
Sunnyside Pan	20 – 25 000	35 – 50 000

* Due to the extent of uranium presence in the fossil teeth from Spitskop, only the early uranium uptake model is given.

Summary

The character of the fauna is Florisian (Table 10), but the predominance of *M. priscus*, as in the Mahemspan assemblage, is noteworthy. *H. amphibius*, *K. leche* and *A. bondi* are also absent from this assemblage, confirming the pattern seen at Spitskop A and Mahemspan. It is noteworthy that both species of wildebeest are represented, as in Spitskop and Mahemspan.

This confirms the periodic overlap of the two species in historic and prehistoric times (Plug & Engela 1992; Brink *et al.* 1999). The fact that both species of *Damaliscus* are present is not unusual, since it is known that *D. niro* becomes extinct in the interior only at the end of the Late Pleistocene (Klein 1984).

Table 10. Taxonomic list of fossil mammals from Sunnyside Pan according to the number of identified specimens (NISP). Extinct species are indicated with an asterisk.

	NISP
Carnivora	
<i>Crocuta crocuta</i>	1
Artiodactyla	
<i>Phacochoerus aethiopicus/africanus</i>	1
<i>Connochaetes taurinus</i>	2
<i>C. gnou</i>	9
* <i>Megalotragus priscus</i>	15
* <i>Damaliscus niro</i>	19
<i>D. pygargus</i>	4
<i>A. marsupialis</i>	8

Florisbad spring

Introduction

The Florisbad fossil site (32° 46' S; 26° 04' E) consists of a sequence of Quaternary deposits associated with a thermal spring situated 45 km NNW of Bloemfontein in central South Africa (Figure 13). The spring erupts at the contact of an igneous intrusion of dolerite and the Permian Karoo Ecca shale. Groundwater is forced to the surface because the intrusion acts as an impervious barrier to ground water (Loock & Grobler 1988). Through geological time sediments accumulated around the springs to produce fossil bearing deposits. The Florisbad Quaternary spring sedimentary sequence is one of the most extensively studied fossiliferous Quaternary deposits in the interior (Rubidge & Brink 1985; Butzer 1988; Grobler & Loock 1988; Loock & Grobler 1988; Visser & Joubert 1991).

Florisbad is primarily known for its mammalian fossil record (Dreyer & Lyle 1931; Cooke 1964; Brink 1987, 1988, 1993, 1994; Brink & Lee-Thorp 1992; Table 11), which includes an archaic human skull fragment (Dreyer 1935; Clarke 1985; Grün *et al.* 1996). Additionally the site has produced an important fossil pollen record (Van Zinderen Bakker 1957, 1989; Scott & Brink 1992; Scott & Nyakale 2002) and Middle Stone Age (MSA) archaeological material (Dreyer 1938; Kuman & Clarke 1986; Kuman 1989; Brink & Henderson 2001). Most recently fossil oribatid mites have been discovered in Holocene and MSA levels (Coetzee & Brink 2003).

In the present phase of research at Florisbad, the question of the geological age of Florisbad was addressed by the application of new dating techniques. The problem of dating fossil material older than the limit of radiocarbon dating has been a limiting factor in the study of the past in the interior of southern Africa. An ESR/OSL dating programme conducted at Florisbad has provided an indication of the age of the Florisbad deposits (Grün *et al.* 1996), which extend beyond the range of radiocarbon. In this section the Florisbad dating exercise is explained and the results are given in more detail than in the initial publication. This temporal framework developed for Florisbad and other sites provides the basis for the chronological ordering of the fossil material of black wildebeest and *M. priscus*.

Summary of excavations

During the late 1920s and in 1932 T.F. Dreyer conducted the first excavations at Florisbad (Dreyer & Lyle 1931; Dreyer 1935, 1938; Brink 1987). In 1952 A.C. Hoffman and J. D. Meiring followed this up by a short season of fieldwork (Hoffman 1955; Brink 1987). R.J. Clarke initiated the first systematic excavations at Florisbad in 1981, soon after the site was acquired by the National Museum for research purposes. Clarke found Middle Stone Age artefacts and bone remains in apparent association and exposed this occurrence in an 8 X 20 m² cutting. Excavation of the primary context MSA horizon continued from 1982 until April 1984 (Brink 1987; Kuman 1989). After the departure of Clarke and Kuman in February 1984, exploration of the spring mound resumed. From 1984 to 1987 the author excavated two test cuttings. These were positioned as close as possible to the present-day centre of spring activity with the aim of exploring the spring sediments. In the course of this work sediment samples from an auger drill programme were analysed (Rubidge & Brink 1985), and the old

collections of fossil materials were restudied (Brink 1987, 1988). The two test cuttings did not uncover spring sediments, but the second pit exposed the Middle Stone Age horizon approximately 30 m to the east of Clarke's exposure. Based on the discovery of the Middle Stone Age horizon in the second test pit and given its archaeological importance it was decided to extend the existing exposure of this occurrence in an easterly direction (Brink 1987; Brink & Henderson 2001; Henderson 2001).

In continuing the exploration of the spring mound and to establish a sedimentary profile to serve as a reference section for the site as a whole, a third test pit was started in 1987 and completed in 1993 (Figure 14). The third test pit was planned with new dating techniques, such as ESR and OSL, in mind. The main reason for the pit being some distance north of the present-day spring area was the greater depth of Quaternary deposits in that area.

The Florisbad spring mound

Although the Florisbad spring mound has a complex depositional history (Brink 1987; Butzer 1988; Grobler & Looek 1988; Rubidge & Brink 1985; Scott & Brink 1992; Visser & Joubert 1991), it is this complexity, which allows unusual insights into past environments and human behaviour. There are two contexts in which fossils occur at Florisbad. One represents naturally accumulated material from ancient spring vent structures, mainly the result of ancient carnivore activity around palaeo-waterholes. This material includes the human skull fragment. The other is represented by debris of human activity, such as the Middle Stone Age horizon (*vide* Brink 1987; Kuman 1989; Brink & Henderson 2001). These remains of human habitation activities are found in horizontal deposits and are more or less undisturbed by post-depositional spring action (Figure 15).

Most of the horizontal deposits, excluding the upper aeolian deposits, appear to have formed subaqueously or were postdepositionally modified under saturated conditions. It appears that the saltpan to the northwest of Florisbad was a fluctuating perennial lake in pre-Holocene times, when pans of the central interior formed locally interconnecting perennial lakes. This is evident from the Florisbad sediments, the fossil vertebrates and regional geology (Brink 1987, 1988; Grobler & Looek 1988; Visser & Joubert 1991; Scott & Brink 1992). The western and central panveld of the interior would have been analogous to the internal drainage basin of the modern Okavango area in Botswana (Figure 16). Thus, contributing factors to the

deposition of the spring mound are subaqueous deposition of water-borne sediment, aeolian deposition during periods of intensified aridification during the Late Pleistocene and the Holocene, and autochthonous spring production and reworking.

Another point of interest is that the Florisbad Quaternary deposits appear to consist of two adjacent spring mounds. When the sections from the augur drill programme are projected as a north-south section through the mound (*vide* Rubidge & Brink 1985; Brink 1987; Figure 17), it appears that the present position of the spring is in a smaller, southern mound. However, this applies only to the upper sedimentary levels at Florisbad, since the basal horizons seem to continue without interruption (Coetzee & Brink 2003). The larger of the two mounds is separated from this smaller, southern mound by a slight depression in the landscape, which had been artificially filled in recent years. The apparent existence of two adjacent spring mounds supports the suggestion that migration of the spring eyes occurred in the past (Brink 1987).

The fossil fauna

The Florisbad spring fauna, also termed the “Old Collection” (Brink 1987), is the type assemblage of the Florisian Land Mammal Age (LMA). It is characterised by six extinct species, *Equus capensis*, *E. lylei*, *Homoiceras antiquus*, *Megalotragus priscus*, *Damaliscus niro* and *Antidorcas bondi* (Brink 1987, 1994; Table 11). The Florisian large mammal fauna reflects two palaeo-ecological components. *Hippopotamus amphibius*, *Kobus leche*, a form of waterbuck, possibly *K. ellipsiprymnus* and Hippotragini represent an aquatic component. This component indicates the existence of fluctuating, but perennial lakes, of which the modern-day pans are remnants. The water-rich habitat of open grasslands, interspersed with numerous lakes, would have been highly productive. The diverse range of extinct grazing ungulates, which co-existed with extant grazers in a facilitating grazing system, is reminiscent of the Serengeti today (Table 11; Brink 1987; Brink & Lee-Thorp 1992). The Florisian LMA can be defined not only on the basis of a range of extinct grazing ungulates, but also on the presence of taxa indicating a highly productive palaeo-ecosystem that accommodated specialised aquatic grazers, such as *K. leche* and Hippotragini, which today are extinct in the central interior of southern Africa.

Table 11. Taxonomic list of fossil mammals from the Florisbad spring according to the number of identified specimens (NISP), modified after Brink (1987). Extinct species are indicated with an asterisk.

	NISP
Primates	
<i>Homo helmei</i> (archaic)	1
Lagomorpha	
<i>Lepus</i> sp.	6
Rodentia	
<i>Pedetes</i> sp. cf. <i>P. capensis</i>	8
Carnivora	
<i>Aonyx capensis</i>	3
<i>Galerella sanguinea</i>	1
<i>Atilax paludinosus</i>	3
<i>Canis mesomelas</i>	6
<i>Lycaon pictus</i>	3
<i>Crocuta crocuta</i>	7
<i>Panthera leo</i>	1
Perissodactyla	
* <i>Equus capensis</i>	73
* <i>Equus</i> sp. cf. <i>E. lylei</i> .	61
<i>Equus</i> sp. cf. <i>E. quagga</i> subsp.	97
<i>Ceratotherium simum</i>	3
Artiodactyla	
<i>Hippopotamus amphibious</i>	333
<i>Phacochoerus africanus/ aethiopicus</i> .	33
<i>Taurotragus oryx</i>	24
* <i>Homoiceras antiquus</i>	25
<i>Kobus leche</i>	60
<i>Kobus</i> sp.	4
<i>Hippotragus</i> sp.	16
* <i>Damaliscus niro</i>	111
<i>D. pygargus</i>	9
<i>Alcelaphus buselaphus</i>	8
<i>Connochaetes gnou</i>	284
* <i>Megalotragus priscus</i>	30
* <i>Antidorcas bondi</i>	889
<i>A. marsupialis marsupialis</i>	107
<i>Raphicerus campestris</i>	4

The application of the ESR and OSL dating techniques

Introduction

Besides the limitations of the conventional radiocarbon method, the dating of the Florisbad fossil materials was complicated by the initial uncertainty of their sedimentary context and taphonomy. This was compounded by the coarse excavations methods, which were employed before the 1980s. These problems have been solved by the systematic restudy of old fossil collections and by the insight gained from new excavations (Brink 1987, 1988; Kuman 1989). These showed that the old fossil collections, including the human skull, derive from vertically intrusive spring bodies into the sub-horizontal deposits (Figure 15). The spring acted as a sampling agent over time by accumulating the natural scatter of objects around the ancient eyes, which were focal points of human and animal activity. Because the spring eye migrates over time, renewed events of spring activity would repeatedly rework fossil material, but would also continue to accumulate new material from contemporary land surfaces. In this way the Florisbad springs accumulated fossil material of varying geological ages (*vide* Brink 1987, 1988), while on the undisturbed land surfaces slightly removed from the area of spring activity, archaeological materials could accumulate mostly unaffected by spring action. The revised interpretation of the Florisbad fossil deposits prepared the way for the application of new dating methods.

The third test pit sequence

Figure 18 gives a composite west-facing view of the sedimentary profile of the southern part of the Florisbad spring mound. Section A is the remaining profile of the western part of the spring area, which had been destroyed almost entirely by previous excavations and swimming pool construction. Section B is the sedimentary profile of the third test pit and the insert (section C) is an enlarged profile of the upper portion of the spring section, which Dreyer termed “Peat III” and “Peat IV” (Dreyer 1938). Section A illustrates the vertically intrusive nature of spring sand bodies, which is the sedimentary context of the old collection (*vide* Brink 1987; Visser & Joubert 1991). The dental specimens of hippopotamus and of *C. gnou*, which were used for dating the spring fossil occurrence (see below), were recovered from such vertically intrusive spring sand bodies over a large area in the vicinity of the present-day spring area (Dreyer 1938; Brink 1987, 1988). Scott and Nyakale (2002) sampled the upper part of the spring section, which is the enlarged insert in Figure 18, in order to study the

Holocene fossil pollen content of the sediments. The radiocarbon dates from the organic component in these sediments range from early to late Holocene. This package of sediment is roughly equivalent to the chronological hiatus, which separates the two upper aeolian sand units, as indicated in the section of the third test pit (Figure 18).

The uppermost unit of the sedimentary profile from the third test pit (Figure 18) consists of a late Holocene brown aeolian sand unit, which contains LSA artefacts, pottery and some vertebrate remains. Below this was another aeolian sand unit, which is lighter in colour due to the leaching out of carbonates. It contains a terminal Pleistocene/early Holocene LSA assemblage, commonly referred to as a Lockshoek industry (Sampson 1974). Leaching has destroyed the bone material in this horizon and only occasional fragments of tooth enamel were recovered.

Underlying the package of aeolian deposits is a dense yellow-green sandy-clay unit with very few and poorly preserved fossil inclusions. Decayed clasts of hornfels are the remains of stone artefacts. Below this is a unit of light grey quartz sand with organic lenses. Middle Stone Age artefacts and bone remains occur at the base of this sand unit, which overlies an old land surface or palaeosol (Coetzee & Brink 2003). This palaeosol represents the top of a sandy organic clay unit, which previously was referred to as “Peat II” (Dreyer 1938; Visser & Joubert 1991; Scott & Brink 1992). This unit approaches a metre in thickness, and overlies a grey sand, which contains occasional Middle Stone Age artefacts and bone fragments. Below this unit is a black clay unit, which can be correlated with Dreyer’s “Peat I”. The basal horizon of the Quaternary sequence in the third test pit is a green sandy clay, formed from decomposed shale. The bedrock is Ecca shale (Karoo Supergroup).

Sampling for ESR/OSL analysis

In 1992 an ESR/OSL dating project was initiated in collaboration with R. Grün of the Australian National University, Canberra. Sampling was carried out in 1993, 1994 and 1995.

- From the third test pit 17 dental samples were taken for ESR analysis, five sediment samples for OSL and two bone samples from the upper aeolian sands for radiocarbon dating. In order to establish the gamma dose rate for Florisbad, readings were taken with a

portable gamma detector at all the points in the sedimentary sequence of the third test pit where tooth samples were taken for ESR analysis. Additional sediment samples from the third test pit were collected in light tight containers.

- One additional sediment sample was taken from the MSA horizon, which were later measured for OSL.
- From the old collections 18 hippopotamus dental specimens and six black wildebeest dental specimens were analysed for ESR. - These specimens derive from spring contexts and the ESR age determinations on these specimens are in particular relevant to this study, as explained below.

Results

All teeth measured for ESR, those found *in situ* and those from the old spring collections, contained very little uranium. This is surprising as the site is generally very wet. The low uranium concentrations in the teeth minimised the differences in the results interpreted by the early uranium uptake and linear uranium uptake models. For this reason only the closed system early uranium uptake ESR ages have been considered (Table 12; R. Grün pers. com. – For details on the ESR dating technique *vide* Grün 1997).

Table 12. ESR age estimates from the third test pit at Florisbad: the results of the early uranium uptake model and the linear uranium uptake model are given as averages (R. Grün pers. comm.) .

Positions of samples above bedrock (m)	Number of samples	Early U-uptake (x 1000 years)	Linear U-uptake (x 1000 years)
7.15	1	2.1 ± 0.8	2.1 ± 0.8
6.45	2	13.7 ± 1.3	14.7 ± 1.2
3.65	8	176 ± 23	207 ± 33
3.25	5	184 ± 24	211 ± 29

2.95	2	159 ± 7	188 ± 9
2.05	2	254 ± 1.4	292 ± 18
1.45	4	187 ± 41	196 ± 37
1.2	1	124 ± 9	136 ± 10
0.65	2	154 ± 18	161 ± 18
0.25	6	200 ± 22	204 ± 20

From a plot of the ESR results from the third test pit (Table 12; Figure 19), it appears that in the lower two-thirds of the deposit there is hardly any trend for dates to become progressively older. This is ascribed to the dependence of ESR dating results on the external dose rate and the uncertainty regarding the effects of water saturation on the lower deposits. The ESR age estimates range between about 130 000 and 250 000 years ago. However, a notable feature is the tight cluster of ESR results for the MSA horizon ($120\,000 \pm 5000$ years BP), suggesting a Last Interglacial age, the equivalent of the Marine Oxygen Isotope Stage 5e. There is a greater degree of uncertainty in the OSL results from the MSA horizon ($135\,000 \pm 31\,000$ years BP), as they appear marginally older and cluster less tightly. They broadly support the Last Interglacial age estimate, suggested by the ESR results. The OSL dating method technique is still under development. In the future there will be the opportunity to test these results further using the single grain luminescence technique.

On the basis of the taphonomy and general sedimentary context of the archaeological materials from the MSA horizon, which suggest a short-lived occupation event (Brink 1987; Kuman 1989; Brink & Henderson 2001; Henderson 2001), a limited age range for the MSA horizon was predicted. The ESR age estimates for this horizon, which cluster around 125 000 years ago, and to a lesser degree the OSL age estimates, are in agreement with this prediction.

The ESR age estimate of the MSA horizon allows for interpretation of the remaining ESR estimates of the third test pit. If one assumes that a relatively steady sedimentation rates applied through time and, given that the MSA horizon is roughly in the middle of the sedimentary column, then the age estimate for the base of the third test pit of around 250 000 years ago or somewhat older would be plausible. Since it is unlikely that sedimentation was continuous it is more likely that the basal ESR dates from the third test are underestimations

of the real age of these deposits. Therefore, one may argue for an age approaching 300 000 years BP for the base of this section.

The taphonomy of the spring fossils predicts that they accumulated at different times when the spring was active and that some temporal spread in the ESR age estimates had to be expected (Brink 1987). However, the extremely wide range in ESR age estimates on dental samples from the spring, which can be grouped in age clusters ranging between c. 100 000 and 400 000 years BP, was initially cause for concern.

When the dating project was planned it was hoped that the spring material would provide a sufficiently restricted temporal range to provide a proxy age estimate for the human skull. When the first set of dental samples from the spring, consisting of 18 hippopotamus teeth, produced the wide scatter in age estimates (Figure 20), it was speculated that the local aquatic niche of the hippopotamus may have been the cause of this dispersed temporal pattern. Because hippos are dependant on the presence of water and since they inhabit lakes, it was thought that perhaps they would have occupied the vicinity of the spring even when submerged by the water of the palaeo-lake represented by the present-day Soutpan. In such a case hippos would have had access to the spring area even when terrestrial animals would not have had. Therefore it was thought that hippo remains might show a wider temporal span than the remains of terrestrial animals. Consequently, six teeth of black wildebeest, occupying a very different terrestrial niche, were selected for analysis from intact mandibles. However, the ESR results on the black wildebeest teeth supported the temporal pattern of the hippopotamus sample (Figure 20).

These results were disappointing from the point of view of dating the Florisbad hominid, since they did not provide a restricted age estimate, which would have dated the human skull by proxy. Although this was not entirely unexpected in the light of the taphonomy of the Florisbad Spring fossils, which predicted some temporal spread in geological age of the spring fossils, the extent of the temporal span of the ESR results was unexpected. However, given the fact the ESR age estimates essentially accorded with the taphonomy of the Florisbad spring assemblage, these results give some confidence in the reliability of the technique, as also suggested by the results of the third test pit.

The problem of dating the Florisbad hominid skull was solved by means of a non-destructive technique of ESR measurement on a sample of tooth enamel from the third molar associated with the human skull (Dreyer 1935; unpublished). This provided an age of *c.* 260 000 BP. Although this non-destructive technique was pioneered for the purpose of dating the Florisbad human third molar, it is now commonly applied to Pleistocene human dental material (Grün *et al.* 1996; R. Grün pers. com.).

Discussion

The primary significance of the ESR/OSL dating exercise for this study is the temporal framework that is provided by the results from the spring. The fact that the ESR results of the black wildebeest fossil sample from the Florisbad support the temporal pattern derived from the hippopotamus specimens give confidence in the ESR age estimates. The ESR dating of the Florisbad Spring material to between *c.* 100 000 and 400 000 years BP is the basis for the discussion of the evolution of the black wildebeest in Chapter 9.

In addition the ESR results from the Florisbad Spring provided a new appreciation of the time depth of the Florisian LMA. Since the Florisian LMA is defined on the basis of the Florisbad spring assemblage (Ewer & Cooke 1964; Wells 1969; Hendey 1974b; Brink 1987), the ESR results from the spring assemblage need to be taken into account in this definition (*vide* Chapter 6).

The advanced pre-modern morphology of the Florisbad specimen and the age estimate of some 260 000 years ago have encouraged a re-instatement of the original name of the specimen, *Homo helmei* Dreyer, to refer generally to a pre-modern stage in African human evolution (Foley & Lahr 1997). The dating of Florisbad has also contributed to re-opening the debate on the position of this specimen in the evolution of modern humans in Africa. For example McBrearty & Brooks (2000) are of the opinion that archaic human populations represented by *H. helmei* may be the direct ancestors of the first modern *H. sapiens* in sub-Saharan Africa.

Cornelia-Uitzoek

Introduction

The Cornelia-Uitzoek fossil site (27° 10' S; 28° 52' 30'") is the type locality of the Cornelian Land Mammal Age. It is known primarily for its rich vertebrate fauna, but also for the occurrence of Acheulian artefacts (Cooke 1974; Clark 1974). The site was discovered in the 1920's and became known through the fieldwork of E.C.N. van Hoepen and his pioneering work on the fossil bovids, equids and suids (Van Hoepen, 1930, 1932a, 1932b, 1947). In 1953 A.C. Hoffman and A.W. Crompton conducted excavations there, while in 1960 R.J. Mason made a collection of stone artefacts (Clark 1974). In 1974 a summary volume was published on the sedimentology, archaeology and palaeontology of this site (Butzer 1974; Clark 1974; Cooke 1974). Almost no fossil collecting was done at the site after the publication of this volume and it was commonly assumed that the site had ceased to be productive. In 1989 the author visited the site at the invitation of G. Botha, Council for Geoscience, Pietermaritzburg, and found it to be a rich source of fossil material. Since then regular visits have been made in order to collect material eroding out of the deposits (Bender & Brink 1992). In 1998 a systematic excavation was started and continued in 2000, in 2001 and in 2002 (Brink & Rossouw 2000; Figure 21). During the field season of 2000 the first human material was found at Cornelia-Uitzoek, a first upper molar (Brink 2002). This find is noteworthy, as in the period of between a million years ago and the last 10 000 years human remains are rare in southern Africa. The work being carried further at Cornelia-Uitzoek follows on the programme initiated at Florisbad in the early 1980s and is an attempt to investigate older geological times.

The early work at the site predates the development of research interest in taphonomy and palaeontological site formation (Brain 1981, 1993; G. Avery 1988, Cruz-Uribe 1991, Fosse *et al.* 1998), and accordingly at the beginning of the 1990's very little was known of the context of the Cornelia-Uitzoek vertebrate fossils. The new excavations at Cornelia-Uitzoek were aimed at addressing questions, such as the taphonomy of the vertebrate fossils, their sedimentary context, the nature of their association with the Acheulian stone artefacts and the geological age of the occurrence. In addition, unresolved taxonomic issues demanded an increased sample of the fossil vertebrates from Cornelia-Uitzoek. Other lines of investigation include the application of dating methods, such as ESR and palaeomagnetism, the study of the

newly discovered human molar and studies of the fossil phytoliths and fossil pollens. For the purpose of this study Cornelia-Uitzoek is important, because it has produced the earliest ancestral black wildebeest.

New field work

The 1998 the author cut a test excavation, an area of four square metres, into the basal part of the sequence where abundant surface fossils were known to occur (Figure 21; Brink & Rossouw 2000). In the years 2000 - 2002 the cutting was extended to an area of 40 square metres (Brink in press). This cutting has produced a dense scatter of *in situ* fossil vertebrate remains. Standard techniques of excavation were applied and all finds were recorded *in situ* in three dimensions from an arbitrary base line and an arbitrary datum. Sieving of sediments did not produce any microvertebrates and only occasional fragments of bone specimens of larger taxa.

In addition, occasional specimens have been found eroding out of the sections at Cornelia-Uitzoek. These were mapped and collected and appear to derive from old land surfaces. The fossils occur at the bases of upward fining micro sequences (J. Hancox pers. comm.), and represent a different taphonomic entity from the dense scatter of vertebrate remains (Brink in press).

Sedimentary context

The site consists of Quaternary alluvial and colluvial gravels and clays in a small basin of Permian Karoo (Ecca) shale (Figure 22). A small stream, the Schoonspruit, which flows northwards into the Vaal River, cuts through this pocket of Quaternary sediments, which have been described as valley fill sediments (Butzer 1974). The down cutting of the Schoonspruit into the Quaternary fossil-bearing sediments was initiated when the level of the flow of the Schoonspruit was lowered through the upstream migration of the nickpoint of the drainage. This resulted in the erosion of the Quaternary and Ecca sediments and the exposure of the Quaternary fossil occurrence (J. Hancox, pers. com.).

Butzer identified eight stratigraphic horizons. His basal horizon, Unit 1, is a “fine-to-coarse-grade shale gravel” and Unit 2 is a “compact, pale-yellow, moderately sorted silty clay”,

which he considered the main fossil-bearing horizon. The rest of the sedimentary sequence represents various horizons of fine-grained valley floor sediments, which is capped by a vertisol (Butzer 1974). Although more than one fossil-bearing horizon could be identified in the stratigraphic sequence at Cornelia-Uitzoek, in agreement with Butzer's observation (Butzer 1974), the 1998 test excavation was made into the lowermost of these occurrences at a locality where an abundance of fossils were continually eroding out after rains (Figures 21 & 22). Our test excavation has shown that the gravel layer, Butzer's "Unit 1", is not basal in the sequence, but rather that it is banked against an older horizon, an underlying dense yellow clay, Butzer's "Unit 2" (Figure 22). The vertebrate fossils that were found in the new excavations crosscut both these stratigraphic horizons and appear to be intrusive. A vertical north-facing plot of the fossil specimens superimposed on an inverted south-facing section of the sedimentary layers illustrates the intrusive nature of the occurrence (Figure 23), suggesting that the *in situ* occurrence postdates the two layers.

A noteworthy aspect of the underlying yellow clay sediment matrix was that it was less consolidated around the fossils, but more compact and hard in areas slightly removed from the occurrence. The softer consistency of the sediment around the fossils made it easier to follow the bone occurrence. It appears that some specimens were post-depositionally mobilised along the inclination of the palaeo-surface on which the fossils were deposited. However, specimens tend generally to be intact, excluding pre-depositional damage, and they show no signs of rolling, suggesting that post-depositional movement was limited and characterised by low energy. The indication that the *in situ* specimens and the matrix slumped down a palaeoslope suggests post-depositional saturated conditions and that there was considerable loading of overlying sediment (Reineck & Singh 1975).

The intrusive nature of the occurrence, the linear nature of the horizontal distribution of specimens (Figure 24), their limited vertical distribution on an old surface, the minor post-depositional displacement of some specimens along a palaeo-surface and the fact that the sediment matrix is less consolidated around the fossils suggest that the occurrence represents an intrusive depositional event, such as when bones are deposited within a burrow. Bone accumulations in burrows are commonly associated with hyaena behaviour (Kruuk 1972; Mills, 1990), and often produce linear concentrations of bone remains (G. Avery 1988; G. Avery *et al.* 1984). The *in situ* fossil occurrence at Cornelia-Uitzoek is, therefore, likely to

represent the minimally disturbed remains of an ancient hyaena lair. Although it is not possible yet to identify the species of hyaena with certainty, there are indications that it was an active hunter of large game, such as the spotted hyaena, *Crocuta crocuta* (Table 13). This interpretation is tentative, since typical indicators of hyaena presence, such as a high proportion of specimens showing gnawing and hyaena coprolites, are not present in the assemblage (Brink in press).

Apart from the *in situ* occurrence, which is presently interpreted as the contents of an ancient hyaena burrow, there are fossil occurrences from intact sedimentary horizons. In the course of the new work at Cornelia-Uitzoek fossil material has been found on what appear to have been short-lived, but stable landsurfaces. An example of such an occurrence is a large bovid rib and the basal part of the horn cores of *Megalotragus eucornutus* (Figure 25), which were found at a higher elevation in the sedimentary sequence in a sedimentary horizon that would correlate with Butzer's "Unit 2". This part of the sequence is characterised by laminations of upward fining micro sequences (J. Hancox pers. comm.). The fossils illustrated in Figure 25 lie at the base of such a micro sequence. From the sedimentary context it is evident that material from these intact palaeo-surfaces predates the intrusive occurrence. Therefore, there are potentially at least two kinds of fossil occurrence at Cornelia-Uitzoek; one derives from intrusive burrows and the other from older land surfaces. This has important implications for interpreting the taxonomic composition of the old collections in relation to the new material.

Mammalian fauna and its geological age

Because the old collection was excavated by a number of workers and because records of recovery are not available, it is not possible to determine the context of the individual specimens in the old collection. However, given what is now known of the sedimentary context of the fossil vertebrates from Cornelia-Uitzoek, the old collection can contain elements from both old land surfaces and from intrusive burrows. The intrusive nature of the newly excavated fossils from the burrow structure suggests that these specimens postdate the samples from the palaeo-surfaces. In this context it is noteworthy that an archaic component in the Cornelia-Uitzoek fauna is found only in the old collection, but not in the assemblage from the intrusive occurrence. The archaic component includes hipparions, primitive forms of Suidae and *Hippopotamus gorgops* (Table 13). The presence of archaic taxa in the old

collection, but not in the assemblage from the intrusive structure, gives support to the suggestion that the fossils from the intrusive burrow postdate those from intact landsurfaces.

This leads to the question of the scale of the difference in geological age between the two taphonomic components. The question can be addressed by noting the morphological state of those taxonomic elements in the fossil assemblages, which are known to have undergone morphological change over approximately the last million years. Such taxa are *C. gnou laticornutus*, *D. niro* and *A. bondi* (Brink 1993; Thackeray *et al.* 1996; Chapter 9). When comparing these taxa from the intrusive burrow assemblage with those from the old collection there are no obvious shifts in morphology in these taxa. Therefore, in spite of a minor difference in geological age between the two taphonomic components at Cornelia-Uitzoek, it can be assumed for the purpose of faunal correlation that the new material and the old collection reflect a confined temporal span.

There is remarkable taxonomic similarity between the Cornelian fossil assemblage and the assemblages from Olduvai Beds III – IV (Cooke 1974; Gentry & Gentry 1978; Harris & White 1979). Taxa common to both Olduvai and Cornelia are the hipparions, *Hipparion steyleri* and *H. cornelianum*, the suids *Kolpochoerus limnetes*, *Metridiochoerus compactus*, and *Phacochoerus modestus*, and the artiodactyls, *Hippopotamus gorgops* and an archaic temporal form of *Damaliscus niro*, although somewhat more evolved (Thackeray *et al.* 1996). With the exception of *D. niro*, these taxa are referred to above as the archaic component in the faunal assemblage from Cornelia-Uitzoek and they suggest a much older age than for the typically Florisian sites (Klein 1984; Brink 1987; Grün *et al.* 1996). Previously, the conventional age estimate for Cornelia-Uitzoek, based on faunal correlation with East Africa, was some 700 000 BP (Gentry & Gentry 1978; Vrba 1997). A recently revised magnetostratigraphy of the Olduvai sequence indicates that the upper beds of Olduvai may be somewhat older than previously thought, probably around 1.0 to 1.2 million years in age (Tamrat *et al.* 1995). The inferred age for the older component of the Cornelia-Uitzoek assemblage may be of this order or somewhat younger.

Biogeographic factors in the mid to later Quaternary, which may have contributed to regional differentiation between southern and East Africa, have to be considered in attempts at faunal correlation between the two evolutionary centres. The most obvious difference between the

fossil vertebrate assemblages from the upper levels of Olduvai and Cornelia-Uitzoek is the presence in the latter of early forms of local endemics, such as *C. gnou laticornutus*, *A. bondi* and “*Gazella*” *helmoedi*. This may represent both biogeographic and evolutionary shifts. The former two taxa are not found in East Africa, and probably indicate a locally derived component in the Cornelian fauna and this together with the somewhat more evolved state of *D. niro* suggests that the assemblages from Cornelia-Uitzoek may postdate the upper levels of Olduvai. “*G.*” *helmoedi* appears to be a local form of the impala, *Aepyceros melampus*.

Another point of interest is the presence of *Rabaticeras arambourgi* in Beds II to IV of Olduvai and Elandsfontein, but its absence in Cornelia-Uitzoek. This may reflect the peripheral position of the Cape coastal zone in relation to the central interior and the younger geological age of the older component at Elandsfontein (Gentry & Gentry 1978). Since *R. arambourgi* and *Theropithecus* occur in ‘Cornelian’ contexts in North and East Africa respectively, it is possible that both these taxa at Elandsfontein represent a relict occurrence. This interpretation may also apply to the machairodont and *Gazella* sp. The absence of *R. arambourgi* from Cornelia-Uitzoek suggests that in the Cornelian it was extinct in the central interior of southern Africa, but that it survived in the Cape coastal zone after the time represented by the Cornelia-Uitzoek assemblages. *R. arambourgi* is known to have ranged from North Africa, through East Africa and to southern Africa in the Early/Middle Pleistocene (Vrba 1997). This suggests that there was a dispersal of *R. arambourgi*, that its distribution became disjunct subsequently and that this eventually led to its extinction. Some researchers consider it likely that *R. arambourgi* evolved into the modern hartebeest (e.g. Kingdon 1982), but this opinion is not supported by evidence presented in Chapters 7 & 8.

The taphonomic and taxonomic evidence presented here suggests that the Cornelia-Uitzoek fauna dates to a relatively restricted time span, estimated to be around a 1.0 million years ago. It may be somewhat younger, but is unlikely to be significantly older.

Table 13. Taxonomic list of Cornelia-Uitzoek: a comparison of new material excavated from a slumped hyaena burrow (1998 to 2002), with previously collected material (old collection) Extinct species are indicated with an asterisk.

	1998 – 2002	Old collection
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Primates		
<i>Homo</i> sp.	1	-
Carnivora		
<i>Panthera leo</i>	-	5
Indet.	1	-
Proboscidea		
Indet.	2	2
Perissodactyla		
* <i>Hipparion steytleri</i>	-	4
* <i>H. cornelianum</i>	-	2
<i>Equus</i> sp. cf. <i>E. capensis</i>	19	69
Rhinocerotidae indet.	1	2
Artiodactyla		
* <i>Hippopotamus gorgops</i>	-	49
<i>Phacochoerus</i> sp.	4	-
* <i>P. modestus</i>	-	11
* <i>Metridiochoerus compactus</i>	-	2
* <i>Kolpochoerus limnetes</i>	-	4
* <i>Sivatherium maurusium</i>	-	4
* <i>Homoioceras antiquus</i>	7	54
* <i>Damaliscus niro</i>	65	237
* <i>Megalotragus eucornutus</i>	1	24
<i>Connochaetes gnou laticornutus</i>	36	150
* <i>Antidorcas bondi</i>	84	257
" <i>Gazella</i> " <i>helmoedi</i>	2	1
<i>Sylvicapra grimmia</i>	5	2

FOSSIL LOCALITIES FROM THE CAPE COASTAL ZONE

Introduction

In this section brief descriptions of the Cape sites with fossil black wildebeest samples are given (Figure 5). These sites include Elandsfontein, the Klasies River main site, Swartklip and Sea Harvest. No suitable fossil elements of *C. gnou* were available from the Last Glacial Nelson Bay Cave assemblages and only very limited samples are available from the early Last Glacial assemblage from Herolds Bay Cave (Klein 1972, Brink & Deacon 1982). An important Cornelian site from the Cape coastal zone, which contains fossil black wildebeest material, is Duinefontein 2 (Klein *et al.* 1999), but it is not included in the present study as the materials were not yet available for study. All the fossil black wildebeest materials from the Cape coastal zone, which are used in this study, are housed in the collections of the Dept. of Cainozoic Palaeontology, Iziko South African Museum.

Elandsfontein

Elandsfontein has produced taphonomically mixed fossil vertebrate assemblages with Middle and Late Pleistocene elements (Singer & Wymer 1968; Hendey 1974a; Hendey & Deacon 1977; G. Avery 1988; Klein & Cruz-Uribe 1991; Brink 1993; Deacon 1998).

The site is situated in the Saldanha Bay area and consists of a rectangular area of approximately 4.5 km² of Pleistocene mobile sand deposits referred to the Bredasdorp Formation (Rogers 1980; Deacon 1998). These deposits, which are now stabilised by recent bush encroachment, are underlain by Plio-Pleistocene sands, which are in excess of 100 m in thickness. The surficial geology has been described as consisting of distinct stratigraphic units. In stratigraphic sequence these units are basal silver-grey sands, calcareous sands, dark or brown sands and calcrete (Mabbutt 1956). Although there appears to be stratigraphic integrity in the fossil deposits at Elandsfontein (Butzer 1973; Klein & Cruz-Uribe 1991), the process of fossil site formation is complicated by a fluctuating water table and by wind deflation. It appears that most of the fossil deposits at Elandsfontein were formed around water bodies or pans within the dune complex. Although there is some evidence that the Acheulian artefacts are associated with the main Middle Pleistocene fossil occurrence, most of these vertebrate fossils were probably produced by carnivore activities and not by human hunting or scavenging (G. Avery 1988).

Deacon initiated systematic excavations at Elandsfontein in 1964 (Deacon 1998), followed by Wymer (Singer & Wymer 1968) and later by G. Avery (1988). However, most of the fossil vertebrate collections from Elandsfontein were unsystematically collected from deflated areas, known as bays, within the sand dunes. The lack of stratigraphic control in these assemblages complicates the interpretation of the Elandsfontein collections. However, these assemblages are useful for the purpose of this study, as it is possible to distinguish the various temporal components of fossil black wildebeest by comparison with interior localities and with coastal sites, such as Klasies River, Swartklip and Sea Harvest.

The older vertebrate component at Elandsfontein is considered to be Cornelian in age, but probably somewhat younger than Cornelia-Uitzoek (Gentry & Gentry 1978). Klein & Cruz-Uribe (1991) mentions an age estimate ranging from 400 000 to 700 000 years ago. In the light of the new evidence from Cornelia-Uitzoek the upper limit of this estimation is more

probable. The younger components of fossil vertebrate assemblages at Elandsfontein can be classified as Florisian in the wide sense, but can be further subdivided into an earlier Florisian and a terminal Florisian, probably late Last Glacial (Chapter 9). The Elandsfontein Bone Circle collection is an example of the latter. These terminal Florisian scatters appear to be the deflated remains of geologically younger brown hyaena burrows (G. Avery 1988).

Klasies River main site

The Klasies River main site encompasses a series of coastal caves on the Tsitsikamma coast in the southern Cape. It is known for producing the earliest dated modern human remains from southern Africa and for producing an important Middle Stone Age archaeological sequence dating to the early Late Pleistocene (Singer & Wymer 1982; Deacon 1995, 1998; Deacon & Deacon 1999). In 1968, Singer & Wymer (1982) first excavated the Klasies River sites. They demonstrated the importance of the deposits, which in the 1980's and 1990's were re-excavated and studied by H.J. Deacon. This work has produced more human remains, has added information on the dating and on the taphonomy of the human remains and has refined the archaeological interpretation of the main site (Deacon 1992; Rightmire & Deacon 1991; Deacon 1998; Wurz 2002).

The stratigraphic sequence in Cave 1 can be summarised as consisting of the basal LBS Member, the SAS Member, the WS Member and a Later Stone Age shell midden, which caps the sequence (Deacon & Deacon 1999). The LBS Member overlies a last Interglacial high sea stand of the Marine Isotope Stage (MIS) 5e and has a minimum age of 110,000 years BP for its lowest levels (levels 38-40). The SAS member (levels 17 upwards) has a maximum age of 100,000 years BP, while the upper WS Member correlates with MIS 5a-4, around 70 000 years BP, which is also the assumed age for the Howiesons Poort substage of the Middle Stone Age (Deacon 1998; Deacon & Wurz 1996).

The fossil black wildebeest specimens utilised in this study come from the Singer and Wymer collection, but can be stratigraphically related to the newer excavations and the dating results.

Sea Harvest

The Sea Harvest site is situated on the coast at Saldanha Bay and consists of calcareous fissure fills in consolidated dune sands. It is adjacent to the Sea Harvest Middle Stone Age

archaeological site, which has produced early evidence of Middle Stone Age shellfish collecting (Volman 1978). The Sea Harvest fissure fills have produced well-preserved Late Pleistocene fossil mammalian remains and are considered to represent hyaena accumulated bone assemblages. Radiocarbon dates on ostrich eggshell from the archaeological midden gave ages beyond the limit of the radiocarbon method. On geological grounds the site is estimated to date to the early part of the MIS 4 (Volman 1978; Klein 1999). The Sea Harvest fissure fills are assumed to be roughly contemporaneous with the Sea Harvest archaeological site.

The sample used in this study was not systematically excavated, but represents occasional collections of material eroding from the fissure fills due to natural weathering (Volman 1978).

Swartklip

The fossil sites of Swartklip 1 and 2 are on the False Bay coast near Cape Town. As in the case of Sea Harvest, they consist of calcareous fissure fillings within consolidated palaeodunes, or aeolianites. The palaeodunes form a modern land surface that is elevated approximately 20 m above the present sea level, while the fossil sites are exposed through weathering approximately 2 m below the top of the cliff. The fossil contents of Swartklip 1 and 2 were studied initially by Singer & Fuller (1963), but were more extensively described and discussed by Hendey & Hendey (1968) and by Klein (1975). The fossil materials from the Swartklip 1 site are the product of denning activities of brown hyaenas (Klein 1975). Ostrich eggshell from the Swartklip 1 assemblage has been radiocarbon dated to > 40 000 years. On geological grounds the fissure filling is considered to date to the early part of the Late Pleistocene, in agreement with the radiocarbon date (Klein 1975). Swartklip 1 is the more prolific of the two occurrences and only material from this occurrence is considered in this study.

The mammalian faunal assemblage from Swartklip is remarkably diverse, with 13 taxa each of carnivores and ungulates. Swartklip has been a key site for illustrating the great diversity of Last Glacial mammalian faunas of the Cape coastal area (Klein 1983). However, for the purpose of this study the presence of taxa in the Swartklip ungulate fauna more usually associated with the interior plateaux is considered the most significant feature of the assemblage. This element includes taxa such as *Ceratotherium simum*, *Equus capensis*, *E.*

quagga, *Homoioceras antiquus*, *Connochaetes gnou* and *Antidorcas marsupialis* (Hendey & Hendey 1968; Klein 1975).

The large black wildebeest fossil sample from Swartklip forms the basis for evaluating the evolution of the black wildebeest in an area outside of its centre of origin (Chapter 9).

FOSSIL LOCALITIES FROM NORTH AFRICA

Introduction

Materials from three fossil localities in North Africa are included in this study, Aïn Jourdel, Aïn Boucherit and Tighenif (= Ternifine = Palikao). Tighenif is situated in the northwest of Algeria, about 20 km west of Mascara near the coastal town of Oran, while the other two localities are in the northeast of Algeria, near the town of Constantine (Arambourg 1970; Geraads *et al.* 1986; Figure 26). The archaeological site of Aïn Hanech, situated in the same sedimentary basin as Aïn Boucherit (Arambourg 1970), is geologically younger than Aïn Boucherit (Geraads *et al.* 2004) and has produced a rich vertebrate fauna (Arambourg 1979), but this is not discussed in detail here.

Aïn Jourdel

The site consists of fossil-bearing fluvio-lacustrine sediments. The fossil material was recovered in the latter part of the nineteenth century, probably in the time after 1871 when political stability was achieved in the area. Thomas (1884) described the type specimen. The fossils from Aïn Jourdel are kept in the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle in Paris.

The site is important mainly for producing the primitive wildebeest-like alcelaphine, *Oreonagor tournoueri*, commonly thought to be part of the lineage leading to the genus *Connochaetes* (Gentry 1978). Although modern dating methods have not been attempted at the site, the relative age of the fossils is inferred from the equids (Eisenmann pers. comm.), the presence of *Palaeoreas gaudryi* and the primitive stage of evolution of the type material of *O. tournoueri* (Thomas 1884). The material from Aïn Jourdel is thought to be older than that of Aïn Boucherit.

Aïn Boucherit

The fossil locality of Aïn Boucherit is situated on the left bank of a stream, the Oued Boucherit. The stream cuts through a sequence of fluvio-lacustrine deposits. The base is a conglomerate, and vertebrate fossils occur at two levels. The lower of these is referred to as Aïn Boucherit, while the upper occurrence is referred to as Aïn Hanech. The sediments of the lower Aïn Boucherit fossil occurrence are grey clays and conglomerates, which overly a lacustrine clay capping. In addition to vertebrate fossils the occurrence has produced terrestrial and freshwater molluscs and ostracods. In the years 1948, 1949, 1952, 1953 and 1966 systematic excavations were conducted at Aïn Boucherit (Arambourg 1970), and the fossil collections from these excavations are housed in the Laboratoire de Paléontologie, Paris.

Arambourg (1979) described the vertebrate remains from Aïn Boucherit, together with material from other North African localities. He referred some of the alcelaphine material from Aïn Boucherit to the species *O. tournoueri* (Thomas 1884) and redescribed the species on the basis of a neotype and as neosyntypes from Aïn Boucherit (Arambourg 1979). The material is pertinent to the question of origins of the genera *Connochaetes* and *Megalotragus*. The fact that the species *O. tournoueri* has been described on material from more than one locality has resulted in some confusion in the literature (*vide* Gentry & Gentry 1978; Vrba 1997). This issue is further discussed in Chapter 8.

Tighenif (Ternifine)

The site is an accumulation of sediments associated with an artesian spring and appears to have some similarities with Florisbad (Geraads *et al.* 1986). In the 19th century vertebrate fossils and Acheulian stone artefacts were discovered through quarrying and were described by Pomel (Pomel 1878, 1893 – 1897, as quoted in Geraads *et al.* 1986). In 1882 Pomel attempted a small-scale excavation in collaboration with an archaeologist Tommasini (Tommasini 1886, as quoted in Geraads *et al.* 1986). Between the years 1954 and 1956 Arambourg and Hofstetter conducted a large-scale excavation, which increased the vertebrate samples and produced hominid remains referred to *H. erectus* (Arambourg & Hofstetter 1963). This phase of fieldwork was terminated when the water levels of the spring rose and

made it impossible to continue with systematic excavations. However, when water levels dropped due to the drying out of the spring at Tighenif systematic excavations were re-continued from 1981 to 1983 by a team consisting of researchers of the French CNRS, the University of Paris VI, and of the Algerian ONRS.

The site is dated by a normal polarity reading in the basal clays and by faunal correlations with other North African and East African localities (Geraads *et al.* 1986, 2004), which suggest that it is in the order of 0.7 million years old. It also appears that the Acheulian artefacts are chance inclusions into the deposits and that they are not directly associated with the vertebrate remains (Geraads *et al.* 2004).

The locality of Tighenif has produced the type material of the fossil subspecies of the blue wildebeest, *C. taurinus prognu* Pomel. The name *C. taurinus olduvaiensis* Leakey, which is the taxon to which some of the Olduvai specimens in Beds II, III & IV are referred (Gentry & Gentry 1978), is considered a junior synonym of *C. taurinus prognu* Pomel (Geraads 1981). The Tighenif wildebeest fossils together with the material from the Middle Awash (Vrba 1997), Olduvai (Gentry & Gentry 1978), Turkana (Harris *et al.* 1988; Harris 1991) and Sterkfontein (Vrba 1976), show that the ancestral forms of *C. taurinus* had an African-wide distribution in the Early Pleistocene. This is important for understanding the appearance and evolution of *C. gnou*, which is discussed in more detail in Chapter 9.

CHAPTER 6. THE CHRONOLOGY AND PALAEO-ECOLOGY OF THE CORNELIAN AND THE FLORISIAN LAND MAMMAL AGES

INTRODUCTION

Land Mammal Ages (LMA) are periods of geological time, which can be distinguished by their distinctive faunal character over a large area such as a continent or a sub-continent (Savage & Russel 1983). The faunal character of a LMA is defined on the basis of presence or absence of time sensitive taxa and on the evolutionary stages of certain taxa. The use of Land Mammal Ages as a biochronological method to provide temporal order to the Cainozoic fossil record is well established, including in southern Africa (Savage & Russel 1983; Hendeby 1974b; Chapter 2). In Hendeby's (1974b) revision and summary of southern African large mammal biochronology and in later works by Klein (1980, 1984) it was assumed that the Cornelian LMA can be equated with the 'Middle Pleistocene' and the Florisian LMA with the 'Late Pleistocene'. However, the temporal frame of this biochronological scheme was based on undated fossil assemblages, except for those younger than the c. 40 000 years limit of the conventional radiocarbon method. This limitation and the lack in southern Africa of volcanic deposits suitable for radiometric dating meant that the Cornelian LMA and Florisian LMA were effectively undated.

To address this problem the ESR and OSL dating techniques were applied to fossil assemblages and sediments from localities in central southern Africa (Chapter 5). These dating results and new data on the palaeo-ecology of large mammal species provide an opportunity for a revised definition of the Cornelian LMA and the Florisian LMA. In this chapter a revision is provided of the palaeo-ecology and biochronology of large mammal evolution in southern Africa of approximately the past 1.0 million years. This revision serves as background and as chronological framework for assessing the fossil history of the black wildebeest.

THE CORNELIAN LMA

Taxonomic definition

It is possible to distinguish an interior from a coastal Cornelian fauna. Interior localities with Cornelian faunas include the type locality on the farm Uitzoek near the small town of Cornelia and the near-by locality on the farm Mara (Butzer 1974; Chapter 5). The interior Cornelian is characterised by the absence of extinct Carnivora and of the bovid genera *Pelorovis*, *Gazella*, *Beatragus*, *Parmularius* and the species *Megalotragus kattwinkeli* (Table 13). However, it can be defined on the presence of archaic taxa such as *Hipparion steytleri*, *H. cornelianum*, the suids *Kolpochoerus limnetes*, *Metridiochoerus compactus*, and *Phacochoerus modestus* and *Hippopotamus gorgops*. It can be defined further on the presence of certain taxa, some of which are endemic to southern African. These taxa can be distinguished from their Florisian descendants in their less derived morphologies. They would include the earliest form of the black wildebeest, *C. gnou laticornutus*, the post-Olduvai Bed IV/ pre-Florisian form of *Damaliscus niro* (Thackeray *et al.* 1996), an early morphotype of *A. bondi* and a very large form of *S. grimmia* (Table 13). The presence of archaic forms allows correlation with the East African fossil mammal assemblages, in particular those from Olduvai (Gentry & Gentry 1978). The incipiently endemic character of the fauna from Cornelia-Uitzoek and Cornelia-Mara suggests that the Cornelian LMA represents an early stage in the process of southern vicariance, where the large mammal faunas of southern African evolved an increasingly distinctive character from those of East Africa.

The Cornelian fauna of the Cape coastal zone is mainly represented by the older component in the Elandsfontein assemblage, but also by the new material from Duinefontein 2 (Klein *et al.* 1999). This fauna has a slightly different taxonomic composition from that of the interior Cornelian faunas. Animals such as the local kudu, *Tragelaphus sp. cf. T. strepsiceros*, the extinct hippotragine, *Hippotragus gigas*, *Redunca arundinum*, *Rabaticeras arambourgi*, machairodonts, *Theropithecus sp.* and gazelles are not found at Cornelia-Uitzoek or Cornelia-Mara, while the genera *Beatragus* and *Parmularius* have been tentatively identified at Elandsfontein (Gentry & Gentry 1978). The relatively isolated biogeographical position of the Cape coastal region may account for the presence of these forms as either the product of endemic evolution, or vicariance (*e.g. Tragelaphus sp. cf. T. strepsiceros* and *R. arundinum*), or as relict forms (*e.g. Hippotragus gigas*, *R. arambourgi*, *Gazella*, machairodonts and extinct

baboons). However, it should be noted that it is possible that some of these archaic taxa may be associated with deposits that predate the Cornelian LMA, given the open site context at Elandsfontein.

Temporal definition

Correlation of the Cornelia-Uitzoek fauna with the upper levels of the Olduvai sequence, with a presumed age of some 1.0 million years ago, provides an estimate for the maximum age of the Cornelian LMA (Cooke 1974; Gentry & Gentry 1978; Harris & White 1979). In a recent study of the decalcified breccia deposits at the Gladysvale Cave in the Sterkfontein Valley an age estimate, based on ESR and palaeomagnetism, of between 700 000 and 550 000 BP was obtained. The character of the large mammal fauna from these deposits at Gladysvale is essentially Florisian (Lacruz *et al.* 2002). This effectively establishes the terminus ante quem of the Cornelian LMA. If the Gladysvale dating can be considered reliable, then the Cornelian LMA grades into the Florisian LMA at c. 700 000 BP to 550 000 years ago. From this it follows that the age of the Cornelian assemblages from the Cape coastal zone, *i.e.* the Elandsfontein older materials and the Duinefontein 2 assemblage (Klein *et al.* 1999) should not be younger than this temporal limit.

This revised estimate of the dating of the Cornelian LMA has bearing on the geological age of human fossils from Elandsfontein, Kabwe and Cornelia-Uitzoek. If the Elandsfontein hominid is associated with the Cornelian component of the fossil assemblage, then the age of this component may approach an age of around 700 000 years. It is assumed that the Elandsfontein and Kabwe specimens are of a broadly similar evolutionary stage (Bräuer 1984), and it is encouraging to note that in size the newly discovered human upper first molar from Cornelia-Uitzoek clusters with the Kabwe specimen (J. Moggi-Cecchi pers. comm.). These hominid specimens are substantially older than the Florisbad hominid and represent an earlier phase in human evolution in southern Africa (Bräuer 1984, 2001; Grün *et al.* 1996).

THE FLORISIAN LMA

Taxonomic definition

As in the case of the Cornelian LMA, there is a biogeographic distinction between the Florisian LMA of the interior of southern Africa and that of the Cape coastal zone, although not as pronounced.

The large mammal fauna from the Florisbad spring is the type assemblage for the interior Florisian LMA. It is defined on the absence of archaic Cornelian taxa and on the presence of a number of extinct taxa, which are *Equus capensis*, *E. lylei*, *Homoiceras antiquus*, *Megalotragus priscus*, *Damaliscus niro*, *Antidorcas bondi* and the as yet unnamed new southern African caprine species (Hendey 1974b; Klein 1984; Brink 1987, 1994, 1999; Appendix B). Some of these forms are descendants of Cornelian precursors, such as *E. capensis*, *H. antiquus*, *D. niro* and *A. bondi*. The latter two species are more derived than the ancestral Cornelian forms and can be easily distinguished on morphological grounds. These morphological shifts probably represent drift, or micromutations (*sensu* Goldschmidt 1952), that did not lead to new species. It is probable that *H. antiquus* and *E. capensis* also underwent similar drift, which would allow the Cornelian form to be distinguished from the subsequent Florisian form. In the case of *H. antiquus* this assumption still needs to be tested, while *E. capensis* is presently the focus of a detailed morphological study, which forms part of a larger study of equid evolution (Eisenmann 2000, 2004). In addition, the new caprine species from montane areas in southern Africa seems to show similar evidence for evolutionary drift in that it became more specialised as a grazer from early to later in the Florisian LMA (Appendix C). Morphologically the caprine has much in common with the Pliocene *Makapania broomi* from the Makapansgat Limeworks deposits. However, the question of its Cornelian, or pre-Cornelian, evolutionary roots is not yet clear. Therefore, the list of extinct species that characterises the interior Florisian can be modified from that given by Klein (1984) to include *E. lylei* and the new caprine. However, contrary to the suggestion by Klein (1984), the available fossil evidence (Brink 1987; Lacruz *et al.* 2002) does not suggest the existence of the extinct giant warthog genus, *Metridiochoerus*, during the Florisian LMA.

In addition to the above, the interior Florisian can be defined on the appearance in the fossil record of immigrant species. The alcelaphines, *A. buselaphus* and *D. pygargus*, the lechwe, *K. leche*, the modern hippopotamus, *H. amphibius* and probably *E. lylei* are examples of such new arrivals (Brink 1987; Vrba 1997). These taxa have no Cornelian forerunners and seem not to have evolved locally. It is likely that *M. priscus* also was an immigrant species. This contention rests on the morphological evidence given in the next chapter, which suggests that it is probably not a descendant of *M. eucornutus* (Chapter 7).

It appears that the taxonomic composition of the large mammal faunas of the Florisian LMA in the Cape coastal zone was stable over time, as in the interior. However, an important difference between the two areas is the more pronounced effects of the global glacial-interglacial cycle on palaeo-environments of the Cape. Additional habitat was formed during glacial times due to the eustatically-exposed continental shelf. During the maximum of the Last Glacial the sea level dropped to around a 100 m below present-day level (Deacon & Lancaster 1988). This created open plains-habitat in the palaeo-environment that was reminiscent of the plains of the interior and consequently a very pronounced “interior” element is present in fossil assemblages of glacial age. This is illustrated by the fossil materials from the Middle Pleistocene Hoedjies Punt hyaena den, the Swartklip 1 locality and the archaeological site of Nelson Bay Cave (Klein 1983; Stynder *et al.* 2001; Chapter 5). These assemblages include the typically extinct Florisian forms, such as *E. capensis*, *H. antiquus*, *M. priscus*, *D. niro*, but also extant species associated with the modern-day open grasslands of the interior, such as *E. quagga*, *C. gnou*, *A. buselaphus*, *D. pygargus* and *A. marsupialis*. It appears that in interglacial deposits, illustrated by the lower levels of the Klasies River main site, frequencies of plains-living ungulates are reduced and species more typically associated with closed habitats, such as the Cape Fynbos, are more predominant (Klein 1976, 1983).

It should be noted that the plains-living ungulates of the glacials in the Cape coastal zone show incipient differentiation from their interior counterparts. This is illustrated by the small black wildebeest materials from Swartklip (Brink 1993; Chapter 9) and by the southern springbok, *Antidorcas marsupialis australis* (Hendey & Hendey 1968). The living bontebok, *Damaliscus pygargus pygargus*, is another example of glacial vicariance in the Cape coastal zone. The bontebok survived as a relict population on the southern Cape coast after the Last

Glacial, when climatic amelioration and a high sea level reduced the glacial plains habitat. It is the only Florisian glacial form that survived the end-Pleistocene extinction event in the Cape coastal zone (see also discussion in Hendey 1974a). The glacial black wildebeest materials from the Cape coastal zone also show size reduction and changes in body proportions, which reflect reproductive isolation from interior populations (Chapter 9).

In addition, the Florisian glacial mammal faunas of the Cape coastal zone include the descendants of some of the local Cornelian forms, such as *R. arundinum* and *T. strepsiceros* (Hendey & Hendey 1968; Klein 1975). However, these forms are not found in terminal Pleistocene assemblages in the southern Cape, such as at Nelson Bay Cave (Klein 1972). There is also no evidence for *E. lylei* and *A. bondi* in Florisian assemblages from the Cape coastal zone.

Temporal definition

Before the ESR/OSL dating exercise at Florisbad the conventional estimate of the upper age limit of the Florisian LMA was around the Middle and Late Pleistocene boundary, at 125 000 years BP (Klein 1984). This limit was revised to c. 400 000 years BP, following the Florisbad dating exercise (Grün *et al.* 1996), and is now revised to c. 700 000 to 550 000, based on the Gladysvale evidence (Lacruz *et al.* 2002). The lower limit of the Florisian LMA is well established on the basis of the terminal Pleistocene/early Holocene extinction of the suite of Florisian species in the interior and in the Cape coastal zone (Klein 1984; Brink & Lee-Thorp 1992).

In the Cape coastal zone Hoedjies Punt represents the earliest Florisian fauna. The Hoedjies punt assemblage includes hominid remains and may be as old as around 300 000 years (McBrearty & Brooks 2000; Stnyder *et al.* 2001). However, it can be assumed that the Cornelian-Florisian boundary in the Cape coastal zone would have been as old or slightly younger than its estimate for the interior. The latest occurrence of a Florisian fauna is in the terminal Pleistocene deposits of Nelson Bay Cave at c. 10 000 years ago (Klein 1972, 1983).

The palaeo-ecology of the interior Florisian

The range of extinct and extant ungulates of the interior Florisian can be considered to reflect a highly productive open grassland ecosystem in which a range of grazing ungulates, some now extinct, interacted in a facilitating grazing system analogous to the grazing succession described for the Serengeti (Bell 1971; Brink & Lee-Thorp 1992). This ecosystem included an aquatic component, which is reflected by the presence of hippopotamus and lechwe in the fossil record (Brink 1987). Seen in conjunction with geological evidence, that the pans of the central interior record Middle and early Late Pleistocene high lake levels (Loock & Grobler 1988; Visser & Joubert 1991), the aquatic component of the Florisian LMA can be interpreted to reflect the presence of perennial lakes in the palaeo-environment. The pans of the modern landscape of central southern Africa contain water only seasonally and are the relicts of the Florisian lake system.

It can be predicted that the global glacial-interglacial cycle would have caused some cyclicity in the regional palaeo-climate of the central interior and that there would have been fluctuations in lake levels. This indeed can be seen in the sedimentary record of the fossil-bearing deposits at Florisbad (Visser & Joubert 1991). However, the taxonomic composition of the interior Florisian LMA was essentially stable for a period of around half a million years in that extinction only occurred at the end of the Late Pleistocene. This suggests that the Florisian ecosystem, and the network of palaeo-lakes, survived palaeoclimatic fluctuations predicted by the global glacial-interglacial cycle. Geographically the Florisian lake system seems to have extended over most of central and western southern Africa, including the Highveld and the Karoo areas. This can be deduced from the widespread occurrence of Florisian ungulates, including the lechwe, in areas as far south as the town of Cradock. The fossil deposits of the thermal spring near Cradock produced an interior Florisian fauna, which includes hippopotamus and lechwe (Wells 1970; personal observation).

Today the only analogue of this ecosystem survives in the Okavango region of Botswana, where a pronounced aquatic component is maintained not by climatic factors, but by the configuration of the modern landscape that causes the Okavango River to drain internally (McCarthy *et al.* 2000). Therefore, the lechwe occurs today in the Okavango and adjacent areas where suitable habitat allows it to survive as a Florisian relict.

DISCUSSION

The roots of the Florisian ecosystem

The roots of the Florisian ecosystem can be found in the Cornelian. The interior Cornelian fauna has an ecological character, which reflects three distinct habitat types, grassland, aquatic habitat and closed/woodland habitat (Figure 27). The interior Florisian LMA, however, is sharply differentiated from the preceding Cornelian LMA, because of the absence of a closed/woodland habitat component and the presence of a marked aquatic and open grassland component in the fauna. This reflects a temporal trend in faunal turnover. This trend resulted in the extinction of the closed habitat and woodland component of the Cornelian faunal spectrum. One may view this element as plesiomorphic in a palaeo-ecological sense in that it reflects an ancestral condition in the palaeo-environment. The Cornelian extinction event can be described as a response to the disappearance of woodland habitat in the palaeo-environment with the formation of the central open grassland ecosystem as a dominant aspect of the Florisian landscape.

The formation of open grasslands, as the predominant habitat type in the central interior at the end of the Cornelian LMA, would have had the effect of creating an ecological island of open habitat within a wider area of savannahs or wooded grasslands (Chapter 4).

The grassland and aquatic components of the interior Cornelian fauna can be seen as an incipiently Florisian aspect of the fauna. These components include the ancestors of typically Florisian taxa, such as the black wildebeest, *A. bondi* and *D. niro*. However, the balance of the list of Florisian grazing ungulates consists of immigrant forms, such as *A. buselaphus*, *D. pygargus* and possibly *M. priscus* and *E. lylei*. The appearance of these taxa in the fossil record followed or coincided with Cornelian extinction and combined with the *in loco* ancestral Florisian taxa to form the grazing component of the new Florisian grazing ecosystem (Brink & Lee-Thorp 1992). Associated with this process was the appearance of a Florisian aquatic component represented by the immigrant species *H. amphibius* and *K. leche* (Brink 1987).

The demise of the Florisian ecosystem

The first evidence for the existence of the Florisian ecosystem is found in the decalcified deposits at Gladysvale Cave (Lacruz *et al.* 2002). From this time, estimated to be around 700 000 to 550 000 years ago, until the end-Pleistocene/early Holocene extinction of the typical Florisian grazers (Chapter 5), the faunal composition of the Florisian LMA remained stable. This suggests continuity and stability in the Florisian LMA over a period of at least 500 000 years, despite the effects of periodic drier conditions possibly associated with glacials.

The Florisian ecosystem was evidently disrupted towards the end of the Pleistocene by intense aridification, when the palaeo-lakes dried up to be transformed into the modern pan system (Loock & Grobler 1988). The interior fossil assemblages dating to around the Last Glacial maximum record this transformation by a decline in frequencies and eventual disappearance of aquatic indicators, such as lechwe and hippopotamus (Chapter 5). The extinction of the Florisian grazing ungulates followed on the extinction of the aquatic forms and occurred somewhat later at the end of the Late Pleistocene and early Holocene. The Serengeti-like grazing succession system ceased to function due to prolonged and intense aridification, which had the effect of reducing primary productivity to levels below the threshold necessary for the maintenance of the system. Because of the disruption of this ecosystem, extinction affected only the more specialised of the grazers (Chapter 5; Brink & Lee-Thorp 1992). Those grazers specialised in having very large body size are *Equus capensis*, *Homoiceras antiquus* and *Megalotragus priscus*. *Antidorcas bondi* was specialized as a small-bodied grazer. In addition those with close competitors, such as *Damaliscus niro* and *E. lylei*, also became extinct. Therefore, the spectrum of extinct Florisian grazers, being either specialized in terms of body size or those with close ecological competitors, is consistent with the prediction that aridification disrupted the Florisian ecosystem through a marked reduction in primary productivity (Brink & Lee-Thorp 1992). This hypothesis accords with sedimentary evidence for aridity during the last Glacial Maximum in the central and western interior of southern Africa (Thomas & Shaw 1993). In summary, the modern grasslands of the central interior are not different in structure from those of the Florisian LMA. They are the impoverished continuation of the Florisian ecosystem without the aquatic component and with a substantially reduced diversity of grazing ungulates.

In taxonomic terms the end-Pleistocene extinction event affected the Cape coastal zone and the interior almost equally. In the Cape coastal zone the return to high sea levels and an increase in Fynbos at the cost of grassland reduced the habitat necessary for the survival of plains-living ungulates. This caused the extinction of the coastal counterparts of the Florisian extinct grazers and of the extant plains-living taxa of the interior, with the exception of the bontebok, which survived as a Last Glacial relict in the southern Cape. In the interior the initial effect of intense aridification around and after the Last Glacial maximum was that the aquatic component disappeared from the landscape. This was followed by the disruption of the Serengeti-like facilitating grazing system and the extinction of the Florisian grazers.

By the end of the Pleistocene the process of extinction was complete in the interior and in the Cape coastal zone and the causes were seemingly palaeo-environmental rather than anthropogenic.

A CHRONOLOGICAL ARRANGEMENT OF FOSSIL ASSEMBLAGES

Based on the evidence and discussion provided in Chapter 5 and in this chapter, a correlation of sites from the interior of southern Africa and from the Cape coastal zone is given in Figure 28. This represents a revision of the mammalian biochronology of southern Africa and provides the temporal framework for the data presented in Chapters 8 and 9.

CHAPTER 7: ALCELAPHINE COMPARATIVE OSTEOLOGY

INTRODUCTION

The systematic comparison of southern African Alcelaphini given in this chapter serves as a morphological reference to address the questions of the origin of the genus *Connochaetes* (Chapter 8) and the evolution of the black wildebeest (Chapter 9). It also serves as the basis for addressing the discovery of the first Quaternary caprine from southern Africa (Appendix C). This chapter concludes with a reconstruction of the body plan of *M. priscus*.

Based on the osteological comparisons, the blueprint, or morphological reference, is presented as discrete characters. In the anatomical illustrations a fixed sequence is usually followed, except where otherwise indicated:

- *D. pygargus* (A)
- *A. buselaphus* (B)
- *M. priscus* (C)
- *C. taurinus* (D)
- *C. gnou* (E).

The numbers of characters given in the figures correspond to those in the text. The osteological comparison follows the natural sequence of skeletal parts, starting with cranial material (the skull, horn cores and dentitions), which is followed by the postcranium (the axis, front limb and hind limb). Conventionally the atlas, axis and the sacrum are used in postcranial osteological comparisons, since these elements are known to be diagnostic (*vide* Boessneck *et al.* 1964; Peters 1986; Peters & Brink 1992; Peters *et al.* 1997; Plug & Peters 1991). However, for the purpose of mapping changes in the neck anatomy in fossil alcelaphines, the axis was chosen, because it is considered to be more representative of neck dimensions than the atlas. The atlas often reflects functional aspects of the skull. The axis also happens to be better preserved in the fossil record than the atlas and the sacrum. The anatomical comparison of the appendicular skeleton does not include the phalanges. In the distal phalanx it is difficult to establish whether a given specimen is of a fully-grown adult or

not. This is because there are no epiphyses to determine the state of fusion and therefore maturity. Although proximal and medial phalanges are useful in osteometry they are not taken into account, because they are relatively underrepresented in the fossil samples and because they usually duplicate the patterns visible in the metapodials. In considering the fossil material of *Oreonagor tournoueri* and of *C. gnou* in the following chapters, the same anatomical order is followed, except that in the case of *O. tournoueri* upper dentitions are included.

In evaluating the dentitions of early wildebeest-like fossils from North Africa the dentitions of the impala, *Aepyceros melampus*, and the Indian black buck, *Antilope cervicapra*, are used as reference. The published accounts of the early alcelaphine/caprines materials from Fort Ternan, an early Middle Miocene locality in East Africa (Gentry 1970b), and of the materials from Langebaanweg, an early Pliocene locality in the south-western Cape (Gentry 1980) provide additional information. On this basis a list of blueprint characters for the upper and lower dentitions for primitive and advanced alcelaphines is given. It was not considered necessary to provide separate lists of primitive and advanced characters for the postcrania of alcelaphines, since in certain respects the living blesbok and hartebeest are examples of primitive alcelaphines. In discussing the primitive condition of alcelaphine postcrania the morphological blueprint characters are complemented by published accounts of the osteomorphology of caprines and antilopines (Boessneck *et al.* 1964; Peters 1986; Plug & Peters 1991; Peters & Brink 1992).

The fact that the two species of wildebeest are genetically close enough to allow interbreeding with fertile offspring, poses the problem of the inclusion of hybrid individuals in the black wildebeest study sample. However, it was possible to distinguish between hybrids and non-hybrids in the modern comparative sample by using a small number of specimens, which were collected before 1930's bottleneck. These specimens predate the present-day problem of hybridisation. The black wildebeest male skull, NMB-F 84, is an example of such a specimen and it is used for the skull comparison in this chapter. Furthermore, *C. gnou* X *C. taurinus* hybrids can be identified easily on their unusually large body size, unusual body proportions and deformities. Where these characteristics were identified in specimens, they were not included in the black wildebeest modern comparative sample.

POTENTIAL CONFUSION IN THE DIAGNOSIS OF ALCELAPHINE FOSSILS

Superficially, the extant *C. taurinus* and *C. gnou* are very similar and fossil postcranial materials of the two species can be confused. This problem applies particularly to geologically older material, because ancestral forms of *C. gnou* were larger than extant forms (Brink 1993). Because of repeated events of range expansion of *C. taurinus* in the past and periodic overlap between the two wildebeest species (Skead 1980; Brink *et al.* 1999), the geographic location of a site within the modern range of *C. gnou* is not in itself grounds for referring a specimen to this taxon. However, even the oldest material of ancestral *C. gnou* from Cornelia-Uitzoek shows *C. gnou*-like characters. This also applies to other early samples such as those from Elandsfontein. In geologically younger samples, the degree of body size reduction in *C. gnou* makes it easily distinguishable from *C. taurinus* on size, in addition to other morphological characters.

M. priscus can be confused with ancestral *C. gnou* and *C. taurinus*, because *M. priscus* shows convergent morphology with *C. gnou*. However, the large size of *M. priscus* provides sufficient grounds for distinction from the genus *Connochaetes*. Even though *A. buselaphus* approaches *C. gnou* in size, the differences between *C. gnou* and *A. buselaphus* are very marked. Furthermore, it is only in the Florisian and in more recent times that *A. buselaphus* is recorded in the fossil record of the interior (Chapter 6), and so can be discounted when trying to identify pre-Florisian black wildebeest fossils. *Damaliscus niro* is morphologically very similar to *D. pygargus*, but these taxa cannot be confused with *C. gnou*, since they are too small and because morphologically they resemble small hartebeest.

HORNCORES AND SKULL

Introduction

The skull is treated differently from the other skeletal elements, as it is a more complex morphological system. Since the focus of this study is on wildebeest evolution, the skull morphologies of *C. gnou* and *C. taurinus* are given in detail. The skull morphologies of *D. pygargus* and *A. buselaphus* are discussed in the literature (Vrba 1976, 1979; 1997; Gentry 1978, 1992; Gentry & Gentry 1978). The skull of *M. priscus* is described from available fossil

specimens. Although no complete skull of *M. priscus* has been found, it is possible to reconstruct the skull with some degree of confidence.

The skulls of *C. taurinus* and *C. gnou*

The morphological characters (char.) given below refer to Figure 29.

- The curvature of the horns in *C. gnou* is down and forward, while in *C. taurinus* they curve sideways and then upwards (char.1).
- Basal bosses are enlarged in *C. gnou* (char. 2).
- The horns are positioned more posteriorly than in *C. taurinus* and the sinuses of the frontals are enlarged.
- The forehead and nasals in *C. gnou* tend to be in a straight line or concave (char. 3), while in *C. taurinus* they are slightly convex.
- The face in *C. gnou* is shortened, due mainly to the shortened premaxillae, nasals and lacrimals.
- In *C. taurinus* the frontal suture remains unfused, even in old individuals, while in *C. gnou* it fuses early in life (char. 4).
- In *C. gnou* the orbits are enlarged and laterally projecting (char. 5). This character appears to be more pronounced in males.
- The ossa incisiva (premaxillae) are as wide in *C. gnou* as in *C. taurinus* in absolute terms, but proportionally wider in *C. gnou*, because of the difference in skull size (char. 6).
- The paracondylar processes are smaller in *C. gnou* (char. 7).
- The skull in *C. gnou* is dorso-ventrally flattened, as is reflected by the dorso-ventral reduction in the maxillary (char. 8) and a dorsal shift in the position of the articular facet for the mandible (char. 9). The flattening of the skull in *C. gnou* is accentuated by a greater angle of the brain case to the face.
- The fossa temporalis, is greater in *C. gnou* than in *C. taurinus* (char. 10). This character in *C. gnou* is associated with a number of features, such as a more anterior placement of the orbit, a reduced crista pterigoidea, narrower temporal processes of the zygomatic.

- The braincase in *C. gnou* is shorter than in *C. taurinus*, as reflected by the shorter distance between the tubercula muscularia (= “anterior tuberosities of the basioccipital”, *sensu* Gentry 1970b) and “posterior tuberosities”.
- The tubercula muscularia are sharply demarcated and point-like in *C. gnou*, but are inflated and more rounded in *C. taurinus*.
- The longitudinal valley between the tubercula muscularia is better defined in *C. taurinus*, while in *C. gnou* this area tends to be flattened.
- The bullae tympanicae are larger in *C. taurinus* than in *C. gnou*.

Discussion

Territoriality

A remarkable aspect of the morphology of the skull of *C. gnou* is the extent to which it is convergent with the skulls of caprines. These caprine-like features, listed in Table 14 (characters 1-8), represent derived morphologies and reflect the more fixed territorial behaviour of *C. gnou* in relation to *C. taurinus* (Chapter 3). The structural changes to the skull and horns can be classified into two broad categories - modifications to the posterior and basal parts of the skull, which give structural support to the skull to withstand the frequent head-to-head contact when territories are defended and the need to survey territories visually. Both categories are directly related to the maintenance of breeding territories. These adaptations will be considered in more detail.

Enlarged basal bosses, the forward curvature of the horns, enlarged frontals' sinuses and fused frontals' sutures are adaptations to absorb the impact of head butting and horn clashing when males defend territories. The early ontogenetic fusion of the mid-frontal suture in young black wildebeest has the effect of buttressing and strengthening the region of the forehead and the area in between the horn bases. This adaptation stabilises the cranium where the horn bases attach to the frontals. Fusion of the mid-frontal suture is seen also in *Ammotagus lervia*, in which it is a parallel adaptation to withstand the aggressive use of horns during head butting and horn clashing. Although *A. lervia* is considered to be a primitive sheep (Geist 1971), this character represents a derived state. Enlarged frontals' sinuses are also present in *A. lervia* and in North American bighorn sheep, where it serves as protection against head-to-head impacts

(Geist 1971). Although enlarged sinuses in the frontals is an alcelaphine characteristic (Gentry 1992), the extreme enlargement of the basal bosses and of the frontals' sinuses in black wildebeest are further examples of structural adaptations that parallel those in caprines.

In the black wildebeest skull there is a greater development of features associated with vision over those of smell. Compared to *C. taurinus* the orbits of *C. gnou* are enlarged and protruding in relative and absolute terms. It should be noted that orbital protrusion in *C. gnou* is relatively moderate and not as pronounced as in *Megalotragus kattwinkeli* in which it is a characteristic feature (Gentry & Gentry 1978; Vrba 1997). Orbital protrusion is commonly found in caprines (Gentry 1992) and its presence in *C. gnou*, *Megalotragus*, and *Aepyceros melampus* represents parallel adaptations and convergence on a caprine blueprint.

Another feature associated with the importance of vision in black wildebeest is the flattening of the forehead and nose profile and the reduction in the size of the face and snout in relation to the posterior parts of the skull (Table 1, features 5 & 6). These adaptations allow less space for the turbinalia and olfactory organs. This suggests reduced olfactory ability in black wildebeest compared to blue wildebeest. In the blue wildebeest the structures associated with smell are better developed as can be seen in the pronounced convex profile of the frontal and nasal parts of its skull.

A feature that may also reflect an emphasis on vision over other senses, besides that of smell, is the reduced size of the auditory bullae in *C. gnou*. All modern specimens of black wildebeest in the Florisbad comparative collections show small auditory bullae. Where enlarged auditory bullae are found in assumed black wildebeest specimens, they should be checked for being possible hybrids. This was found to be the case in the hybrid specimen NMB-F 6029. It has not been established in field observations whether black wildebeest has reduced capacity for hearing. However, on the basis of the size of the auditory bullae this can be predicted.

Table 14. Functional interpretation of the skull features of *C. gnou* in relation to *C. taurinus*.

Feature	Functional interpretation
1. Horns curve downwards and forward 2. Large basal bosses 3. Horns more posteriorly positioned with larger frontals' sinuses 4. Frontals' suture fused early in life	These features reflect aggressive behaviour, especially in defending territories. The fusion of the frontals' suture strengthens and stabilises the skull for head-to-head contact and increased use of horns to modify environment etc.
5. Forehead and nasals flat or concave 6. Face shortened 7. Proportionally enlarged braincase that is widened and flattened	The reduced face and nasals reflect a reduced reliance on smell in favour of vision in open environments. The braincase appears enlarged due to the reduction of the face, which is a by-product of the re-organisation of the skull base.
8. Enlarged and projecting orbits	Related to the need for vision in open environments, where reliance on smell is reduced.
8. Premaxillae as wide as in <i>C. taurinus</i> . 9. Relatively enlarged fossa temporalis	The width of the premaxilla and the large fossa temporalis in <i>C. gnou</i> reflect a feeding niche similar to <i>C. taurinus</i> .
10. Reduced paroccipital processes 11. Increased angle between the brain case and the face 12. Flattening of the longitudinal valley between the tubercula muscularia	The reduced paroccipital processes are related to the greater angle of brain case and face, and the general flattening in the skull of <i>C. gnou</i> . The flattened area between the tubercula muscularia is caprine-like, but may also be related to the re-arrangement of the posterior part of the skull.

The dorso-ventral flattening of the black wildebeest skull is reminiscent of the flattened skulls of aurochs and bison and is another example of the superficial resemblance of black wildebeest to bovines and caprines. Other examples are a lowered head position and the shortened ox-like morphology of the axis (see below). In cladistic analyses of the family Bovidae a large angle between brain case and face is sometimes referred to as a plesiomorphic condition (Vrba 1979). In the case of the black wildebeest the greater angle between the braincase and face clearly is not plesiomorphic, but is related to the backward shift of the horn cores and flattening of the posterior part of the skull, which accompanied the process of its evolution and is, therefore, a derived character. Since *C. gnou* appears to have evolved out of a *C. taurinus*-like ancestor (Gentry & Gentry 1978; Brink 1993), the greater basicranial flexion in the skulls of *C. gnou*, compared to modern *C. taurinus*, represents an evolutionary reversal.

Feeding niche

In spite of a reduction in skull size black wildebeest has a wide premaxilla, of which the width is statistically indistinguishable from that of *C. taurinus* (Figure 30). In ruminants the width of the premaxilla reflects the degree of selectivity in cropping plant leaf material so that more selective feeders will have narrower premaxillae, while more generalised feeders, such as grazers, will tend to have wider premaxillae (Bell 1969, quoted in Attwell 1977). The fact that the premaxilla is virtually equal in width in two species of extant wildebeest suggests that there is no significant distinction in their respective feeding niches. Other derived characters related to the specialised grazing niche of the black wildebeest, as suggested by the width of the premaxilla, are the large space for the m. temporalis and dental adaptations discussed below. The space for the temporal muscle of *C. gnou* is roughly equal to that of *C. taurinus*, but is proportionally larger, given the smaller body size of the former. Such functional adaptations are aimed at maintaining efficiency in mastication and support the suggestion that *C. gnou* maintained its position as a grazer of grass leaf material in the course of its evolution and that it has a feeding niche comparable to that of the blue wildebeest.

The specialised grazing niche of *C. gnou* may appear to be at odds with the known flexibility in its diet, since it has been demonstrated that extant black wildebeest can shift its diet to include a substantial proportion of karoid shrub, from 3% to 37%, when necessary (Van Zyl

1965; Vrahimis in press). However, this flexibility is not expressed in the morphology of black wildebeest skull, but rather it appears that in ecological terms the species strived to maintain its niche as a specialized grazer of fresh grass (Hofmann & Stewart 1972). This is consistent with the view that the role of black wildebeest in the Florisian grazing succession was generally similar to that of extant blue wildebeest in East African grasslands (Bell 1971; Brink & Lee-Thorp 1992).

The skull of *M. priscus*

Introduction

It is a commonly held view that all very large-bodied African alcelaphines belong to one genus, *Megalotragus* Van Hoepen 1932, and that the various fossil species of this genus are closely related (Gentry 1978; Gentry & Gentry 1978; Gentry *et al.* 1995; Vrba 1979, 1997). Furthermore, it is commonly accepted that *M. kattwinkeli*, an East African species, is ancestral to the southern African *M. priscus*, which includes two temporal forms, *M. priscus eucornutus* Van Hoepen 1932 and *M. priscus priscus* Broom 1909. However, it was noted recently that there are grounds for maintaining the specific distinction between *M. priscus* and *M. eucornutus* (Bender & Brink 1992). For the sake of clarity this taxonomic distinction is adopted in this study in order to describe the skull morphology of *M. priscus* and to discuss the phylogenetic relationships of *M. priscus*, *M. eucornutus* and *M. kattwinkeli*.

The suggestion of Gentry is followed to use Van Hoepen's genus, *Megalotragus*, for the species "*Bubalis*" *priscus* Broom 1909. The type specimen of *M. priscus* (Broom, 1909) is a cranial fragment with part of the left horn core preserved (SAM 1741). The specimen was recovered from the Modder River between Bloemfontein and Kimberley, an area rich in Quaternary fossil material. The newly discovered fossil-rich donga system on the farms Erfkroon and Orania (Churchill *et al.* 2000), which is in the vicinity of the find locality of the type specimen, has produced a virtually complete horn core pair and complete braincase of *M. priscus* (Figure 31). This specimen appears very similar to the type specimen, but is more complete, and serves as the basis for an expanded description and discussion of the skull of *M. priscus*. The Mahemspan material, Florisbad material and other specimens from the Free State Province complement the Erfkroon specimen.

The type of *Megalotragus eucornutus* Van Hoepen 1932 is from Cornelia-Uitzoek. So far, no material is known from other localities in southern Africa. The Sydney-on-Vaal specimen is evidently a primitive form of *M. priscus* and not *M. eucornutus* (*vide* Wells 1964a). In East Africa numerous Plio-Pleistocene localities have produced material of *M. kattwinkeli* (Vrba 1997), while a closely related Late Pleistocene taxon, *Rusingoryx atopocranium* Pickford & Thomas 1984, was discovered on Rusinga Island. The type of the Plio-Pleistocene East African giant alcelaphines was originally described on material from Olduvai as *Rhynotragus semiticus* Reck. This material was thought to have been destroyed in Munich during World War II. Consequently a later name given to giant alcelaphine material from Olduvai, *Alcelaphus kattwinkeli* Schwartz 1932, was adopted as the new type (Gentry *et al.* 1995). Because of the obviously close relationship between the East African and South African giant alcelaphines, these forms are thought to be congeneric (Gentry & Gentry 1978). Since Van Hoepen's name, *Megalotragus*, has taxonomic priority, the East African Plio-Pleistocene material and the Late Pleistocene material from Rusinga were referred to this genus, as *M. kattwinkeli* (Schwartz, 1932) and *M. atopocranium* respectively (Pickford & Thomas, 1984) (Gentry & Gentry 1978; Vrba 1997). The original type material of *Rhynotragus semiticus* was rediscovered in Munich recently and an application was made to the International Commission on Zoological Nomenclature to retain the generic name *Megalotragus* and the specific name *kattwinkeli* on the grounds of their common use in recent years (Gentry *et al.* 1995).

Originally the Florisbad giant alcelaphine material was named *Bubalis helmei* by Dreyer & Lyle (1931). Van Hoepen (1932b) described an isolated find of an incomplete horn core pair with intact pedicels from the farm Doornberg, on the Sand River near Kroonstad, Free State Province, as *Pelorocerus elegans*. The Mahemspan material was initially described as *Pelorocerus mirum* by Van Hoepen (1947). The Florisbad *B. helmei* was redescribed as *Lunatoceras mirum* (Van Hoepen, 1947), but later referred to *Alcelaphus helmei* by Cooke (1952) and again to *Pelorocerus helmei* by Hoffman (1953). Cooke (1964) referred the Florisbad material to both *Pelorocerus helmei* and to *Lunatoceras mirum*. Eventually Gentry & Gentry (1978) included the Florisbad material and all other Florisian giant alcelaphine materials in *M. priscus*. This was followed by Vrba (1979) and by Brink (1987).

Genus *MEGALOTRAGUS* Van Hoepen 1932

1932 *Megalotragus* Van Hoepen: 63

1932 *Pelorocerus* Van Hoepen: 65

1953 *Lunatoceras* Hoffman: 48

1965 *Xenocephalus* Leakey: 62

1984 *Rusingoryx* Pickford & Thomas: 445

Generic diagnosis: See Gentry & Gentry (1978) and Vrba (1997).

Type species *Megalotragus priscus* (Broom, 1909)

1909 *Bubalis priscus* Broom

1931 *Bubalis helmei* Dreyer & Lyle

1932 *Pelorocerus elegans* Van Hoepen

1947 *Pelorocerus mirum* Van Hoepen

1951 *Connochaetes grandis* Cooke & Wells

Specific diagnosis: An alcelaphine with large horns; horns are inserted towards the back of the head and on the same plane as the face; the basal parts of the horns overhang the braincase; the basal parts of the horns are dorso-ventrally compressed; the horn pedicels are fused and contain large sinuses, which extend into the basal parts of the horn cores (modified after Broom 1909b).

Horns and braincase of M. priscus

The Erfkroon specimen (Figure 31) consists of a braincase and horn core pair. The left horn core tip is not preserved. The horns are dorso-ventrally compressed near the bases, but become rounded towards the last third of its course. Horn pedicels are fused and overhang the occipital surface. Horns are bent down sharply and diverge with a mutual angle of around 150°. In mid-course they are sub-horizontal before they curve up and forward and there is clockwise torsion on the right. The horns have faint transverse ridges near the bases, an indication of nodes on the horn sheath. Near the base of the horn on the cranial surface there is a slight swelling, also present in the Florisbad specimen FLO 2274 (see below). The

frontals' suture is less extremely fused than in *C. gnou*. There is no postcornual fossa. The braincase is antero-posteriorly shortened in dorsal view. This is due mainly to the reduction in the parietals, which are visible only in lateral view so that the occipital makes contact with the frontal. The combined effect of the reduction in the braincase and the posterior projection of the fused pedicels is that the braincase appears hidden beneath the horn bases. The posterior shortening of the braincase appears to have caused the nuchal crest to have become inverted to form a concave structure in order to allow sufficient area for the attachment of the neck muscles. Although the specimen is somewhat damaged in this region, it appears that the nuchal furrow extends into a very pronounced supramastoid crest anteriorly, while posteriorly it links with the petrosal part of the temporal to form a very strong structure for neck muscle attachment. The occipital condyles are very wide. The basi-occipital is short, wide and flattened with large anterior tubercula muscularia. There is a relatively wide angle, around 140° , between the basi-occipital and the sphenoid. The bullae tympanicae are not preserved, but the spaces in which they were situated are preserved and it can be deduced that they were moderately large and rounded. The foramina ovalia are moderate in size. The braincase is not very high. From the remaining part of the frontal it is evident that the angle of the braincase to the face is small, approaching 90° . There is enough of the posterior margin of the orbits preserved to suggest that they would have been at least moderately projecting.

An almost complete set of horn cores from Florisbad, FLO 2274, is virtually identical to the Erfkroon specimen in terms of size, horn shape and horn curvature, but lacking the braincase.

In another Florisbad specimen, FLO 2273, the horns tend to be more sharply curved, they extend further backwards at their bases before curving sideways and forwards. The bases of the horn cores lack the protuberance on the cranial surface, as seen in the Erfkroon specimen and in FLO 2274. The mutual angle between the horn bases is somewhat smaller, while the specimen is generally more gracile. This specimen is believed to be female, while the Erfkroon specimen and FLO 2274 appear to be males.

In addition the horn core of *M. priscus* from the Ongers River near Britstown, central Karoo (Brink *et al.* 1995; Appendix D), has a base that is not antero-posteriorly extended and appears to be somewhat rounded in cross section. There is no basal protuberance and, while it is difficult to estimate the degree of pedicel fusion in this specimen, it appears to have had a

reasonably wide mutual angle between the horn cores. The specimen is very gracile and in size comparable to the specimen from Doornberg, C. 1711. Of all the specimens assigned to *M. priscus* the Doornberg specimen has the smallest mutual angle between the horn core bases, a condition that is considered to be plesiomorphic for *Megalotragus*. For this reason it is probable that the Doornberg specimen is geologically older than the other specimens of *M. priscus* under consideration here. The Ongers specimen resembles the Doornberg specimens in gracility, but has a wider mutual angle between the horn bases. The horn core bases of the Doornberg specimen are also less expanded antero-posteriorly than the Ongers River specimen and have no basal protuberances, which is also a plesiomorphic condition for *M. priscus*. Both these specimens are likely to be female.

In the type specimen of *P. mirum* (C. 2013) from Mahemspan the horn pedicels are not as extremely fused as in the Erfkroon and Florisbad specimens and the area of pedicel fusion is less elevated above the frontals. The mutual angle between the horn bases is reduced, resembling the Doornberg specimen. The basal parts of the horn cores are not as robust as in the large specimens from Erfkroon and Florisbad. The cranial sides of the horn bases are not preserved and it cannot be established whether there were protuberances. This specimen appears to be male.

In specimen C. 2537 from Mahemspan, a frontal fragment with the basal parts of the horn cores preserved, there is a marked posterior projection of the horn bases and the horn bases are much thinner. There is a reduced mutual angle between the horn core bases, a reduced degree of pedicel fusion, while the frontals' suture appears less fused than in the Erfkroon and Florisbad specimens. C. 2537 is also more gracile than Mahemspan specimen C. 2013 and very similar to the Doornberg specimen and, consequently, is likely to be female.

Mahemspan specimen C. 2246 has an equally narrow mutual angle between the horn core bases. In contrast with the Erfkroon specimen the nuchal crest forms a convex relief, and is not inverted, and it is not as wide as in the Erfkroon specimen. In the co-type of *P. mirum*, C. 2292, the horn base appears not to have a protuberance and it is not antero-posteriorly extended. The curvature of the horns is intermediate between the large forms from Florisbad and Erfkroon and the small specimens from Doornberg and Mahemspan. These specimens are probably female.

Discussion

Sexual dimorphism and geographic variability in the horn cores of *M. priscus*

Although there is considerable variability in size, the horn core specimens of *M. priscus* can be separated into categories of male and female. Females are those with more gracile horn cores, with less dorso-ventral extended basal parts and with slightly shorter horn curvature. Males, on the other hand, have generally larger horn cores, with dorso-ventral expanded horn bases and with a thickening, or protuberance on the dorsal side. Male horns tend to be more horizontally positioned, as seen in the Erfkroon specimen, and to be less sharply curved (Figure 32). This supports the observation that the mutual angle in *M. priscus* horn cores is a sexually dimorphic character with males tending to have more downward pointing horns than females and that a greater mutual angle is associated with greater robusticity (Brink *et al.* 1995).

The type specimen and the specimens from Florisbad and Erfkroon are considerably larger than those from Mahemspan, Doornberg and the Ongers River. In the Mahemspan specimens there is a lesser degree of horn pedicel fusion, the fused pedicels are less elevated above the frontals and the horn cores are generally more vertically inserted.

Previously it has been suggested that morphological variability in *M. priscus* horns represent a temporal cline in that horns become more downward and forward pointing in the course of geological time (Cooke 1974). This statement was based on the assumption that Mahemspan predates the Florisbad spring assemblage. However, it appears now that Mahemspan is of Last Glacial age (Chapter 5; Table 15) and that a more likely explanation for the variability is that it reflects geographic variability in populations. This is supported by the similarity of the Mahemspan and Doornberg horn cores and the likelihood that the Doornberg specimen is substantially older than the Mahemspan specimens.

Therefore, on the available fossil evidence *M. priscus* can be divided into two morphological entities, which may have represented two geographically distinct populations. The type specimen, the Erfkroon specimen and Florisbad specimens form one entity, which may have

represented a north-eastern population, while the Doornberg, Ongers River and Mahemspan specimens may have represented a south-western population. The varying geological ages of these specimens suggest that these geographic morphotypes may represent distinct and probably stable populations over time (Table 15; Figure 32).

Table 15. Geological age of fossil assemblages that include specimens of *M. priscus*.

Fossil assemblage	Estimated geological age (in years BP)
Florisbad spring	100 – 400 000 (ESR)
Erfkroon	100 – 200 000 (Luminescence & ESR)
Mahemspan	12 – 17 000 (ESR)
Ongers River	? Late Pleistocene
Doornberg	? Middle Pleistocene

The Doornberg specimen, C. 1711, named *P. elegans* by Van Hoepen (1947), is an early and very gracile female version of *M. priscus*. Similarly, the description of two forms of giant alcelaphine from Florisbad, *P. helmei* and *L. mirum*, reflects sexual dimorphism, with the former being male and the latter female. With more complete and dated material available for comparison it has been possible to develop an appreciation of the level of sexual dimorphism and geographic variability in *M. priscus*.

Sexual selection in *M. priscus*

There is some suggestion of sexual selection in horn evolution of *M. priscus*. Certain characters in *M. priscus* male horn cores are indications that social interactions may have been aggressive. For example there is a tendency for the horns of males to be more horizontally orientated and to be more robust with evidence of basal protuberances. These characters parallel those seen in *C. gnou* and can be interpreted that the behaviour of *M. priscus* was in some degree territorial.

The horn shape of *M. priscus* is remarkably like that of the aurochs, *Bos primigenius* (Boessneck 1985). This may be a further indication of aggressiveness in the behaviour of *M. priscus* and of parallel evolution in the family Bovidae.

The lower jaw of *M. priscus*

There are numerous lower teeth and several *M. priscus* lower jaw fragments from Mahemspan, including a complete lower jaw, C. 2472 (Figure 33), which was referred to by Hoffman (1953). From Florisbad there are several teeth, but only a ramus fragment, C. 2900.

The lower jaw of *M. priscus* is unusually elongated compared to other alcelaphines. The corpus of the lower jaw is extended both anteriorly and posteriorly. Anteriorly, the diastema is enlarged to balance the increase in the posterior extension of the ramus, while the angle between the ramus and the corpus is widened to around 135°. These features are adaptations to allow the mandible to fit the extremely elongated skull. It appears that there is a structural balance between the elongation of the anterior and posterior parts of the lower jaw.

The closest parallel to this extreme morphology of the lower jaw can be found in the hartebeest and the Barbary sheep, *Ammotragus lervia*. In both the latter species there is some degree of fusion of the horn pedicels and the horn bases are positioned posteriorly on the skull, which is reflected in the widened angle between the ramus and corpus of the mandible. In *C. taurinus* the lower jaw is also somewhat elongated, but less so than in the hartebeest, while the angle of lower jaw is not as wide. In *C. gnou* and blesbok the ramus is sub-vertical and the corpus relatively short and stout (Figure 33).

Discussion

*Reconstructing the skull of *M. priscus**

The reconstruction of the skull of *M. priscus* is based on the horn core pair and braincase from Erfkroon, the upper jaw fragment (C. 1804) and the lower jaw (C. 2472), both from Mahemspan (Figure 34). Because these specimens are not from the same individual and because the upper jaw fragment and the horn cores and braincase do not conjoin, the proportions of the skull and the relative position of the components were estimated on the basis of the complete lower jaw from Mahemspan. Because it is possible to estimate with

reasonable certainty the position of the jaw articulation on the Erfkroon braincase, the Mahemspan lower jaw allows the estimation of the length of the face and the angle of the braincase to the face. Although the Mahemspan materials represent a different geographic population from the Erfkroon and Florisbad materials, this will result in only marginal distortion to the skull proportions, since the dentitions from Florisbad and Mahemspan seem to be almost identical in morphology and size (see below). Because the Erfkroon specimen is used as the basis for the reconstruction, it represents the geographic population to which the type specimen and the Florisbad spring specimens belonged. At present nasal bones of *M. priscus* are not known in the fossil record and this reconstruction suggests only moderately inflated nasals. The nasals represent the most speculative aspect of the reconstruction. The assumption is that the breeding behaviour of *M. priscus* would have resembled *C. gnou* to some degree, given the forward and downward torsion of the horns and the evidence for orbital protrusion. Figure 35 gives a lateral view of the reconstructed skull of *M. priscus*.

The skull of *M. priscus* is characterised by extreme elongation and by the fusion and posterior extension of the horn pedicels, reminiscent of *A. buselaphus*. In the populations represented by the Erfkroon and Florisbad spring specimens fusion and posterior extension of the pedicels are more advanced, very much like the advanced nature of these characters in *A. buselaphus caama* and *A. buselaphus lelwel* (Kingdon 1997). However, the horn curvature in *M. priscus* is clockwise and downward, while the braincase is wide rather than narrow. This is unlike *A. buselaphus* and more similar to *Connochaetes* spp.

Phylogenetic relationships in the genus Megalotragus

There are obvious similarities between *M. priscus* and *M. kattwinkeli* and a number of shared derived characters that unite the two species. These are elongated skulls, horns with transverse ridges near the base, horns inserted far behind the orbits so that there is a tendency for the horn bases to overhang the occipital surface, some degree of pedicel fusion, projecting orbits, and an occipital surface that faces mainly backwards with a median vertical ridge (*vide* Vrba 1997). However, there are some derived characters in *M. priscus*, which are not shared by *M. kattwinkeli*, but there are also some characters in which *M. priscus* is more plesiomorphic. Uniquely derived characters in *M. priscus* in relation to *M. kattwinkeli* are the extreme state of fusion of the pedicels, very large horn size, the almost horizontal angle at which the horns curve outwards from the skull before they curve forward (more extreme in the Erfkroon and

Florisbad specimens), the fact that the fused pedicels of the horn cores overhang the occipital and evidently the very large bullae tympanicae. In the past, shared derived characters and the uniquely derived characters of *M. priscus* have been considered as ground for suggesting an ancestor-descendant relationship between the two species (Gentry & Gentry 1978; Vrba 1997). The plesiomorphic characters of *M. priscus* in relation to *M. kattwinkeli*, include a less reduced premolar row, in which the P³ and possibly the P² were still present, and a lower skull. In *M. kattwinkeli* it appears that only the P⁴ was present (Gentry & Gentry 1978). In addition, the horns of *M. priscus* are dorso-ventrally flattened near the bases and not in mid-course. *M. kattwinkeli* is in this respect more typical of the genus *Connochaetes* and may represent a plesiomorphic condition for *Megalotragus*. This mosaic of characters suggests that *M. kattwinkeli* was probably not the ancestor of *M. priscus*, in spite of being closely related.

The fact that *M. kattwinkeli* occurs in the fossil record until the end of the Early Pleistocene, and possibly until the Late Pleistocene as *M. atopocranium*, overlapping in time with *M. priscus*, further increases the uncertainty of the suggested ancestor-descendant relationship between *M. kattwinkeli* and *M. priscus*. *M. priscus* is an entirely southern African species, which became extinct early in the early Holocene (Klein 1984). Given the absence of fossil evidence for *M. priscus* in areas outside of southern Africa, it was probably a southern African endemic (Chapter 6).

The ancestor-descendant relationship between *M. eucornutus* and *M. priscus*, suggested by Gentry & Gentry (1978) and Vrba (1997), can be evaluated on the available evidence. The close positioned horn bases, the orientation of the horn bases, the clockwise curvature and the lesser degree of fusion of the pedicels accord with *M. eucornutus* being an ancestor of *M. priscus*. However, the absence of any indication of nodes on the horns of *M. eucornutus* is unexpected. Nodes are not found on the horns of extinct and extant members of the genus *Connochaetes*, but they are common in the genera *Aepyceros*, *Beatragus*, *Alcelaphus* and *Damaliscus*. Nodes on horns indicate a plesiomorphic condition in alcelaphines and their presence on the horns of *M. priscus* would have to be interpreted as an evolutionary reversal in order to accommodate *M. eucornutus* as the ancestor of *M. priscus*. The paucity of fossil material of *M. eucornutus* hampers proper evaluation. Apart from the horn core specimens and a few dental and postcranial elements from Cornelia-Uitzoek, very little of the body of *M. eucornutus* is known. Other than Cornelia-Uitzoek and Cornelia-Mara the only fossil locality

in the interior of southern Africa that may have produced material of *M. euicornutus* is Gladysvale (Lacruz *et al.* 2002), but so far no horn material of *M. euicornutus* has been found. It is noteworthy that at Elandsfontein, which has produced a substantial collection of Cornelian-aged large mammals, *M. priscus* and not *M. euicornutus* is represented. Therefore although the question is not finally resolved, the balance of the evidence suggests that it is unlikely that *M. euicornutus* was ancestral to *M. priscus*. For this reason the giant alcelaphine material from Cornelia-Uitzoek is referred to the species *M. euicornutus*, pending the recovery of more complete fossil material.

Behavioural implications of the skull morphology of M. priscus

Kingdon (1982) ascribes the increased profile of the head of the hartebeest to the importance of head signals in these animals, usually executed in slow movements. This contrasts with blue wildebeest, in which a very small proportion of the horns is visible in profile, but which has very energetic body and head movements during intraspecific encounters. Kingdon further notes that such behaviour in wildebeest may be associated with high densities when large herds form. This is in contrast to the hartebeest and the genus *Damaliscus*. Hartebeest do not congregate in as large numbers as blue wildebeest. They tend to occupy ecotonal habitats rather than the more homogeneous short grass plains, favoured by *C. taurinus* in East Africa and *C. gnou* in southern Africa. The niche of the hartebeest as a roughage grazer is different from the short fresh grass grazer niche of *C. taurinus* (Hofmann & Stewart 1972) and of *C. gnou* (R.C. Bigalke pers. com.; Brink & Lee-Thorp 1992). One may assume that in the course of geological time the lateral profile of the skull of *M. priscus* has become less conspicuous with the more forward position of the horns, but that in frontal view it has become more conspicuous with the extreme elongation of the face and forehead. This may suggest some parallel in behaviour with *A. buselaphus*. However, the forward position and clockwise curvature of the horns resemble that of *C. gnou* and the wild ancestor of cattle, *Bos primigenius*. This accords with the evidence for sexual dimorphism in the horns of *M. priscus* and suggests more aggressive behaviour than seen in for example *C. taurinus*. The picture that emerges is of a large-bodied alcelaphine showing some degree of territorial behaviour where large herds formed and occupying a highly specialised grazing niche in the open grasslands of central southern Africa (*vide* Brink & Lee-Thorp 1992).

DENTITION

Upper dentition

Primitive alcelaphines

In primitive alcelaphines, such as *Damalacra* spp. from Langebaanweg (Gentry 1980), molars tend to resemble caprines and, to some extent, antilopines. There are features evident in the living impala, *A. melampus* (Gentry 1992; Vrba 1997) and in the living Indian black buck, *Antilope cervicapra* (personal observation), which can be considered to be very close to basal Alcelaphini. Based on the dentitions of the impala and on the descriptions of early alcelaphines from Langebaanweg (Gentry 1980), primitive alcelaphine features of the upper dentition are illustrated in Figure 36 and are listed below:

- Lobes of molars are pointed and simple in outline (Figure 36, char. 1)
- Mesial lobes tend to be mesio-distally compressed and bucco-lingually deeper than distal lobes (Figure 36, char. 2)
- There tend to be ridges on the distal lobes of molars, which are equivalent to the goat folds in lower molars. These ridges are termed “upper goat folds” for the sake of convenience (Figure 36, char. 3).
- A pronounced and distally projecting metastyle in M³
- Absence of rib development on the buccal walls of upper molars (Figure 36, char. 4)
- Styles tend to be prominent (Figure 36, char. 5)
- External enamel surfaces tend to be smooth and not rugose
- Central cavities tend to be simple in outline (Figure 36, char. 6)
- The premolar row is moderately reduced
- There is almost no cementum cover on the tooth crowns.

Advanced alcelaphines

The morphological characters of the upper dentitions of modern alcelaphines and of *M. priscus* are illustrated in Figures 37 & 38 and listed below.

- The second and third upper premolars are reduced in *Connochaetes* spp. and in *M. priscus*, but not in the hartebeest and the blesbok. In *C. gnou* and in *M. priscus* this reduction is more pronounced than in *C. taurinus* (Figure 37).
- The upper and lower molars of the hartebeest and blesbok usually have more rugose enamel than is the case in *Connochaetes* spp. and in *M. priscus*.
- All alcelaphines under consideration have rounded lingual lobes, but in the hartebeest and the blesbok the lingual enamel folds tend to be constricted, a phenomenon known as “pinching” (Fig. 37, char. 1).
- In hartebeest and blesbok the styles and the ribs in between them are more pronounced than in *Connochaetes* spp. and *M. priscus* (Figure 37, char. 2). Ribs are more reduced in *C. gnou* than in *C. taurinus* and *M. priscus*, which tend to be more variable.
- In *Connochaetes* spp. and *M. priscus* the metastyle of the M³ tends to project distally (Fig.37, char. 3; Figure 38, char. 1) and has a simple outline. In *A. buselaphus* and *D. pygargus* the metastyle curves mesially, or inwards towards the base of the M³ and tends to have a longitudinal furrow at the base (Figure 38, char 2). Although there is variability in this regard in *C. taurinus*, where it sometimes resembles *A. buselaphus* and *D. pygargus*, it tends to be like *C. gnou* and *M. priscus*.
- It appears that root formation in second and third upper molars of *Connochaetes* and *M. priscus* is postponed until after the teeth had become functional (Figure 38), while in hartebeest and in blesbok roots close earlier (*vide* Watson *et al.* 1991).
- In the hartebeest and blesbok there tends to be a greater degree of cementum cover of the roots and crowns of molars than in *Connochaetes* spp. and *M. priscus*. This feature is variably expressed and should be seen as a tendency, and not an absolute character.

Discussion

As diagnostic characters rugosity of enamel and dental constriction, or “pinching”, should be treated with care, because they are not constant characters and because there is considerable variability within species. However, they can be useful in conjunction with other characters and if viewed as an expression of a tendency. In *A. buselaphus* and *D. pygargus* enamel surfaces are usually very rugose and lobes tend to be constricted. These features are not usually a characteristic of *Connochaetes* spp., but *C. taurinus* can occasionally have quite

rugose enamel. Generally *C. gnou* and *M. priscus* have smooth enamel surfaces and rounded lobes. Given that early alcelaphines were morphologically very similar to caprines and given the fact that the molars of caprines have rounded, unconstricted lobes with smooth enamel surfaces, it can be assumed that constriction and rugosity probably appeared later in the evolutionary history of alcelaphines. If it is considered that *C. gnou* is a descendant species of *C. taurinus* (vide Gentry & Gentry 1978; Brink 1993) and that there is an evolutionary tendency in the genera *Connochaetes* and *Megalotragus* towards more simplified enamel folds and smoother enamel surfaces, then smooth enamel surfaces and unconstricted lobes in *M. priscus* and *C. gnou* re-appeared independently and represents evolutionary reversals.

In *Connochaetes* spp. and *M. priscus* the distally extended metastyle of the M^3 , the tendency for a simpler outline of the metastyle and the fact that it does not curve mesially towards the base of the crown distinguish these species from *Alcelaphus* and *Damaliscus*. The mesial curvature towards the base of the M^3 in the latter species is very characteristic and appears to be also present in *Parmularius* and *Beatragus*. In *Connochaetes* spp. and *M. priscus* the distally extended metastyle in the M^3 is the structural equivalent of the distally projecting base of the M_3 crown (see below). This is probably an adaptation to prolong the functional life of the tooth towards the end of the life span of an individual, when the M^1 has become worn down to the point of not being functional any more. It is also a caprine feature, which has re-appeared in the alcelaphines and, therefore, represents an evolutionary reversal. This is another example of genetically embedded morphology that has re-appeared in the process of evolution, as in the case of the re-appearance of smooth enamel surfaces and unconstricted molars. However, within the context of the Alcelaphini considered here these characters are derived and probably reflect the more specialised grazing niche of the genus *Connochaetes* and *M. priscus* as opposed to *A. buselaphus* and *D. pygargus*.

The early closure of roots in *D. pygargus* is illustrated in Watson *et al.* (1991). A feature, which is possibly linked to the delay in root closure, is the tendency in the M^3 of *C. gnou* to have two roots, instead of three. It seems that the roots of the metacone, hypocone and the protocone merge into one, with only the root of the paracone remaining separate. Delayed root closure in molars is a response to increased hypsodonty. It reflects the more specialized grazing niches of wildebeest and *M. priscus*.

Lower dentition

Primitive alcelaphines

The primitive condition of the alcelaphine lower dentitions is illustrated in Figure 39A. In this figure illustrations provided by Gentry (1980) are compared with the living impala, *A. melampus*. The primitive alcelaphine characters are:

- The premolar row tends to become reduced in advanced forms, so that primitive alcelaphines will tend to have relatively longer premolar rows, as seen in the lower jaws of *Kubanotragus* (= *Oyoceras*) *tanyceras* from Fort Ternan (Gentry 1970b).
- Lobes tend to be pointed (Figure 39A, char. 1).
- The outline of the enamel surrounding the central cavities is simple and buccolingually narrow (Figure 39A, char. 2).
- The lingual walls of the lower molars tend not to be indented (Figure 39A, char. 3).
- A goat fold may be present (Figure 39A, char. 4).
- The lobes of the lower molars are not pinched, but have a simple outline (Figure 39A, char. 5).
- The external enamel walls of the lower molars are not rugose.

Advanced alcelaphines

The diagnostic characters of extant Alcelaphini and *M. priscus*, which are listed below, are illustrated in Figure 39.

- The premolar row is shortened in *Connochaetes* spp. and *M. priscus*, but less so in *A. buselaphus* and *D. pygargus*. In *M. priscus* and *C. gnou* the P₂ is almost always absent, it is usually absent in *C. taurinus*, while in *A. buselaphus* and *D. pygargus* it is usually present. Gentry and Gentry (1978) quote a ratio of around two-thirds of *D. pygargus* specimens with P₂ in the collections of the Iziko South African Museum. Marean and Gifford-Gonzalez (1991) found that 64% of *D. pygargus* in their study sample (n = 25, probably Iziko specimens) showed the presence of the P₂. In the Florisbad comparative collection 82 % of *D. pygargus* (n = 11), 83 % of *A. buselaphus* (n = 6), 9% of *C. taurinus* (n = 11) and 6% of *C. gnou* (n = 17) specimens retain a P₂ on one or the other side of the lower jaw.

- *C. gnou* and *M. priscus* have proportionally shorter premolar rows, than *C. taurinus* and are more derived in this respect. This observation was explored further by plotting premolar row lengths against complete tooth row lengths (Figure 40a) and by comparing the ratio of tooth row length over premolar row length (Figure 40b). In terms of premolar row shortening *M. priscus* has the most extreme morphology, *C. gnou* is somewhat less extreme and both are clearly more derived than *C. taurinus*, *A. buselaphus* and *D. pygargus*. The latter is somewhat more specialised than *A. buselaphus*, as mentioned above.
- As in the upper molars, the roots of the lower molars in *Connochaetes* spp. and *M. priscus* close later than in hartebeest and blesbok, which is a reflection of the greater hypsodonty in the former.
- The base of the M₃ is distally extended in wildebeest and *M. priscus*, while it tends not to be the case in hartebeest and blesbok. As mentioned for the M³, this feature has the effect of extending the functional life of the dentition in the case of a posterior shift in chewing force.
- The lingual walls of the lower molars are deeply indented in all alcelaphine species under consideration (Figure 39. char. 1).
- Buccal lobes of the lower molars are rounded in all species (Figure 39, char. 2), as in the upper molars.
- In *A. buselaphus* and *D. pygargus* the lobes tend to be pinched (Figure 39, char. 3), as in the case of the lingual lobes of the upper molars. The degree in which molars are pinched is variable. Pinching can occur quite often in *C. taurinus* and occasionally in *C. gnou*.
- As in the upper molars, there is a tendency for greater cementum cover in the dentitions of *A. buselaphus* and *D. pygargus* than in those of *Connochaetes* spp. and *M. priscus*.
- The lower teeth of *A. buselaphus* and *D. pygargus* tend to be more rugose than in *Connochaetes* spp. and *M. priscus*.
- Central cavities tend to be more complicated in *A. buselaphus* and *D. pygargus* than in the other species under consideration (Figure 39, char. 4).

Discussion

Shortening of the premolar row evolved independently in various taxa, as can be seen in *M. priscus*, *C. gnou* and *A. marsupialis*, and should not be taken in isolation as indicative of a close phylogenetic relationship. Other similar trends in alcelaphine dentitions, which are functionally related to premolar row shortening in certain cases, are increasing hypsodonty and the tendency for the occlusal surface of the upper and lower M3 to lengthen at the cost of the occlusal length of the M1. These trends coincide with a shift in the focus of mastication towards the back of the toothrow, which may be considered as a common trend in alcelaphines, although variably expressed and often appearing in parallel in the various lineages. However, the primitive features, as seen in *Aepyceros melampus*, can all be seen in the early alcelaphines from Fort Ternan and Langebaanweg, except for goat folds. Although our knowledge of early alcelaphine evolution and variability is limited at the present, one may speculate that there would have been forms of early alcelaphines where the goat fold was consistently present in the lower molars.

Discussion of upper and lower dentitions

Morphological groups as reflected by dental characters

The dentitions of the alcelaphine species can be divided into two morphological groups, (1) *C. gnou*, *C. taurinus* and *M. priscus* and (2) *A. buselaphus* and *D. pygargus*. In the latter group the upper and lower molars tend to have more rugose enamel, the lobes tend to be pinched, central cavities are more complicated and the styles and ribs in the upper molars are more pronounced, which results in a more complicated occlusal enamel pattern. There is a tendency for greater cementum cover on the crowns of *A. buselaphus* and *D. pygargus* relative to *Connochaetes* spp. and *M. priscus*, while the bases of the tooth crowns of the upper and lower third molars of *Connochaetes* spp. and *M. priscus* are distally extended. The distal expansion of the upper third molars is more extremely developed in *M. priscus* and *C. gnou* than in *C. taurinus*. The combination of the distal expansion and the reduced mesostyle of the third upper molar produce a very characteristic wildebeest-like morphology, which is best expressed in *C. gnou* and *M. priscus*, but with some variability in the latter.

C. gnou and *M. priscus* have a more derived overall dental morphology than *C. taurinus*. The less derived condition of *C. taurinus* within the wildebeest morphological group accords with

the fossil evidence of a long period of evolutionary stability in *C. taurinus* (Gentry & Gentry 1978; Geraads 1981). In contrast, *C. gnou* is known to have undergone morphological shifts throughout the Middle and Late Pleistocene (Brink 1993; Brink *et al.* 1995; Chapter 9). The fossil record of *M. priscus* on the other hand is not sufficiently complete to allow an assessment of the tempo and scale of morphological change.

The specialised nature of *C. gnou* is evident from a number of characters. These features are: the greater hypsodonty of *C. gnou*, a reduction in premolar row length versus tooth row length (Figure 40), a reduction in the height of the jaw articulation, the tendency for root fusion in the M³, and the pronounced distal flare of the base of the crown of the M₃. All these characters indicate a shift in focus of mastication towards the distal end of the tooth row. This can be further elucidated by considering aspects of the skull morphology of *C. gnou* versus *C. taurinus*.

Dental specialisation in C. gnou as a response to increased territoriality

The re-organisation of the posterior part of the skull in *C. gnou* relative to *C. taurinus* reflects its more extreme territorial breeding behaviour. This involved the posterior shift of the horns and the enlargement of the basal parts of the horns, which coincided with the dorso-ventral flattening of the skull. This flattening increased the angle between the brain case and the face, which brought the position of the jaw articulation closer to the occlusal plane. This process had two functional responses. The first was a reduction in length of the paroccipital processes. This can be explained by the fact that the length of the paroccipital processes in ruminants seems to be correlated to the elevation of the jaw articulation above the occlusal plane and to the position of the hyoid bones, which need to be aligned with the occlusal plane (W. Hylander pers. com.). Therefore, because the length of the paroccipitals will be decided by the height of the jaw articulation above the level of the occlusal plane (Figure 41), the paracondylar processes are reduced in response to the lowering of the jaw articulation.

The other functional response to the lowering of the jaw articulation was a posterior shift in occlusal pressure during mastication. The lowering of the insertions of the main chewing muscles in relation to the occlusal plane caused the gradient of masticatory force to be steepened distally. The greater occlusal stress on the distal teeth has the effect of reducing the

functionality of the teeth more mesially positioned, and the accompanying loss of the P₂ and a reduction in size of the P₃ and P₄ (Figure 41). Therefore, in the black wildebeest the reduction of the premolar row was not a response to a more specialised grazing niche (*vide* Figure 30), but rather to a distal shift in occlusal pressure due to the re-organisation of the posterior part of skull, which can be associated with its more specialised territorial breeding behaviour (Chapter 3). There is a parallel situation in the jaw mechanics of *M. priscus*, where the lowering of the jaw articulation is even more extreme and as a consequence the reduction of the premolar row is more pronounced (Figure 40B).

If the greater reduction of the premolar row in black wildebeest reflects the fact that it is functionally, but not ecologically, more specialised than blue wildebeest, then premolar row reduction should not correlate positively with other morphologies that indicate a specialised grazing niche, such as hypsodonty. In a test to see whether the proportional shortening of the premolar row was positively correlated with hypsodonty, it was found that in *Connochaetes* spp. and *M. priscus* mandibular depth, as a measure of hypsodonty, does not increase with a proportional increase in toothrow length/premolar row length (Figure 42A). Therefore, shortened premolar rows may not necessarily imply hypsodonty. This point is well illustrated by the marked reduction in the premolar row of *A. marsupialis*, which is well known to be a mixed feeder and not a grazer (Bigalke 1972; Liversidge 1972).

Figure 42 also suggests that there is a functional limit to ramus depth of the lower jaw in ruminants. Therefore, mandibular depth does not seem to increase beyond a certain stage, even if the molars become more hypsodont. This is made possible by the postponement of root formation and root closure in molars, which allows the mandible to accommodate molars of which the real crown height exceeds the depth of the mandible. A parallel to this is seen in extant and extinct warthogs, where the third molar has become so deep-crowned that the roots tend to stay open for some time after the crown has come into wear. In grazing suids this extreme form of hypsodonty is coupled to a mesio-distal expansion of the tooth crown so that the third molar dominates the toothrow in mature and old individuals (Cooke 1974). A similar adaptive response is seen in the third molars of proboscideans. The posterior expansion of the upper and lower third molars in wildebeest and *M. priscus* is likely to be a parallel phenomenon. Therefore, the delayed root formation in wildebeest, but in particular *C. gnou* and *M. priscus*, is a by-product of increased hypsodonty and reflects the more specialised

nature of the dentitions, as opposed to those of the hartebeest and blesbok, where roots close earlier in life.

Flexibility in the feeding behaviour of A. buselaphus and D. pygargus

If hartebeest and blesbok have structurally less specialised dental adaptations for grazing than *Connochaetes* spp. and *M. priscus*, it is surprising that the occlusal enamel patterns of *A. buselaphus* and *D. pygargus* are consistently more complex than *C. taurinus*, *C. gnou* and *M. priscus*. Intuitively one would associate a more complex occlusal enamel pattern with greater resistance to dental attrition and a more specialised coarse grass diet. In this respect the ecological classification of bovids based on stomach structure is instructive as it suggests that hartebeest is indeed a grazer of coarse grass stem material (Hofmann & Stewart 1972). However, in spite of this the geographic distribution of *A. buselaphus* suggests that it is less specialised than wildebeest, as it has tolerance for a greater variety of habitats, often preferring ecotone environments (Kingdon 1982; Skinner & Smithers 1990). The less specialised adaptation in *A. buselaphus* is also reflected in its previous pan-African distribution, which extended into the Middle East (Uerpmann 1987). The fact that both wildebeest species are dependent on short grass habitat, which is often facilitated by specialised bulk feeders such as equids and large-bodied ruminants (Bell 1971), reflects the more restricted adaptation of the two wildebeest species as fresh grass grazers and accords with their structurally more specialised dentitions. The apparently anomalous complexity of occlusal enamel patterns in *A. buselaphus* molars may be a plesiomorphic feature that is genetically fixed in *A. buselaphus* and *D. pygargus*, reflecting an earlier specialisation.

Parallelism between C. gnou and M. priscus towards a caprine blueprint

The parallelism between wildebeest-like alcelaphines and caprines is striking. The lack of pinching and the tendency for occlusal simplicity in the molars of *Connochaetes* spp. and *M. priscus* are noteworthy, since these characters represent a departure from the morphology represented by the genera *Alcelaphus* and *Damaliscus*. Extant alcelaphines do not have the caprine “goat fold”, which is typical of almost all modern and fossil caprines and probably certain primitive alcelaphines. The caprine-like morphology in wildebeest-like alcelaphines may be genetically deeply embedded (*sensu* Turnbull 2002), harking back into the evolutionary past to alcelaphine-caprine connections (Gentry 1992, 2000). It is apparent that

C. gnou and *M. priscus* have evolved a more extreme form of caprine-like morphology than *C. taurinus*. Given that *C. gnou* is probably the descendant species of *C. taurinus* and is more distantly related to *M. priscus*, the caprine-like morphologies probably evolved independently in *C. gnou* and *M. priscus*. This is an example of parallel evolution (*vide* Mayr 2001).

POSTCRANIUM

Introduction

Except where otherwise indicated, the morphological illustrations given in the figures follow a fixed taxonomic sequence, which is *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E).

Axis

Description

Figures 43 and 44 give ventral and lateral views of the axes of Alcelaphini.

- The axes of modern black wildebeest are short and compact, approaching the shape of axes of caprines and bovines, while blue wildebeest axes tend to be more elongated and less wide across the corpus of the vertebra. This reflects the longer neck and proportionally lighter horns in blue wildebeest. From the plots of length and corpus width of axes it is evident that *C. gnou* and *M. priscus* have proportionally more robust and compact axes than *C. taurinus* (Figure 45), while the axes of *A. buselaphus* and *D. pygargus* are even more slender. The metrical values suggest that in general proportions *M. priscus* had a neck that was as stout as that of *C. gnou*.
- In *C. gnou* on the ventral side of the axis there is a lesser degree of hollowing of the surface on either side of the crista ventralis than in *C. taurinus* and *M. priscus* (Figure 43, char. 1; Figure 44, char. 1).
- A reflection of this is the lack of prominence of the crista ventralis in *Connochaetes* spp., in which it tends to be rounded. In *A. buselaphus* and *D. pygargus* it is sharply offset from the adjacent ventral surface (Figure 43, char. 2; Figure 44, char. 2). This seems to be

more pronounced in females, but can be a useful feature for distinguishing between wildebeest-like as opposed to the hartebeest-like Alcelaphini.

- The transverse processes in males are generally larger, straighter and more caudally extended than in females. In female *A. buselaphus* and *D. pygargus* there is a tendency for the transverse processes to be slightly recurved, which is also evident in some females of *C. taurinus*. In very large males of *A. buselaphus* the transverse processes are longer, more robust and approach the shape of male *C. taurinus* (Figure 43, char. 3). In male and female *C. gnou* the transverse processes are more robust than in *A. buselaphus* and *C. taurinus*.
- The axis in *C. taurinus* has more a pronounced “waist” than in *C. gnou* (Figure 43, char. 4), and in this respect *C. taurinus* resembles *A. buselaphus*.
- The size and shape of the processus spinosus is a sexually dimorphic feature – in males it tends to be higher and cranio-caudally longer. It provides the most obvious differentiation between *Connochaetes* spp. and *M. priscus*, on the one hand, and *A. buselaphus* and *D. pygargus*, on the other. In *Connochaetes* spp. it is higher and cranio-caudally shorter than in *A. buselaphus* and *D. pygargus* (Figure 44, char. 3).
- In *C. gnou* the processus spinosus is higher and shorter and the caudal articulation facets are more upright and raised than in *C. taurinus*. Although there are no *M. priscus* specimens in which complete processus spinosi are preserved, it seems that *M. priscus* was more like *C. gnou* than *C. taurinus* (Figure 44, char. 4). In a well-preserved specimen of *M. priscus* from Mahemspan, which seems to have been a male on account of its robust corpus, the more upright angle of the caudal articulation facets is reminiscent of *C. gnou*. (Figure 44).
- The ventral rim of the cranial articular surface of the axis is thinner in females than in males and it tends to be thinner generally in hartebeest-like than in the wildebeest-like alcelaphines. *C. gnou* and *M. priscus* have the most extreme morphology in this regard, where the extended ventral rim may form a flattened surface (Figure 43, char. 5).
- The foramen laterale is bigger in *A. buselaphus* and *D. pygargus* than in *Connochaetes* spp. (Figure 44, char. 5).
- The axes of *Connochaetes* spp. and *M. priscus* have wider cranial articular surfaces than those of *A. buselaphus* (Figure 43; Figure 46, char. 1). A plot of width of the cranial articular surface (BFcr) against length of the corpus and the dens (LCde) (Figure 47) confirms this distinction.

Discussion

In bovids the length of the axis reflects the overall size of the neck, while the smallest width of the body of the axis is a function of stoutness of the neck. Although these dimensions are related to function, *i.e.* the need for bearing the weight of the neck and horns, there appears to be a difference between *Connochaetes* spp. and *M. priscus* relative to *A. buselaphus* and *D. pygargus*. Even in extremely large male hartebeest (Figure 43B) the slenderness of the corpus is evident, even though the transverse processes are much enlarged to accommodate the neck muscles, which is a response to the increased weight of the neck. Therefore, constriction of the corpus and extension of the transverse processes are most pronounced in *A. buselaphus* and *D. pygargus*. This gives a very distinctive appearance to the axis in these taxa and they are different in this respect from wildebeest-like alcelaphines. These morphological characters in *A. buselaphus* and *D. pygargus* can be taken as plesiomorphic for alcelaphines, as they resemble an antilopine pattern. The axes of *C. gnou* and *M. priscus* are more derived than *C. taurinus* and convergent on the shape seen in caprines and bovines.

In the extant hartebeest the head is carried in a more upright position than in wildebeest. The wildebeest head hangs in an ox-like position in relation to the body. The axes of *M. priscus*, *Connochaetes* spp., bovines and caprines are of similar proportions (*vide* Nickel *et al.* 1992; Figures 43 & 44). Although a hartebeest-like neck position has been suggested for *M. priscus* (Hoffman 1953), on this evidence it appears that the neck was less upright and similar to the more horizontal position of the neck of extant wildebeest.

Humerus

Description

Figures 48 and 49 give cranial and lateral views respectively of the humeri of extant Alcelaphini and *M. priscus*.

- The humeri in the hartebeest and blesbok are more slender than those in the wildebeest and *M. priscus*. The female specimen in Figures 48 and 49 illustrates the extreme slenderness of the humerus of *A. buselaphus*. The humerus of *C. taurinus* is less slender

than that of *A. buselaphus*, but slightly more slender than that of *C. gnou* and *M. priscus*. A plot of distal breadth over length illustrates these differences (Figure 50A).

- The shape of the tuberculum maius is very distinctive in the Alcelaphini. Although generally the cranial (Figure 49, char. 1) and caudal (Figure 49, char. 2) parts of the tuberculum maius tend to be of equal size and are almost of equal height above the caput humeri, in *A. buselaphus* and in *D. pygargus* there is a greater difference between the two parts than in *Connochaetes* spp. In both *A. buselaphus* and *D. pygargus* the cranial part is marginally elevated above the level of the caudal part, while there is a greater separation between them than in extant wildebeest. However, this feature is also sexually dimorphic and in females of *A. buselaphus* and *D. pygargus* the parts of the tuberculum maius are better differentiated than in males (Figure 49).
- In *C. taurinus* the caudal part of the tuberculum maius is sometimes enlarged compared to its condition in *C. gnou* (Figure 49, char. 3). This character and the fact that in *C. taurinus* the humerus tends to be more slender, provides some degree of distinction between the two species of wildebeest.
- The separation and elevation of the cranial part of the tuberculum maius is also reflected in the degree to which the cranial part overhangs the articular head (Figure 48, char. 1). This feature is marked in Hippotragini and Reduncini and less so in Alcelaphini. In *A. buselaphus* and *D. pygargus* the cranial part overhangs somewhat more than in *C. taurinus* and *C. gnou*, in which there is almost no overhang.
- On the shaft of *M. priscus* there is a well-developed crista humeri (Figure 48, char. 2) and a pronounced tuberositas deltoidea (Figure 48, char. 3). These features give the humerus shaft a medio-laterally compressed appearance. The same features are present in *Connochaetes* spp., and differentiate them from *A. buselaphus* and *D. pygargus*. In the latter the crista humeri and the tuberositas deltoidea are moderately developed, even in large males (Figure 48, char. 4), and the shaft tends to be more rounded in cross section.
- The foramen nutricium, situated in the lower half of the shaft on the caudal side in *Connochaetes* spp. and *M. priscus* (Figure 49, char. 4), tends to be towards midshaft in *A. buselaphus* and *D. pygargus*. In *Connochaetes* spp., and to a greater degree in *M. priscus*, the foramen nutricium is often placed towards the lateral side.
- At the distal end there is a pronounced extension of the lateral epicondyle in *M. priscus* (Figure 48, char. 5), which is mimicked in *Connochaetes* spp., but not in *A. buselaphus*

and *D. pygargus*. In this character *M. priscus* is the most extreme, with *C. gnou* approaching it in compactness and stoutness. In lateral view the stoutness of the lateral epicondyle coincides with the well-developed crista supracondylaris in *M. priscus* and in extant wildebeest (Figure 49, char. 5). The stoutness of the distal humerus in *M. priscus* is comparable to the condition in *C. gnou*, which has the appearance of a reduced version of *M. priscus* (Figure 50B).

- A variable feature, which can provide a distinction between hartebeest/blesbok and wildebeest, is found in the fossa radialis. Medially and immediately proximally to the distal articulation there is a pronounced furrow in which the medial part of the proximal radius articulates in *A. buselaphus* and *D. pygargus*, but is not usually present, or is present in reduced form, in *Connochaetes* spp. (Figure 48, char. 6).
- In the fossa radialis there is another feature that may separate *C. taurinus* from *C. gnou*. Almost in the mid-line of the fossa radialis in *C. gnou* there tends to be a longitudinal ridge, which seems to be absent in *C. taurinus* (Figure 48, char. 7). There is some variability in extant populations in this regard.
- At the distal end, in cranial view, the trochlea in *D. pygargus*, *A. buselaphus* has the appearance of being medio-laterally compressed and, on the medial side, cranio-caudally extended in comparison with *C. gnou* and *M. priscus* (Figures 48, 50B).

Discussion

The slenderness of the humerus in *A. buselaphus* and in *D. pygargus*, its rounded cross section, the elevation of the tuberculum maius craniale and its separation from the t. m. caudale suggest a less derived condition compared to that seen in *Connochaetes* spp. and *M. priscus*. The morphology of the humerus in the latter is reminiscent of that seen in domestic sheep. It is likely that in this regard that there is convergence between sheep and wildebeest-like alcelaphines, since it is known that the wild ancestor of sheep have undergone plains-living adaptations in parallel with alcelaphines (Boessneck *et al.* 1964; Boessneck pers. comm.).

The elevation and separation of the tuberculum maius craniale from the t. m. caudale can be used to separate the Alcelaphini from the Hippotragini and Reduncini. In the latter two tribes the cranial and caudal parts of the tuberculum maius are well separated, with the cranial part much elevated above the caudal part. In *K. ellipsiprymnus* the separation between the cranial

and caudal parts of the tuberculum maius is most extreme (*vide* Peters *et al.* 1997) for a discussion of this feature).

As in the case of the axis, *M. priscus* is wildebeest-like in its overall morphology and approaches *C. gnou* most closely. Given the overall wildebeest-like morphology of *M. priscus*, one may predict that as in *C. gnou* the two parts of the tuberculum maius in *M. priscus* would have been subequal in height without a marked distinction between them.

The tendency for the presence of a well-developed furrow in the fossa radialis in hartebeest and blesbok (Figure 48, char. 6) suggests that the radius pivots in a greater arc around its point of attachment at the distal end of the humerus than in *Connochaetes* spp. and *M. priscus*. It adds to the impression that the hartebeest and blesbok are more cursorially adapted than wildebeest. *M. priscus* again fits the wildebeest pattern rather than that of the hartebeest.

Radius

Description

Figures 51 to 54 provide dorsal, lateral, proximal and distal views of the radii of extant Alcelaphini and *M. priscus*.

- The general proportions of *M. priscus* are more similar to *C. gnou* and *C. taurinus* than to *A. buselaphus* and *D. pygargus* (Figure 55).
- Radii in *A. buselaphus* and *D. pygargus* are more slender and dorso-volarly more curved than in *Connochaetes* spp. and in *M. priscus* (Figures 51 & 52).
- In *Connochaetes* spp. and in *M. priscus* the proximal end of the radius is medio-laterally wider and dorso-volarly flatter than in *A. buselaphus* and *D. pygargus* (Figures 53, 54 & 56). This is partly due to the greater lateral projection of the attachment for the collateral ligament in the former (Figure 51, char. 1; Figure 53, char. 1).
- In dorsal view the attachment for the collateral ligament in *C. gnou* tends to be on the same level as the rest of the proximal articular surface, but in *M. priscus* and *C. taurinus* this attachment is sometimes slightly offset distally, which is the normal condition for *A. buselaphus* and *D. pygargus* (Figure 51, char. 2).

- The incision in the proximal radius for the lateral coronoid process of the ulna is sharp and deep in *A. buselaphus* and *D. pygargus* (Figure 53, char. 2; *vide* Peters *et al.* 1997), but more open in *Connochaetes* spp. and in *M. priscus* (Figure 30, char. 2). In *C. gnou* and *M. priscus* this incision approaches a right angle, while in *C. taurinus* it is often intermediate between the two extremes. This morphology adds to the impression that there is an extreme lateral extension of the proximal radius in *C. gnou* and *M. priscus* and it is emphasized by the dorso-ventral flattening of the lateral part of the proximal articular surface in *C. gnou*
- The tendency in *A. buselaphus* of the shaft of the ulna to be more often attached at the proximal end to the shaft of the radius than in the *Connochaetes* spp is possibly related to the deeper incision of the lateral coronoid process of the ulna. In all specimens used for comparison, only one *M. priscus* ulna from Mahemspan and one *C. gnou* ulna from Deelpan were attached to the radius at the proximal end.
- In *Connochaetes* spp. and in *M. priscus* the radius is dorso-ventrally flatter at the distal end than in the hartebeest and blesbok. Although the distal radius mimics the proximal end in this respect, the dorso-ventral flattening is more pronounced distally than proximally (Figure 54).
- The distal radius is generally very variable in morphology, but the dorso-lateral edge of the facet for the os carpi radiale appears useful for differentiation between *C. gnou* and *C. taurinus*. In *C. gnou* it tends to be flat and in *C. taurinus* it seems to be dorsally extended (Figure 54, char. 1). In *M. priscus* the facets for the os carpi radiale (Figure 54, char. 2) and for the os carpi intermedium (Figure 54, char. 3) seem to be of equivalent size, which reflects the extreme flattening of the distal radius in *M. priscus*. In this respect *C. gnou* is more similar to *M. priscus* than *C. taurinus*, which in morphology approaches that of *A. buselaphus* and *D. pygargus*.
- The dorsal part of the shaft of the radius of *C. taurinus* (Figure 51, char. 3, Figure 54, char. 4) is reminiscent of *D. pygargus* and *A. buselaphus* rather than of *M. priscus* and *C. gnou* in the somewhat better definition of the dorsal muscle attachments on its distal part.

Discussion

In ungulates the main function of the ulna is to stabilise the proximal radius around the trochlea of the distal humerus. This function is reflected in fusion of the ulna to the radius. It

is in its most derived state in equids, where the ulna has largely lost its function as a separate bone. The tendency for greater fusion of the ulna to the radius in *A. buselaphus*, together with the pronounced slenderness of the radius, points to the more cursorial adaptation of *A. buselaphus* relative to wildebeest and *M. priscus*. Cursoriality is also reflected proximally in the more pronounced incision of the lateral coronoid process in *A. buselaphus* and *D. pygargus*. This feature adds to the sagittal stability of the elbow, and distally in the pronounced muscle attachments on the dorsal side. In *C. taurinus* the distal end is less flattened than *C. gnou* and *M. priscus* and approaches the morphology seen in *A. buselaphus* and *D. pygargus*. The generally unfused state of the proximal radius to the proximal ulna in *M. priscus* points to a more distant relationship with *A. buselaphus*, suggesting that the convergence in morphology between *Connochaetes* spp. and *M. priscus* has a genetic basis, and not only a functional one.

The fact that the radius of *C. taurinus* has some morphological similarities with that of the hartebeest and blesbok points to an evolutionary conservative position in relation to *C. gnou*. This would accord with the fossil evidence that *C. taurinus* has changed little over the last 2.5 million years and that *C. gnou* is descended from a *C. taurinus*-like ancestor (Gentry & Gentry 1978; Harris 1991; Brink 1993; Vrba 1997).

Metacarpal

Description

Figures 57, 58, 59 & 60 give dorsal, proximal, volar and lateral views of the metacarpals of extant Alcelaphini and *M. priscus*.

- The metacarpal in *Connochaetes* spp. and *M. priscus* tends to be shorter, more compact and constricted in mid-shaft in comparison to *A. buselaphus* and *D. pygargus*. In the latter species the metacarpal is more slender and like the metacarpals of Antilopini in general proportions, with the shafts tending to be parallel-sided in dorsal and ventral view (Figure 57, char. 1; Figure 61). In extreme cases a small blesbok metacarpal could be mistaken for a large springbok.

- Medially on the proximal articular surface the facet for the os carpale II & III has an angle (Figure 58, char. 1), which is typical for Alcelaphini and, to a lesser degree, for Hippotragini. This “alcelaphine angle” is more prominent in *Connochaetes* spp. and in *M. priscus* than in *A. buselaphus* and *D. pygargus* (see also Gentry & Gentry 1978: 374). *C. gnou* and *M. priscus* appear to have more accentuated alcelaphine angles than *C. taurinus*.
- There is a greater degree of dorso-ventral flattening of the proximal articular surface in *M. priscus*, compared to the other alcelaphine species under consideration (Figures 58, 62A & B). This and the prominent alcelaphine angle produce a flattened and squared profile in the proximal metacarpal of *M. priscus*.
- On the dorsal side of the proximal end of the metacarpal, the tuberositas ossis metacarpalis is strongly developed in *A. buselaphus* and, to a lesser degree in *D. pygargus* (Figure 58, char. 2). This tuberosity is better developed in *C. taurinus* than *C. gnou* and *M. priscus*.
- On the volar side of the metacarpal, immediately below the proximal end, there is a pronounced concavity in all the alcelaphine species considered here (Figure 59, char. 1). This concavity extends distally for up to a quarter of the length of the shaft and is linked to the incomplete ventral fusion of the third and fourth metacarpal rays. It is a diagnostic alcelaphine character, but does not allow distinction among these alcelaphine taxa.
- In *C. gnou* and *M. priscus* the distal end of the metacarpal is flared more than in *A. buselaphus* and *D. pygargus* - in this respect *C. taurinus* resembles the latter (Figure 57, char. 2; Figure 63).
- At the distal end of the metacarpal the condyles in *A. buselaphus* and *D. pygargus* are deeper both dorso-volarly (Figure 60, char. 1) and proximo-distally (Figure 60, char. 2) than in *Connochaetes* spp. and in *M. priscus*.
- In dorsal view immediately proximal to the distal articulation there is a raised area in *A. buselaphus* and *D. pygargus*, which tends to be flattened in wildebeest species (Figure 57, char. 3). This raised area in hartebeest and blesbok gives the impression that the shaft merges with the distal condyles without interruption and is antilopine-like in morphology. The flattening in the distal metacarpal and the distal flare (Figure 63) give a very distinctive appearance to *Connochaetes* spp. and *M. priscus* - *M. priscus* is most extreme in this regard.
- In dorsal and volar view the lateral and medial margins of the distal part of the shaft in *C. taurinus* does not flow evenly into the distal articulation, as in the case of *M. priscus* and

C. gnou, but it tends to form an angle (Figure 57, char. 4; Figure 59, char. 3). This tendency in *C. taurinus* can create the impression that the two distal condyles are more separated than in *C. gnou*.

- In extant wildebeest species the peripheral parts of the condyles (Figure 60, char. 3) are more reduced in relation to the achsial parts than in *A. buselaphus* and *D. pygargus*. In this respect *M. priscus* is exceptional, being more hartebeest-like (Figure 64). However, this character is masked by stoutness and great distal flare, so that the metacarpal of *M. priscus* resembles that of *C. gnou*, but is much enlarged.

Discussion

The metacarpals can be separated into two morphological groups; hartebeest-like, including *A. buselaphus* and *D. pygargus*, and wildebeest-like, including *Connochaetes* spp. and *M. priscus*. Morphologically the metacarpal of *M. priscus* gives the impression of being a much-enlarged version of *C. gnou*, except in the proportions of the achsial versus the peripheral parts of the distal condyles. In this morphology *M. priscus* is not wildebeest-like. It probably reflects a plesiomorphic condition in *M. priscus* and is likely to refer back to an ancestral condition close to *A. buselaphus* and *D. pygargus*. This would be another example of a morphology that is genetically deeply embedded and less prone to functional modification. However, in general the metacarpals of *C. gnou* and *M. priscus* have similar derived morphologies. This may be partly due to convergent evolution between these two alcelaphine species, but it is likely that there is a genetic basis for the tendency to evolve convergently. One may envisage that common ancestry and the presence of shared genetic material, which is not necessarily expressed in the phenotype, will predispose two taxa to evolve homoplastic morphologies.

In distal flare and in dorso-ventral flattening of the distal metacarpal *C. taurinus* is less extreme, when compared to *C. gnou* and *M. priscus*. This fits the phylogenetic position of *C. taurinus* as close to the ancestral form of *C. gnou*.

In alcelaphines generally the third and the fourth metacarpal rays do not join ventrally to form a closed connection (Figure 58, char. 3). This unfused condition of the ventral parts of the third and fourth metacarpals is useful for separating alcelaphines from other bovid tribes, but

the degree to which these bones are unfused appears to be randomly variable within the Alcelaphini.

Femur

Description

All observations on the femur of *M. priscus* are based on one complete specimen from the site of Erfkroon (*vide* Churchill *et al.* 2000) and additional near-complete specimens from Mahemspan (Figures 65 – 68). Length measurements of *M. priscus* femora from Mahemspan, given in the plots (Figure 69), are estimates extrapolated from the complete specimen from Erfkroon. These results should be seen as tentative, until more complete specimens become available.

- The femora in *A. buselaphus* and *D. pygargus* are more slender and more curved than in wildebeest. The femur of *M. priscus* is wildebeest-like being robust and not markedly curved in lateral view (Figures 65, 66, 67, 69).
- At the proximal end the lateral rim of the femoral head is well defined and sharply demarcated in all the alcelaphines (Figure 65, char. 1).
- In cranial view the trochanter major is bigger, extends further proximally and laterally in *Connochaetes* spp. and *M. priscus* than in *A. buselaphus* and *D. pygargus* (Figure 65, char. 2).
- Cranio-caudally the trochanter major is also more flared in *Connochaetes* spp. than in *A. buselaphus* and *D. pygargus* (Figure 66, char. 1). This is due to the ligament attachment on the cranial side of the trochanter major, which is more prominent in *Connochaetes* spp and *M. priscus* (Figure 66, char. 2).
- The femora in *Connochaetes* spp and *M. priscus* have broader facies asperae than in *A. buselaphus* and *D. pygargus* (Figure 67, char. 1). In *A. buselaphus* the facies aspera is broader than in the hippotragine genera *Addax* and *Oryx* (Peters *et al.* 1997) and in wildebeest this feature is extreme and approaches the morphology found in cattle (Nickel *et al.* 1992). The functional meaning of this is not apparent, but it accords with the superficially ox-like body shape of extant species of wildebeest.

- The line forming the lateral demarcation of the facies aspera, the labium laterale, is sharper in *Connochaetes* spp. and *M. priscus* than in *A. buselaphus* and *D. pygargus* (Figure 67, char. 2).
- The fossa supracondylaris is deeper in *M. priscus* and *C. taurinus* than in the other Alcelaphini (Figure 67, char. 3). The deepening of the fossa supracondylaris may be a function of the larger body size of *M. priscus* and *C. taurinus*, since in *C. gnou* it is similar in size to *A. buselaphus*.
- In *Connochaetes* spp and *M. priscus* the distal end of the femur is absolutely and proportionally wider than in *A. buselaphus* and *D. pygargus* (Figure 68, 69).
- The lateral ridge of the trochlea is more curved outwards in *A. buselaphus* and *D. pygargus* than in the wildebeest clade (Figure 68, char. 1). The two ridges formed by the medial and lateral margins of the distal trochlea are more parallel sided in *Connochaetes* spp. and *M. priscus*.
- The medial ridge of the trochlea is more pronounced in *Connochaetes* spp. and *M. priscus* than in *A. buselaphus* and *D. pygargus* (Figure 68, char. 2; Figure 70). This is manifested in lateral view as a strong dorsal projection of the medial ridge, where it sometimes terminates in *C. gnou* and *M. priscus* in a thickened tubercle (Figure 66, char. 3), reminiscent of the tuberculum trochleae in equids (*vide* Nickel *et al.* 1992). This is evidently a derived feature, which evolved independently in *C. gnou* and *M. priscus* and, again, is somewhat cattle-like.
- On the lateral side of the distal end of the femur the attachment for the *M. vastus lateralis* of the quadriceps is stronger in *C. gnou* than in the other Alcelaphini (Figure 66, char. 4). The function of this muscle, together with the other component muscles of the quadriceps, is to extend the knee joint in locomotion and to help stabilise the knee. The prominence of this feature accords well with the characteristic running and jumping behaviour of black wildebeest, which is associated with its territorial behaviour. Functionally this feature may be related to the great dorsal projection of the medial ridge of the trochlea, but this needs to be tested by dissection. In *M. priscus* this feature seems to be less developed.

Discussion

The femora of Alcelaphini can be divided into those that are wildebeest-like, *Connochaetes* spp and *M. priscus*, and those that are hartebeest-like, *A. buselaphus* and *D. pygargus*. The

most striking difference between these two groups is the slenderness and accompanying greater curvature of the femur in the hartebeest-like group. This is evidently a plesiomorphic condition in alcelaphines and reflects back to their antilopine ancestry. The femur of wildebeest-like alcelaphines has undergone adaptation that is in parallel with bovines and caprines, in being shorter, stouter and less curved.

The cranial projection of the medial condyle at the distal end of the femur is paralleled in bovines and in *Antidorcas marsupialis* (Peters & Brink 1992), but is not seen in caprines (Boessneck *et al.* 1964). Although this morphology probably had a functional origin, which is presently not evident, it appears to be a morphological marker for wildebeest-like alcelaphines distinguishing them from the hartebeest-like alcelaphines.

Tibia

Description

The observations on the tibia of *M. priscus* are illustrated on a complete specimen from Florisbad, FLO 1982. Figures 71, 72, 73 and 74 give dorsal, plantar, lateral and distal views of the tibiae of extant Alcelaphini and *M. priscus*.

- The tibia in *Connochaetes spp.* and *M. priscus* is not as slender as in *A. buselaphus* and in *D. pygargus*. In *D. pygargus* it is the most slender (Figures 71, 72, 73 & 75).
- The corpus of the tibia in *C. gnou* is unusual in being recurved in dorsal and plantar views (Figures 71, 72). In lateral view it is also more curved than in other Alcelaphini (Figure 73).
- In lateral view the angle of the tuberositas tibiae is less steep in *C. gnou* and *M. priscus* than in *C. taurinus* and *A. buselaphus* (Figure 73, char. 1). In *D. pygargus* this angle seems to be intermediate.
- In dorsal view *A. buselaphus* and *D. pygargus* can be distinguished from *Connochaetes spp.* and *M. priscus* by the medio-laterally flattened margo cranialis of the tibia, giving a sharp-edged and pinched impression (Figure 71, char. 1).
- The medio-lateral flattening of the margo cranialis in *A. buselaphus* and *D. pygargus* is accentuated by the prominence of the attachment for the musculus semitendinosus (Figure

71, char. 2; Figure 73, char. 2). In extant wildebeest and in *M. priscus* this attachment is not prominent and the margo cranialis merges evenly into the middle part of the shaft of the tibia.

- On the lateral side of the proximal tibia the remnant of the fibula is less developed in *C. gnou* and *M. priscus* than in the other Alcelaphini (Figure 71, char. 3; Figure 73, char. 3). Although this feature is not preserved on the illustrated specimen, FLO 1982, it is present on many *M. priscus* specimens from Mahemspan.
- On the plantar side of the shaft, immediately distal to the proximal articular surface, there is a concavity in *C. gnou*, which extends distally for approximately a third of the length of the shaft (Figure 72, char. 1). In *M. priscus*, *C. taurinus*, *A. buselaphus* and *D. pygargus* this part of the shaft is rounded. This concavity in *C. gnou* causes the lateral edge of the tibia shaft and, to a lesser degree, the medial edge, to be sharp-edged. In this regard *M. priscus* is unlike *C. gnou*, and more like *C. taurinus*, which has an intermediate morphology between the extremes of *C. gnou* and *A. buselaphus/D. pygargus*.
- The muscle attachment on the dorsal side of the distal part of the shaft is variable in its placement and orientation in the alcelaphines. However, it tends to be more distally placed and more angled inwards in *Connochaetes* spp. than in *A. buselaphus*, *D. pygargus* and possibly *M. priscus* (Figure 71, char. 4). In *A. buselaphus*, *D. pygargus* and *M. priscus* the muscle attachment appears more isolated, although more extreme in *M. priscus*.
- In *A. buselaphus* and *D. pygargus* the plantar indentation between the articulation facets on the distal tibia is deeper than in *Connochaetes* spp. and *M. priscus* (Figure 74, char. 1).
- There is a greater difference between the dorso-plantar depth of the medial articulation facet of the distal tibia as opposed to the lateral furrows in *A. buselaphus* and *D. pygargus* than in *Connochaetes* spp. and *M. priscus* (Figure 74, char. 2).
- On the distal tibia the plantar facet for the os malleolare dominates the articulation to the extent that there is no dorsal facet in *M. priscus* (Figure 74, char. 3). This feature is unique for *M. priscus*, since the dorsal and plantar facets for the os malleolare are sub-equal in size in the other alcelaphine species considered here. The functional meaning of this highly distinctive character in *M. priscus* is not clear, but it has the effect of making the distal tibia proportionally wider than in the other alcelaphine taxa (Figures 76).
- In *A. buselaphus* immediately proximal of the plantar articular facet of the malleolare on the distal tibia there is usually a well-defined ridge of additional bone formation. It is the attachment for the long part of the ligamentum collaterale tarsi laterale (Figure 73, char.

4). Although this feature is variable, it is more pronounced in *A. buselaphus*, than in *M. priscus*, in which it may be well developed, but it is usually less emphasized in *Connochaetes* spp. and *D. pygargus*.

Discussion

In general the tibia is more conservative than the other skeletal elements considered so far. The exception is *C. gnou*, in which the tibia is very distinctive. Tibiae can again be grouped into wildebeest-like and hartebeest-like. Examples of shared morphologies between *Connochaetes* spp. and *M. priscus* include the lesser degree of plantar indentation between the distal articulation facets. This provides a concavity, which allows the calcaneus to extend into the distal tibia when the hind leg is extended. Functionally this means that the tarsal joint of hartebeest and blesbok have greater freedom of movement, a feature that one would associate with more specialised runners, as suggested by Gentry & Gentry (1978). This observation accords with the fact that the extant hartebeest and tsessebe, *D. lunatus*, are known to be among the fastest runners of all antelope species (Kingdon 1982; Skinner & Smithers 1990). A feature, which is likely to be functionally linked to the previous character, is the dorso-ventral depth of the medial and lateral furrows in which the proximal talus articulates. This morphology evidently enhances stability in the tarsal joint during locomotion and is, therefore, also a cursorial adaptation. In *D. pygargus* this morphology seems to be less extreme, but still greater than in *Connochaetes* spp. The measuring system employed in this study does not allow graphic illustration of this feature.

Although the tibia of *M. priscus* is essentially wildebeest-like, it has some morphological attributes that appear hartebeest-like. This is evident in the ‘hartebeest’ rounding of the plantar side of upper part of the shaft. However, in *C. taurinus* this feature is also found to some extent. Another ‘hartebeest’ feature of the tibia of *M. priscus* is its extreme length (Figure 75). The most striking aspect of the tibia of *M. priscus* is the articulation of the distal fibula, the os malleolare, with the distal tibia. This feature probably represents a uniquely derived character in *M. priscus*. The tibia of *M. priscus* is less predictably wildebeest-like than the radius, which is its structural equivalent in the front limb.

Superimposed on the attributes of the morphology of the tibia of *M. priscus* that have been noted are a number of convergent features with *C. gnou*, such as the remnant of the proximal fibula being less developed. The reduction in the fibula is commonly found in advanced ungulates, such as equids. In this respect *M. priscus* and *C. gnou* are equally derived.

Metatarsal

Description

Dorsal, plantar and proximal views of the metatarsal of extant Alcelaphini and *M. priscus* are given in Figures 77, 78 and 79.

- The metatarsals of *A. buselaphus* and *D. pygargus* are more slender than *Connochaetes* spp. and *M. priscus* (Figures 77, 78 & 80).
- Although the metatarsal of *M. priscus* is more robust than in the other alcelaphines, it is unusually elongated relative to the metacarpal. In terms of absolute dimensions it is the most extreme of all the Alcelaphini under consideration (Figure 77 & 80A).
- The plantar projection at the proximal end of the articulation facet for the os tarsale I is greater in *Connochaetes* spp. and *M. priscus* than in *A. buselaphus* and *D. pygargus*. In *M. priscus* it projects more than in *C. gnou* and *C. taurinus* (Figure 79, char. 1; Figure 81). The intra-specific linear relationship between the degree of plantar projection (Dp) and proximal width (Bp) is different among the species (Figure 81). In *C. gnou* proximal depth reduces with increased width, in *M. priscus* this trend is most extreme and in *C. taurinus* it is the least extreme.
- On the plantar side of the shaft, immediately below the proximal articulation at the fusion of the third and fourth rays of the metatarsal, the hollow in which the foramen nutricium is situated is deeper in *Connochaetes* spp. than in *A. buselaphus* and *D. pygargus* (Figure 78, char. 1). In this regard *M. priscus* resembles *Connochaetes* spp.
- On the plantar side the mid-shaft cross-section tends to be more concave and medio-laterally more compressed in *A. buselaphus* and *D. pygargus* than in *Connochaetes* spp. (Figure 78, char. 2; Figure 80A). *M. priscus* is wildebeest-like in this respect.
- At the distal end of the shaft there are two raised areas dorsally on either side of the vascular groove at the area of fusion of the third and fourth rays in *A. buselaphus* and *D.*

dorcas (Figure 77, char. 1). These areas are not as prominent in *Connochaetes* spp. or in *M. priscus*.

- In dorsal or plantar view the shafts of the metatarsals of *A. buselaphus* and *D. dorcas* tend to be constricted immediately proximal to the distal articulation, but not in the genus *Connochaetes* and *M. priscus* (Figure 77, char. 2; Figure 78, char. 3). This adds to the impression of distal flare in the metatarsal of *Connochaetes* spp. and *M. priscus*, which is evident in Figure 82.
- There is little proportional difference between the achsial and peripheral parts of the distal condyles between extant Alcelaphini and *M. priscus* (Figure 83A). Although *M. priscus* appears to have proportionally deeper peripheral parts than the other taxa, the Dpp/Dpa values are statistically indistinguishable (Figure 83B). In this respect the metatarsal is again different from the metacarpal.

Discussion

The distinction between *Connochaetes* spp. and *M. priscus* in contrast to *A. buselaphus* and *D. pygargus* is again evident in the metatarsal. Generally the metatarsals of *Connochaetes* spp. and *M. priscus* are more derived in being more robust, in having a greater plantar projection at the proximal end and in their greater distal flare. *A. buselaphus* and *D. pygargus* are unique in having dorsally raised areas immediately proximal to the distal ends, which grade into the distal articulations. They also have shafts that are medio-laterally more constricted at the distal end.

Not all aspects of morphology observed in metacarpals are equally replicated in the metatarsals. Contrary to the impression given by the metacarpals, *M. priscus* is not simply an enlarged version of *C. gnou*. It is distinguished from the other alcelaphines in having extremely elongated metatarsals in relation to the metacarpals. This is unique to *M. priscus*. Another difference is that there is less distinction in the proportions of the achsial versus the peripheral parts of the distal metatarsals among the alcelaphine taxa. This may reflect the functional differences of the front and hind limbs already noted. The lesser degree of distinction between the achsial and peripheral parts of the distal condyles in *M. priscus* probably represents an underived morphological state.

There is a similar linear relationship between proximal depth and proximal width in *C. gnou* and in *M. priscus* and this is another example of parallelism between the two species. However, the plantar projection of the facet for the os tarsale I is much greater in *M. priscus* than in *Connochaetes* spp. This feature is also present in extreme form in the *A. marsupialis* (Peters & Brink 1992), and may indicate that in *M. priscus* there is increased sagittal stress on the distal part of the hind limb. Although this may hint at a greater cursoriality in *M. priscus*, its body plan was very different from *A. buselaphus* (see below). If the greater plantar projection of the facet for the os tarsale I reflects the energetic jumping behaviour seen in springbok, then it is tempting to suggest that *M. priscus* may have had a similarly energetic component to its behaviour. If this can be linked to territoriality, it would explain the forward pointing horns and other skull characters of *M. priscus*. It also has robust metacarpals that appear to be adapted to accommodate extreme downward pressure, as when the forequarters are used for stabilisation. This would accord with intense activity like jumping. However, it should be noted that shortening of the metacarpals is not characteristic of the springbok.

DISCUSSION

Alcelaphine morphological groups

On the basis of the morphology of the skulls, dentitions and the postcrania the alcelaphine species considered here can be divided in two morphological groups, (1) *Connochaetes* spp. and *M. priscus* and (2) *A. buselaphus* and *D. pygargus*. This basic morphological division is also evident in the body proportions of these taxa, with wildebeest having caprine body proportions and hartebeest having antilopine body proportions (see below). Body proportions are not usually considered in morphological and phylogenetic studies of Bovidae, because of the lack of access to the postcrania. However, the approach adopted in this study, in which postcrania are systematically compared and described, allows such access.

Alcelaphine body proportions

According to Gentry (1992, 2000) the subfamily Caprinae and the tribe Alcelaphini separated after the common stem of both had separated from the tribe Antilopini. The fossil evidence suggests that the initial split between the Antilopini and the Caprinae/Alcelaphini occurred at

the end of the Early Miocene or beginning of the Middle Miocene, approximately 17 to 16 million years ago, while the second split between the Caprini and the Alcelaphini occurred very soon thereafter (Gentry 2000). Therefore, in primitive Alcelaphini one may expect to find characters resembling Antilopini, while in more advanced Alcelaphini one may expect to find characters resembling Caprinae. When the body plans of extant Antilopini, Alcelaphini and Caprini are compared (Figure 84), it is noteworthy that *Aepyceros melampus*, *D. pygargus* and *A. buselaphus*, resemble the Antilopini, while the genus *Connochaetes* and *M. priscus* resemble Caprini (Figure 84). Given that the Caprini and Alcelaphini probably descended from Antilopini (Gentry 2000), the hartebeest group can be described as having underived antilopine-like body proportions, with the wildebeest group having derived caprine-like body proportions.

The antilopine body plan is slender, with the radius and femur tending to be of equal length to the humerus, but with extremely elongated metapodials (Figure 84A). The impala, *A. melampus*, which is considered to be a primitive alcelaphine (Kingdon 1982; Gentry 1992), has the same body plan as the antilopine species, *Gazella dorcas* and *Antidorcas marsupialis* (Figure 84A). Similarly, *A. buselaphus* and *D. pygargus* have an essentially antilopine body plan, except that the metapodials are not as extremely elongated – it appears that *A. melampus*, *D. pygargus* and *A. buselaphus* form a morphological cline, which tends to become progressively less antilopine in character with the proportional elongation of the radius and the shortening of metacarpal. It is noteworthy that the hind limb is essentially conservative in all three species, perhaps with marginal shortening of the metatarsal in *D. pygargus* and *A. buselaphus*, which can be considered as a derived condition for this group (Figure 84A). However, the tendency for distal shortening of the limbs is quite modestly expressed and it does not mask the similarity of the body plans of *A. buselaphus*, *D. pygargus*, *A. melampus* and the Antilopini. It also confirms the many antilopine-like characters in the osteology of *A. buselaphus* and *D. pygargus*, as described above. In a structural sense *A. buselaphus* and *D. pygargus* can be considered as underived, which is remarkable in the light of the long geological time span of the separation between Antilopini and Alcelaphini. Although the present comparison does not include the genus *Parmularius*, it appears that the species *P. altidens* from Olduvai Bed I had antilopine body proportions very similar to *A. buselaphus* (Gentry & Gentry 1978: 376). It is assumed that other species of the genus *Parmularius* would also conform to the antilopine body plan.

The caprine body plan, in contrast, is compact and stocky, with the distal limb elements being shortened in relation to the humerus and the femur (Figure 84B). The bodyplans of *Connochaetes* spp. and *M. priscus* are markedly different from the antilopine blueprint in that the tibia and metapodials are proportionally shorter. In *M. priscus* the metatarsals are not as extremely reduced as in the case of the metacarpals. *M. priscus* is also distinguished by the shortening of the metacarpal in relation to the radius and by the elongation of the hind limb in proportion to the front limb, suggesting that the hind limb in *M. priscus* has less derived proportions. There are only minor proportional differences between *C. taurinus* and *C. gnou*, in that the tibia and metatarsal of the latter are marginally elongated in relation to the rest of the body. In a general sense the bodyplans of the wildebeest taxa can be described as caprine-like. If it is considered that the caprine body plan is derived from that of the Antilopini (*sensu* Gentry 2000), then the bodyplans of *Connochaetes* spp. and *M. priscus* represent an intermediate position between the extremes those of the Antilopini and Caprini, but tending towards being caprine.

The shortening of the metacarpal, and the accompanying increased medio-lateral width in *M. priscus*, is likely to be a function of the need to accommodate greater proximo-distal stress, as discussed above. The elongation of the hind limb in *M. priscus*, which is seen in somewhat reduced format in *C. gnou*, may well be linked to the greater and more energetic use of the hindquarters, unlike in *A. buselaphus* and *D. pygargus*, where the hind limb is primarily used for locomotion and less for kicking, jumping and display behaviour (Kingdon 1982).

In terms of body proportions the tribe Alcelaphini can be divided into those species with antilopine-like and those with caprine-like bodyplans. These two categories coincide with the two morphological groups identified in this study, so that those species with antilopine bodyplans have hartebeest-like morphologies, *i.e.* *Damaliscus* and *Alcelaphus*, while those with caprine bodyplans have wildebeest-like morphologies, *i.e.* *Connochaetes* spp. and *M. priscus*. Given the assumed antilopine origins of both the Alcelaphini and the Caprini, the antilopine-like body proportions can be taken as underived, while the caprine-like body proportions can be taken as the derived condition. The question of when the derived caprine-like body plan of the wildebeest group became manifested in the fossil record is addressed in the next chapter (Chapter 7).

Caprine-like characteristics of *C. gnou*

The caprine-like bodyplans of *Connochaetes* spp. and *M. priscus* are of interest in the light of the many caprine and sheep-like cranial and postcranial characters of *C. gnou*. Almost all the unique skull characters of *C. gnou* can be correlated with its more specialised territorial social behaviour, as listed in Table 14. The marked territorial behaviour of *C. gnou* is perhaps most visibly expressed in its horn shape and related morphologies. These adaptations are functional responses to a behaviour pattern characterised by frequent head banging and horn clashing, which is also a characteristic of evolved sheep (Geist 1971). Therefore, the morphological convergence in the skull and horn morphologies between *C. gnou* and sheep is driven by functional needs in response to social behaviour patterns, which are similar to advanced sheep. It is suggested that the predisposition of black wildebeest to converge on sheep, both in terms of social behaviour and in terms of morphology, has an underlying genetic basis, which refers back to the common ancestor of alcelaphines and caprines (*vide* Gentry 2000). Therefore, it can be concluded that there is a 'caprine genetic component' in certain alcelaphines species, which predisposes them to evolve caprine behavioural patterns and morphologies when suitable circumstances present themselves. These alcelaphine taxa have been diagnosed and grouped in this study as 'wildebeest', as opposed to 'hartebeest'. In the latter there is no evidence of caprine morphology or behaviour.

In addition to the cranial morphology of *C. gnou* there are numerous postcranial as well as external, soft tissue characters, which confirm the surprisingly caprine-like nature of black wildebeest cranial adaptation. Besides its cranial morphology, visually the most striking external features of the black wildebeest are its elongated white tail, its mane and its throat beard, which extends to between the forelegs. In Table 16 these characters are listed and interpreted as either generally caprine, primitive caprine or sheep-like in character.

Table 16. External and osteological characters of *C. gnou* that can be described as caprine or sheep-like.

CHARACTER	INTERPRETATION
External characters 1. Throat beard 2. Extension of throat beard to forelegs 3. Sagittal dorsal hair, or mane 4. Stocky body build	Primitive caprine – cf. <i>A. lervia</i> Primitive caprine – cf. <i>A. lervia</i> Primitive caprine, as seen in <i>A. lervia</i> , but also in reduced form in Cameroon dwarf goats Generally caprine
Skull 5. Forward horn curvature 6. Enlarged basal bosses 7. Increased pneumatization of frontal 8. Fused frontals' suture 9. Projecting orbits 10. Flattened area between t. muscularia 11. Reduced bulla tympanica	Advanced sheep-like Advanced sheep-like Advanced sheep-like Advanced sheep-like (seen in <i>A. lervia</i> *) Sheep-like Sheep-like Primitive caprine
Dentitions 12. Distal projection of M ³ metastyle 13. Smooth enamel surfaces 14. Simple outlines of enamel folds 15. Reduced cementum cover	Generally caprine Generally caprine Generally caprine Generally caprine
Axis 16. Short and compact 17. High and cranio-caudally short p. spinosus	Generally caprine (also seen in Bovini) Sheep-like
Humerus 18. Shortened and stouter 19. Tuberculum maius craniale less elevated above T. m. caudale 20. T. m. craniale tends not to overhang the proximal articular surface 21. Medio-laterally compressed shaft 22. Medio-laterally expanded distal end	Generally caprine Sheep-like Sheep-like Sheep-like Sheep-like

Radius 23. Shorter 24. Greater lateral projection of proximal end	Generally caprine Sheep-like
Metacarpal 25. Shorter and stouter 26. Medio-laterally flared distal end	Generally caprine Sheep-like
Femur 27. Medio-laterally flared proximal end	Sheep-like

* Although *A. lervia* is an underived form of sheep in terms of its behaviour and general morphology (Geist 1971), there are aspects of its skull morphology, which can be considered advanced. The posterior position of the horn bases, incipient fusion of the pedicels and the tendency for the frontals' suture to become fused are derived adaptations, which probably postdate the split from a common ancestor shared with more derived forms of sheep, such as *O. orientalis* and *O. ammon*. These aspects of the cranial morphology of *A. lervia* parallel those of *M. priscus* and *A. buselaphus*.

The degree of caprine-ness in wildebeest species can be used to rank them cladistically. *C. taurinus* appears less derived, with *C. gnou* and *M. priscus* more derived, but in parallel. If one accepts the hypothesis that early alcelaphines were closely related to early caprines (Gentry 2000), then the derived caprine-like behaviour and morphology of *C. gnou* can be classified as evolutionary reversals that converge on a caprine blueprint. Therefore, one may propose the hypothesis that the derived caprine-like morphology of ancestral populations of *C. gnou* was genetically latent, but became expressed in the phenotype once there was a shift towards a more caprine-like social behaviour (*vide* Chapter 9).

Morphological characteristics of *M. priscus*

The wildebeest-like character of *M. priscus* is evident in most of its skeletal elements, but it is more pronounced in the front limb elements and in particular the metacarpal. It can be concluded that *M. priscus* is not a large hartebeest, as formerly assumed on the basis of parallel cranial characters (Hoffman 1953), but rather that it is a large form of wildebeest-like alcelaphine. The wildebeest-like characters of *M. priscus* are listed in Table 17.

Table 17. The wildebeest-like features of *M. priscus*.

1. Clockwise torsion of horn cores
2. Shortened braincase, in which the occipital makes contact with the frontal
3. Shortened premolar row in upper and lower dentitions
4. Simple occlusal enamel pattern of cheek teeth
5. Increased hypsodonty
6. The distal expansion of the base of the crown of the M³ and the M₃
7. A tendency for the metastyle of the M³ to flatten towards the base of the tooth crown
8. A cranio-caudally shortened axis
9. The proximo-distally shortened trochlea of the distal humerus
10. The tendency in the proximal radius for the incision of the lateral coronoid process of the ulna to form a right angle
11. Shortened metacarpal
12. The dorso-volar flattening of the metacarpal
13. Expanded distal width of the metacarpal
14. Short, stout and relatively uncurved femur
15. Enlarged trochanter major
16. Limb proportions

In spite of the general wildebeest-like character of *M. priscus* there are a number of characters, which may be described as hartebeest-like (Table 18).

Table 18. The hartebeest-like features of *M. priscus*.

1. Elongated face, which includes the posterior extension of the horn bases, fused pedicels and elongated lower jaw.
2. The distally positioned lateral tubercle in the proximal radius
3. The roundedness of the plantar side of the shaft of the proximal tibia

Among modern alcelaphines pedicel fusion is seen only in the hartebeest, in which it is variably expressed in different geographic populations, or subspecies. The character is evidently highly derived and represents parallel evolution between the genera *Alcelaphus* and *Megalotragus*. The other characters listed as hartebeest-like can be considered to be primitive or underived, since they all resemble an undifferentiated antilopine (Peters 1986; Peters & Brink 1992). Therefore, the derived morphological attributes of *M. priscus* form a mosaic, which in general can be called wildebeest-like, or ‘caprine’, but its facial elongation can be described as an extreme form of hartebeest morphology.

The many parallel morphologies in *M. priscus* and *C. gnou* may have a behavioural basis: In *M. priscus* the downward and forward pointing horn cores and the tendency for the frontals’ suture to fuse point to a more aggressive use of the horns, which in *C. gnou* is associated with increased territoriality in breeding behaviour. In *M. priscus* these skull characters are complemented by a shortened neck and surprisingly compact forequarters, which may point to social behaviour that may have approached that of the black wildebeest. A reconstruction of the body plan and skeleton of *M. priscus* is given in Figure 85.

It is not common that a single morphological character can be used for identification, but in the case of *M. priscus* there is a character that distinguishes it from all other bovids. This character is found on the distal articular surface of the tibia, where the plantar articular facet for the os malleolare is enlarged to the extent that it dominates the articulation (Figure 74, char. 3). This may be a useful character in distinguishing early *Megalotragus*-like alcelaphines from other forms of wildebeest (*vide* Chapter 7).

Morphological relationships in the Alcelaphini

Previously the position of the genus *Megalotragus* within the wildebeest morphological group, or clade, has not been apparent due to the erroneous assumption that facial lengthening and related changes in horn base morphology are apomorphic characters shared with the genus *Alcelaphus* (Hoffman 1953; Wells 1959b, 1964a; Klein 1994). Gentry (1978) grouped *Megalotragus* close to the wildebeest clade, but separate from a *Parmularius-Alcelaphus-Damaliscus* clade. Later he again questioned the classification of *Megalotragus* within the

hartebeest clade and suggested that *Megalotragus* should be grouped with *Connochaetes* (Gentry 1990). Vrba (1979) initially classified the genus *Megalotragus* in a megagenus that included the genera *Alcelaphus* and *Connochaetes*. In a later work she modified her view and included *Megalotragus*, together with *Oreonagor*, in a “*Megalotragus* – (*Oreonagor*-*Connochaetes*) sistergroup” (Vrba 1997: 189). Although the consensus view of Gentry and Vrba is almost entirely based on the study of skull characters, it is supported by dental and postcranial evidence presented in this study.

However, Vrba (1997) also divided the tribe Alcelaphini into two clades, or subtribes, the Alcelaphina and the Damaliscina. According to Vrba the Alcelaphina include the genera *Damalops*, *Alcelaphus*, *Megalotragus*, *Connochaetes* and *Beatragus*, while the Damaliscina include the genera *Awashia*, *Damaliscus* and *Parmularius*. Figure 86A summarises Vrba’s view on alcelaphine evolution (Vrba 1997). The present study partially supports this taxonomic and phylogenetic arrangement insofar as there is a close morphological relationship between the genera *Megalotragus* and *Connochaetes*. However, the morphological blueprint of *M. priscus* as a large wildebeest-like animal does not agree with its grouping with *A. buselaphus*. Details of the dentitions and the postcranium, as illustrated and discussed above, clearly point to the wildebeest-like nature of *M. priscus*, while *A. buselaphus* has the morphological blueprint of an enlarged version of *D. pygargus*. The close phylogenetic relationship between the genera *Alcelaphus* and *Damaliscus* is further illustrated by cases of hybridisation between hartebeest and blesbok in nature reserves of the Free State Province (P. Strauss pers. com.). Therefore, the position of *Alcelaphus* in the wildebeest clade as a monophyletic group is not supported. In Figure 86 a revised view of alcelaphine classification is given based on the present study. It may be added that Vrba’s choice of names for the subtribes is unfortunate, since both are derived from the same morphological group, the hartebeests.

In the following chapter fossil material referred to the species *Oreonagor tournoueri* is considered. Its position as a hypothetical ancestral wildebeest, suggested by Gentry (1978) and Vrba (1997), is discussed and the question of the evolutionary split between ancestral wildebeest and early *Megalotragus*-like alcelaphines is addressed.

CHAPTER 8. THE EVOLUTION OF THE GENUS *CONNOCHAETES* AND *MEGALOTRAGUS*-LIKE WILDEBEEST

INTRODUCTION

Although the fossil species, *Oreonagor tournoueri*, was originally described from Aïn Jourdel, Algeria, as “*Antilope*” *tournoueri* Thomas 1884, the genus name *Oreonagor* Pomel 1894 was given to the material (Arambourg 1979). Initially, this material was included into the Reduncini by Thomas (1884) and Pomel (1894), but Gentry (1978), Arambourg (1979) and Geraads (1981) considered the material to be alcelaphine. Arambourg also described new material from Aïn Boucherit, Algeria, which he included in *O. tournoueri*, and used as the basis for a revised diagnosis and for the creation of a neotype for the species (Arambourg 1979). In addition to the neotype skull, there were neosyntypes named by Arambourg and numerous dental and postcranial specimens from Aïn Boucherit were also referred to *O. tournoueri* (Arambourg 1979).

O. tournoueri is commonly taken to be the probable ancestor of, or closely related to the earliest members of the genus *Connochaetes* (Gentry 1978; Vrba 1997). The purpose of this chapter is to evaluate the original type material of *O. tournoueri* from Aïn Jourdel as well as the neotype material from Aïn Boucherit as possible ancestors of the genus *Connochaetes*. Since there are two sets of materials that were used for the description of *O. tournoueri* there is a potential for confusion. This is suggested by the uncertain referral of material from the Middle Awash to the taxon ?*O. tournoueri*?/*Megalotragus*, since the specimen evidently resembles the material from Aïn Boucherit rather than that from Aïn Jourdel (Vrba 1997). In contrast, Gentry’s (Gentry & Gentry 1978) reference to *O. tournoueri* appears to refer to the Aïn Jourdel material. Therefore, to prevent further confusion when considering wildebeest origins the original type material and the neotype material are reviewed separately.

FOSSIL HISTORY OF THE GENERA *CONNOCHAETES* AND *MEGALOTRAGUS*

The earliest fossil evidence for the presence of the genus *Connochaetes* is *C. gentryi* Harris 1991 from the Upper Lomekwi Member of the Nachukui Formation, West of Lake Turkana dating to between 3.0 to 2.5 million years ago (Harris *et al.* 1988; Harris 1991). *C. gentryi* also occurs in Olduvai in Beds I and II, between c. 1.8 to 1.5 million years ago and is only

marginally different from presumed descendant forms, such as *C. taurinus prognu* Pomel 1894 and the extant blue wildebeest (Gentry & Gentry 1978; Harris 1991; Vrba 1997). *C. taurinus prognu* (= *C. taurinus olduvaiensis* Leakey), was first recorded at Ternifine (Pomel 1894), estimated to be around 700 000 years ago (Geraads 1981; Geraads *et al.* 2004), but also occurs in Olduvai Beds II to IV (Gentry & Gentry 1978; Geraads 1981; Harris 1991), at Peninj, Tanzania, around 1.1 million years ago and at Bouri, Middle Awash, in Northeast Africa around 1.0 million years ago (Gentry 1978, 1990; Gentry & Gentry 1978; Vrba 1997). *C. taurinus prognu* differs from extant *C. taurinus* only in that the horn cores were less posteriorly inserted and less downwardly curved (Gentry & Gentry 1978; Geraads 1981). It is likely that the *C. taurinus* from the Plio-Pleistocene hominid-bearing cave breccias in South Africa is also *C. taurinus prognu* (Vrba 1976, 1979), which means that ancestral blue wildebeest populations occurred in all three arid centres of Africa with a virtually pan-African distribution. Therefore, from about 2.5 million years ago antecedents of blue wildebeest occurred in East Africa, and later in North Africa and southern Africa, and remained relatively unchanged to appear eventually as the extant *C. taurinus* of southern and East Africa. Since the species had changed so little over time and over such large geographic distances, it can be considered to be evolutionary conservative. The virtually pan-African distribution of *C. taurinus* in the Early and Middle Pleistocene, its flexible social behaviour and its adaptation to a range of habitat types in savannas and grasslands reflect this conservatism (Gentry & Gentry 1978; Geraads 1981; Harris 1991; Vrba 1997; Berry & Louw 1982; Attwell 1977).

The earliest evidence for the genus *Megalotragus* dates to around 3.0 million years ago and is from the Lokochot Member of the Koobi Fora Formation, East of Lake Turkana (Harris 1991). The Shungura Formation of the Omo Group, which is at the north end of Lake Turkana and extends to beyond 3.0 million years, is extremely poor in alcelaphine fossils and there are no certain records of either *Connochaetes* or *Megalotragus* (Gentry 1985). This absence is likely to be the result of local palaeo-environmental conditions reflecting the riverine habitat of the Omo River, which favoured bovids adapted to more closed and water-rich environments, very different from the arid contemporary Lake Turkana conditions (Gentry 1985; Harris 1991). The earliest records of *M. kattwinkeli* are from Matabaietu, Locality 1, Middle Awash, Ethiopia, and from Sidi Hakoma, Hadar Formation, Ethiopia, both dated to 2.5 million years ago (Vrba 1997). In southern Africa and North Africa the fossil record is

less complete and more difficult to date. It has been suggested that *M. kattwinkeli* occurs in Sterkfontein Member 4, which is assumed to be in the order of 2.6 to 2.4 million years old (Vrba 1997).

Although East Africa has the best-dated records of *Megalotragus* and *Connochaetes*, it is not yet possible to know where the genus may have originated. If the North African species *O. tournoueri* represents a forerunner of the blue wildebeest lineage, then *O. tournoueri* must predate the first members of the genus *Connochaetes* and, therefore, should be older than c. 2.5 million years old. The early evidence for *Megalotragus* from the Lokochot Member of the Koobi Formation suggests that ancestral forms of *Megalotragus* should predate c. 3.0 million years ago. However, at present the fossil record of the time range older than c. 3.0 years is too incomplete to resolve the question of the timing of the evolutionary split between the genera *Connochaetes* and *Megalotragus*. The *O. tournoueri* type material from Aïn Jourdel and the neotype material from Aïn Boucherit are undated, but have a minimum estimate of not much younger than c. 2.0 million years (*vide* Chapter 5). Thus, for the present the discussion on the origins of wildebeest *sensu lato* is reliant on the East African chronological record and the morphological evidence provided by the material referred to *O. tournoueri* from North Africa. Figure 87 gives an approximate chronological arrangement of fossil members of the wildebeest group in relation to southern African Land Mammal Ages.

COMPARATIVE OSTEOLOGY OF *OREONAGOR TOURNOUERI* (THOMAS 1884)

Aïn Jourdel

Skull

Material

The original type material that was examined in the Laboratoire de Paléontologie consists of a skull piece, accession number 1885-3, with the left frontal preserved, most of the left orbit, part of parietals, most of the right horn core excluding the tip and the base of the left horn core (Figure 88). The nasals parts, as illustrated by Thomas (1884), are not preserved on the specimen in its present state. Although Thomas illustrates a left mandible with part of the P₄

and the M₁ preserved, a right distal humerus, a right distal radius and a distal metacarpal, no postcranial or dental material referred to “*Antilope*” *ournoueri* from Ain Jourdel were located in the collections of the Laboratoire de Paléontologie. However, a lower molar, which is illustrated and referred to by Thomas as *Palaeoreas gaudryi*, was present in the collections. This specimen is alcelaphine, but appears too large to belong to the same species as the type specimen and, consequently, is not considered further.

Description

The following description takes into account the original description of Thomas (1884: 14), but provides additional observations.

- The skull fragment is that of a medium-sized alcelaphine, about the size of *D. lunatus*.
- The frontals are wide and slightly domed (Figure 88, char. 1).
- The supra-orbital foramina are large
- The rim of the orbit is projects markedly and is thick and rugose (Figure 88, char.2).
- The horns are inserted quite close to the orbits, but also quite far to the back of the skull, as found in *C. taurinus* and domestic cattle. This is reflected in the position of the fronto-parietal (= coronal) suture, which is situated close to the posterior margin of the horn core bases.
- Although the posterior part of the skull is not completely preserved, the available morphology suggests that the nuchal crest was dorsally placed, *i.e.* close to the posterior limit of the horn core insertions.
- In frontal view the bases of the horn cores diverge markedly so that their long axes are at an angle of around 47° to the frontals' suture.
- The frontals' sinuses are moderately large.
- The right horn core has slight clockwise torsion from the base upwards.
- In lateral view the horn cores arise almost on the same plane as the face, after which they curve evenly forward (Figure 88C).
- Pedicels are short (Figure 88, char. 3).
- The horn cores are uncompressed, being almost round in cross section from the base to the tip (Table 19).

- The horn bases are slightly enlarged, suggesting incipient basal bosses (Figure 88, char. 4).
- There are faint indications of transverse ridges near the bases of the horn cores (Figure 88, char. 5), suggesting some development of nodes on the horns.

Since the fragments of the lower jaw and postcranial elements are not available for study, the description of Thomas is summarised and expanded, on the basis of his illustrations (Thomas 1884: 15):

Lower jaw:

- There are no basal pillars between the lobes of the lower molars
- The lower molar has remarkably simple enamel folds, *i.e.* there is no pinching.
- The lobes of the lower molar are medio-laterally compressed.

Postcranial elements:

- The radius appears somewhat flattened dorso-volarly.
- The distal metacarpal is dorso-volarly flattened immediately proximally to the distal articulation.
- In dorsal view the distal articulation of the metacarpal appears primitive in resembling a large antilopine, *i.e.* it resembles the articulation of *A. buselaphus* or *D. pygargus*. In lateral view it appears somewhat compressed dorso-volarly.

Measurements of the cranial fragment are given in Table 19.

Table 19. Skull measurements of the type specimen of *Oreonagor tournoueri* (Thomas 1884) from Aïn Jourdel.

1. Distance between horn bases	73.4 mm
2. Distance between supra-orbital foramen and mid-frontal suture (estimated)	49.0
3. Largest distance between orbit and mid-frontal suture	96.0
4. Smallest distance between orbit and mid-frontal suture	63.5
5. Smallest transverse distance between the lateral margins of the frontals	81.4

5. Medio-lateral (largest) diameter of the base of the horn core	42.4
6. Antero-posterior (smallest) diameter of the base of the horn core	42.9

Discussion

The view of Gentry & Gentry (1978), that the *O. tournoueri* materials from Aïn Jourdel resemble a primitive or ancestral *Connochaetes*, is supported by the morphologies described above. In general the wildebeest-like character of the Aïn Jourdel specimen is evident in the slight doming of the frontals, which is very characteristic of the blue wildebeest and well developed in *M. kattwinkeli* and *M. atopocranion* (Gentry *et al.* 1995), the posterior insertion of the horn cores, the wide forehead, distance between the horn insertions, the projecting orbits, the low angle of the horns to the face and the slight clockwise torsion of the right horn core. The simple enamel outline of the lower molar, with no pinching, the dorso-volar compression of the distal radius and the distal metacarpal confirm this impression. However, the characters that can be considered to distinguish *O. tournoueri* from the genus *Megalotragus* are the wide separation of the horn core insertions and basal swellings on the horn cores. Wide separation of the horn core bases is not a characteristic of the genus *Megalotragus*, except for the southern African material referred to *M. priscus* (Chapter 7). In *M. priscus* this character is likely to reflect recent convergence with the genus *Connochaetes*. Therefore, the presence of this character in an early wildebeest-like alcelaphine, such as *O. tournoueri*, is likely to reflect a closer relationship with the genus *Connochaetes* than to *Megalotragus*. The dorso-ventral flattening of the brain case, which cannot be observed directly, but is suggested by architecture of the preserved portion of the posterior part of the skull, can also be seen as a distinctive feature of the genus *Connochaetes*.

The underived wildebeest characters that one may expect to find in the hypothetical common ancestor of the genera *Connochaetes* and *Megalotragus* are the slight clockwise torsion of the horn cores, short pedicels, the rounded cross section of the horn cores and the indication of nodes on the horns. The latter is found in primitive Alcelaphini, such as *A. melampus* and *Beatragus hunteri* (Kingdon 1982), but not in derived extant *Connochaetes*. The dental and postcranial characters listed above also fall in a generalised underived wildebeest category.

The overall impression of the specimen is that of a relatively unspecialised wildebeest. However, the derived characters shared with the genus *Connochaetes* suggest that it may well represent the immediate ancestor of the genus *Connochaetes*, or a species closely related to such an ancestral form. Given that the type material of *O. tournoueri* from Aïn Jourdel is more primitive than any material assigned to the genus *Connochaetes* from the Turkana deposits, it is likely to be relatively old, possibly in the range of 2.5 - 3.0 million years or older.

Aïn Boucherit

Arambourg (1979) redescribed the species *Oreonagor tournoueri* on the basis of a neotype and neosyntypes. In addition, numerous horn cores, dental and postcranial remains from Aïn Boucherit were referred to *O. tournoueri* (Arambourg 1979). Although Arambourg gives an in-depth description of the type material, which consists of cranial and dental materials, he only provides a general overview of the postcranium. In this section Arambourg's description of the skull is given as a direct translation from the original French. However, this description is expanded, while new descriptions are given of the dentitions and postcranial remains.

Skull

Material

The neotype (1954-8-266) of species *Oreonagor tournoueri*, consists of a complete braincase, right and left horn cores, part of the right orbit and the face above the nasals (Figure 89).

Description

The following is a slightly abridged translation of Arambourg (1979: 96-97):

“The frontals are large and convex in cross-section, but more so towards the mid-line; the frontals' suture can only be distinguished in the area between the horn bases; the junctions between the frontals and the nasals are in the form of two adjacent convex lines, the orbits are large and moderately projecting; the horn cores recurve under the posterior line of the orbits; the horn cores have a triple curvature; for the first c. 10 cm of their length they are almost parallel in an antero-posterior axis, then they diverge outwards virtually at right angles for

approximately two thirds of their length and for the remainder they recurve upwards; the horn cores have a clockwise torsion of around 180° ; the horn bases are robust and are inserted on very short pedicels; the surfaces of the horn bases are uneven and marked by some shallow grooves; the horn cores are compact and generally smooth except for a few grooves.

The braincase is short, but well developed and a little inclined in relation to the face at an angle of 120° ; immediately behind the horn core insertions the braincase widens towards the mastoid area, where it is at its widest; the parietal area is reduced; the lambdoid suture is only 26 mm from the horn bases; the coronal suture approaches the horn bases and form an eminence, as seen in sheep and *Menelikia* from the Pliocene fossil deposits of the Omo; the temporal ridge is not very prominent, but well demarcated nonetheless; the face of the occipital is low and wide, which is an exaggeration of the condition seen in certain reductines (*Kobus*) and *Menelikia*; the occipital face leans forward, as in alcelaphines generally, but still much less than in certain extant forms, such as *Alcelaphus*, where the occipital face sometimes forms an angle with the dorsal face of the braincase in the vicinity of 160° .

The mastoids are particularly wide; the occipital tubercle is rounded, but flanked by two deep fossettes, which give to the parieto-occipital region of the occipital ridge the form of an inverted accent circumflex, reminiscent of the condition in *Menelikia*; the curved line above this, which is the continuation of the occipital protuberance, forms a sharp and prominent ridge that continues as the mastoid ridge, which is rather angular and prominent; the mastoid process is preserved on the right side at the base of a deep depression and is well demarcated.

The occipital crest is short and blunt; it terminates above the foramen magnum in a thick protuberance; the condyles are large, robust and flanked by thick paroccipital condyles; in ventral view the 'basilar apophyses' (= tubercula muscularia = 'anterior tuberosities') are short and wide.

There are numerous horn core pieces recovered from Aïn Boucherit, which are more or less fragmentary, but all correspond to the type; some differences related to age and other details allow an impression of individual variation and sexual dimorphism in the development of the horn core curvature; the cross sections of the horn cores are more or less oval or cylindrical and there is no indication of nodes. “

This description can be expanded as follows:

- The area between the horn bases is inflated (Figure 89, char. 1).
- The horn pedicels are not as short as in the type from Aïn Jourdel. It appears that the pedicels are partially engulfed by the posterior expansion of the frontals (Figure 89, char. 2).
- The frontals' suture is fused, except between the horn bases (Figure 89, char. 3).
- The horn insertions are moderately wide apart (Figure 89, char 4).
- At their bases the horns have an anterior thickened ridge, which resembles a weakly developed keel (Figure 89, char 5).
- The lateral margins of the horn core bases are lower than the medial ones.
- Horns are medio-laterally compressed near the bases, but become rounded in cross section distally (Figure 89, char 6).
- Orbits are projecting (Figure 89, char 7)

Discussion

In contrast to the Aïn Jourdel specimen, the skull material and other cranial elements from Aïn Boucherit that are referred to *O. tournoueri* reflect not only primitive wildebeest-like morphology, but also incipient *Megalotragus*-like characters. These characters are listed in Table 20. Figures 90 and 91 give comparative views of the skull of *C. taurinus*, the type specimen of *O. tournoueri* from Aïn Jourdel, the neotype from Aïn Boucherit and the *M. priscus* skull from Erfkroon.

Vrba gives indirect support to the postulate that the Aïn Boucherit neotype is similar to *Megalotragus*. She identifies a specimen from Bouri 1, Middle Awash (Vrba 1997: 155), as *?Oreonagor/?Megalotragus*, implying that the two genera are close enough to allow some uncertainty in the diagnosis of the Bouri specimen. It appears that Vrba compared the Bouri specimen with the Aïn Boucherit neotype, and not with the original type from Aïn Jourdel. There are a number of derived characters in the Bouri specimen, which are also found in the neotype from Aïn Boucherit. These characters include a moderate medio-lateral flattening of the horn bases, lateral basal margins of the horn cores being lower than the medial ones, each

horn core having a basal upright stem of c. 100 mm and there being a thickened ridge on the anterior side of the basal part of the horn cores. The latter character is described above as resembling an incipient keel. Furthermore, in the Bouri specimen the coronal suture is very close to the posterior horn core bases. Vrba lists these and additional characters, which are shared between the Bouri specimen and the neotype from Aïn Boucherit (Vrba 1997: 156). It is noteworthy that the main differences between these specimens refer largely to details of horn core curvature. Therefore, on the basis of Vrba's diagnosis of the Bouri specimen there can be little doubt that the Bouri specimen and the neotype from Aïn Boucherit are either conspecific or that the Bouri specimen represents a later form in the lineage of the neotype.

The conclusion is that the skull material assigned to *O. tournoueri* from Aïn Boucherit represents an underived form of alcelaphine, which has some resemblances to *Megalotragus*. Therefore, it should not be included in the same taxon as the original type material of *O. tournoueri* from Aïn Jourdel.

Table 20. Some diagnostic characters of the skull material referred to *O. tournoueri* (Thomas 1884) from Aïn Boucherit. The characters are separated into underived characters resembling a generalised wildebeest-like alcelaphine and derived characters resembling *Megalotragus*.

Generally wildebeest -like	<i>Megalotragus</i>-like
1. Clockwise curvature of horn cores	1. Posterior extension of horn pedicels
2. Inflation and doming of the frontals	2. Partial fusion of the frontals' suture
3. Reduction of posterior part of skull	3. Proximity of the parieto-frontal (= coronal) suture to the horn base
4. Reduction of the temporal fossa	4. Forward slanting face of the occipital
5. Low and wide occipital	5. Projection of the orbits
6. Reduced parietals	6. Inflation of the area between the horn bases
7. Extreme width of the mastoid area	

Upper dentitions

Introduction

Shortening of the premolar row, with accompanying loss of mesial premolars, and increasing hypsodonty are universal trends in the evolution of the tribe Alcelaphini. The former is a response to a distal shift of masticatory stress in the jaw, which also has the effect of increasing the size of the third molar at the expense of the first molar (Chapter 7). These character states appear to have evolved repeatedly and, therefore, cannot be used in establishing phylogenetic relationships, except under certain restricted circumstances. The tendency for the distal molars to be more derived than more mesial ones is probably related to the tendency for masticatory stress to be shifted distally. The idea that the distal part of the alcelaphine toothrow can be viewed as evolutionary advanced is taken into account in analysing both the upper and lower dentitions of the material referred to *Oreonagor tournoueri* from Aïn Boucherit.

Material

The neosyntype upper jaw 1966-5-37 is illustrated in Figure 92 together with a well-preserved right side of an upper jaw fragment 1954-8-17. Figure 93 provides buccal views of M³'s. Another partially preserved upper jaw with M¹–M², 1954-22-137, and numerous individual teeth are not illustrated, but are included in the description, given below.

Description

- In the neosyntype the palate is relatively narrow with the tooth rows less convergent and approaching parallel-sidedness, as in *Damaliscus* and in *Alcelaphus*.
- P³ is reduced relative to *Damaliscus* and *Alcelaphus*, and it is probable that P² would have been even more reduced or lost, as in *Connochaetes gnou* and *M. priscus* (Figure 92; char. 1).
- In comparison with extant alcelaphines molars and premolars are not very hypsodont, which is reflected by the imperfect closure of the buccal wall of P⁴ of some specimens (Figure 92; char. 2).
- Ribs between the styles tend to be moderately prominent, as in wildebeest (Figure 92; char. 3).

- Styles are not as rounded as in extant alcelaphines (Figure 92; char. 4).
- Although the mesostyles of M^3 's in the neosyntype tend to be somewhat reduced (Figure 92; char. 5), this character is variable in other M^3 and M^2 specimens. The reduction of the mesostyle appears to increase from the M^1 to the M^3 .
- Although not well developed in the neosyntype, upper goat folds tend to be present on distal lobes of molars (Figure 92; char. 6).
- Central cavities are less complex than in modern alcelaphines (Figure 92; char. 7).
- Rugosity is moderate, but there is a general tendency towards smoother enamel.
- The mesial lobes of the upper first and second molars are bucco-lingually extended compared to the distal lobes. In the third molars the mesial lobes appear less bucco-lingually extended.
- The lobes of the molars tend to be pointed (Figure 92; char. 8). It appears that this character is more pronounced mesially than distally in the molar row.
- In the isolated M^3 specimens the metastyle tends to become flattened and distally expanded towards the base of the tooth crown, a feature that is variably expressed in the study sample (Figure 93, char. 1).

Discussion

The Aïn Boucherit upper dentitions have the morphology of an underived alcelaphine. This impression is due to the coincidence of the bucco-lingually extended mesial lobes of the first and second molars, the tendency for lobes to be pointed, the presence of upper goat folds, the simplicity of the enamel surrounding the central cavities and a lesser degree of hypsodonty. In these respects the upper dentitions from Aïn Boucherit are less derived than those of extant alcelaphines (*cf.* Figures 36 & 37). The second upper molars from Aïn Boucherit appear more primitive than the Omo specimen illustrated by Gentry (1980: 285; Figure 36), suggesting that it predates the Omo specimen. However, because Gentry does not indicate from which member the illustrated specimen derives, it does not allow further speculation on the geological age of the Aïn Boucherit upper dentitions.

The advanced characters of the upper dentitions include the tendency for reduction of the mesostyle of the M^3 and for the distal expansion of the metastyle. The distal projection of the metastyle, which is considered a derived character of the wildebeest morphological group

(Chapter 7), but is also typical of caprines, appears to be in a stage of evolutionary change, since it occurs distally in the toothrow and it is variably present. The distal projection of the metastyle of the M^3 is interpreted as the re-appearance of a goat-like feature. This feature may have been lost in early alcelaphines, as represented by the morphology seen in *Beatragus hunteri*. *B. hunteri* is considered to represent an underived stage in the evolution of the Alcelaphini (Kingdon 1982). If this interpretation is correct, the process of the re-appearance of the distally projecting metastyle represents an evolutionary reversal. It also suggests that the Aïn Boucherit dentitions referred to the *O. tournoueri* are wildebeest-like, since these two characters, that is a reduction in prominence of the mesostyles and a distally projecting metastyle in the M^3 , can be considered apomorphic for the wildebeest morphological group in relation to the hartebeest group. Their variable presence in *Oreonagor* material from Aïn Boucherit may indicate that the species was undergoing a morphological shift towards being wildebeest-like.

Lower dentitions

Material

The syntypes consist of a right lower jaw with $M_1 - M_3$ (1966-5-133) and a left lower jaw with $P_4 - M_3$ (1954-8-16) (Figure 94).

Description

- Lobes of lower molars tend to be more pointed than in extant alcelaphines (Figure 94; char. 1).
- Enamel surrounding the central cavities tends to be simple in outline (Figure 94; char. 2).
- Lingual indentations are slightly less developed than in extant alcelaphines (Figure 94; char. 3).
- Goat folds are present in reduced form (Figure 94; char. 4).
- Pinching occurs variably, but decreases distally in the toothrow (Table 21).
- Molars are often rugose, but decreases distally in the toothrow (Table 21).
- The premolar row is reduced, with P_2 absent.

Table 21. Quantification, according to the number of observations, of some of the characters on the lower molars referred to *Oreonagor tournoueri* from Ain Boucherit.

Character	M ₁	M ₂	M ₃
One or more pointed lobes	4 (26.7%)	3 (27.3%)	5 (35.7%)
Goat folds	10 (66.7%)	7 (63.6%)	8 (57.1%)
Pinching	5 (33.3%)	1 (9%)	1 (7.1%)
Rugosity	10 (66.7%)	5 (45.5%)	4 (28.6%)
TOTAL NO. OF SPECIMENS	15 (100%)	11 (100%)	14 (100%)

Discussion

In the lower teeth there is a mosaic of advanced and primitive characters (*vide* Figure 39). The characters that can be described as caprine, the presence of goat folds and pointedness in the lobes of the lower molars, do not become more dominant towards the distal part of the toothrow, suggesting that these characters are not evolving. This is in contrast to caprine-like characters in the upper teeth, which are in the process of appearing and can be seen as an advanced condition. However, pinching and rugosity, characters usually associated with the genera *Alcelaphus* and *Damaliscus*, are decreasing distally in the toothrow. This suggests that they were in the process of becoming lost and should be seen as primitive in this context. The overall picture of the dentitions is that they show a tendency to become more caprine in character. This trend is shared with *C. gnou* and *M. priscus*. In *C. gnou* this trend resulted in the evolution of increasingly caprine-like characteristics seen in the dentitions, the skull and the postcranium (Chapter 7).

Humerus

Material

The material consists of six specimens, of which one is complete and another virtually complete specimen, but with damage to its proximal end: 1954-8-218 (complete), 1953-22-112 (almost complete), 1953-22-59, 1954-22-59, 1953-22.114, 1966-5-40.

Description

- The humeri are moderately slender.
- In the complete specimen, 1954-8-218, the tuberculum maius is somewhat squared off, but not as completely as in *Connochaetes* spp. (Figure 95, char. 1).
- The pars cranialis of the tuberculum maius is short and does not overhang the articular head of the humerus (Figure 95; char 2), which is very similar to *Connochaetes* spp. and unlike *A. buselaphus* and *D. pygargus*.
- The crista humeri (Figure 95; char. 3) and the tuberositas deltoidea (Figure 95; char 4) are both well developed and similar to the condition found in *M. priscus* and *Connochaetes* spp.
- The lateral epicondyle is extended (Figure 95; char. 5).
- There is a marked fossa supracondylaris (Figure 95; char. 6), as in wildebeest.

Discussion

The fact that the pars cranialis of the tuberculum maius in 1954-8-218 does not overhang the caput humeri can be considered to be a derived condition, since an overhanging pars cranialis is typical for antilopines, as seen in *A. marsupialis* (Peters & Brink 1992). Although this morphology is observed on only one specimen, it is so extreme that it is unlikely that the reverse of this condition would have been found in the population. At the distal ends the lateral projection of the distal humerus gives the impression of greater width, which is again a wildebeest character.

The humeri from Aïn Boucherit are wildebeest-like in most details. The wildebeest-like derived morphology of the humerus from Aïn Boucherit can be interpreted as an evolutionary trend towards being wildebeest-like, as in the case of the dentitions.

Radius

Material

There are three radii available for study. The most complete of these, 1954-8-218, is from a sub-adult individual and lacks the distal epiphysis. The other two, 1954-13-36 & 1953-22-55, are proximal pieces.

Description

- In lateral view the radii from Ain Boucherit appears slender and curved, as in *A. buselaphus*.
- The attachment for the collateral ligament appears somewhat more laterally extended, as in *C. gnou*.
- Medially there is some degree of dorso-volar compression in the An Boucherit radii. This feature is found more typically in *Connochaetes* spp. and *M. priscus*.

Discussion

Although the incomplete immature radius appears slender and curved, like in *A. buselaphus*, the derived aspects in the radii resemble wildebeest, rather than hartebeest.

Metacarpal

Material

There are two complete specimens, both of the right side, 1954-8-219 and 1953-22-118, and one almost complete left metacarpal, 1954-8-207. Other specimens include a proximal piece, 1954-8-222 and a distal piece, 1954-8-215 (Figure 96).

Description

- The metacarpals are slender, as in hartebeest and specifically *D. pygargus* (Figure 97A).
- The proximal articulation facet is dorsally rounded, as in hartebeest (Figure 96; char. 3).
- Proximally and distally the metacarpals tend not to flare, as in hartebeest (Figure 96; char. 1).
- The part of the shaft immediately proximal of the distal articulation is thickened, as in wildebeest (Figure 96; char. 2).
- The achsial parts of the distal articular condyles are enlarged relative to the distal width (Figure 97B), which is a hartebeest-like morphology.

Discussion

In virtually all respects the metacarpals from Aïn Boucherit are hartebeest-like, except in the thickening of the distal part of the shaft. The obvious similarity of the Aïn Boucherit metacarpals with those of hartebeest-like alcelaphines is illustrated in Figure 97, in which they appear most similar to the blesbok. This may indicate a generally underderived condition for the Aïn Boucherit metacarpals and that they are structurally primitive, as seen in Antilopini. This accords with the greater depth of the achsial part of the distal articular condyles. If the dentitions and the more proximal elements indicate an evolving wildebeest-like morphology, then the metacarpals do not show this. On a general level this is noteworthy, as it may seem to contradict the common assumption that distal elements in ungulates are usually more derived than those more proximally situated. If one accepts that the Aïn Boucherit material was in an evolutionary phase, in which progressively more wildebeest-like morphology was appearing, then these changes are more evident in the skull, dentitions and proximal elements of the manus.

Femur

Material

There are two specimens available for study - a shaft piece, 1953-22120, and a distal piece, 1953-22-108 (Figure 98).

Description

- The femur shaft is relatively slender
- The medial ridge of the trochlea extends cranially, but not as far as in wildebeest (Figure 98, char 1; Figure 99).

Discussion

The femur appears to be relatively gracile, or hartebeest-like. This impression is supported by the plot in Figure 99, which shows that the cranial extension of the medial ridge of the trochlea does not differ from that found in extant hartebeest. This is in contrast to the situation in the front limb, where the humerus, the structural equivalent of the femur, shows indications of advanced wildebeest-like morphology.

*Tibia*Material

Of the five distal tibiae assigned to *O. tournoueri* by Arambourg, one specimen (1953-22-19) appears to be too small and it is not included in this description. The other specimens are all distal pieces: 1954-15-36, 1949-5-4, 1953-22-113, 1966-5-154 (Figure 100).

Description

- The dorsal articulation facets for the os malleolare are reduced (Figure 100; char. 1).
- The plantar articulation facets for the os malleolare are enlarged (Figure 100; char. 2).

Discussion

The enlargement of the plantar articulation facets is a unique feature of *M. priscus* and it can be considered a certain indication of relatedness when found in other alcelaphines (*vide* Chapter 6). The variability in the distal tibiae from Aïn Boucherit suggests that this feature may have been in the process of evolving.

*Metatarsal*Material

The metatarsal remains consist of two proximal specimens, 1954-5-38 and 1954-13-52, and a distal fragment, 1954-13-87.

Comments

The metatarsal material is very fragmentary and little can be deduced from their study, except that they resemble a hartebeest-like medium-sized alcelaphine.

Body proportions of the Aïn Boucherit alcelaphine

In a plot of the body proportions of the Aïn Boucherit material (Figure 101), it is clear that they match those of structurally underived alcelaphines and antilopines. This is particularly evident in the elongation of the metacarpal.

DISCUSSION

In order to discuss the position of the species *O. tournoueri* in the evolution of the genus *Connochaetes*, it is necessary to know whether the original type material from Aïn Jourdel and the neotype material from Aïn Boucherit belong to the same taxon. The answer to this question lies in the comparisons of the skulls and horn cores of the two sets of material (Figures 90 & 91) and in the study of the postcranial elements from Aïn Boucherit, given above. The comparisons suggest that the type material from Aïn Jourdel is unlikely to belong to the same species as the neotype material from Aïn Boucherit. This is particularly evident in the primitive *Connochaetes*-like character of the skull and horn cores of the Aïn Jourdel specimen as opposed to the incipiently *Megalotragus*-like character of the Aïn Boucherit specimen. The advanced characters in the Aïn Boucherit specimen are not found in ancestral or later forms of *Connochaetes* and they are considered to reflect an early stage of *Megalotragus*-like morphology.

The postcrania assigned to *O. tournoueri* from Aïn Boucherit confirm the observations on the skull and horn core materials. The body proportions are primitive, as one may expect in an underived *Megalotragus*-like alcelaphine. The wildebeest-like morphology is better expressed in the front limb and particularly in the humerus, which parallels the extreme development of wildebeest-like morphology in the front limb of *M. priscus* (Chapter 6). Finally, the unique character observed on the tibia of *M. priscus*, which is the enlargement of the plantar articulation facet for the os malleolare (Chapter 6, Figure 74), is also present in incipient form in the Aïn Boucherit material.

If the Aïn Boucherit material represents an underived form of *Megalotragus*-like alcelaphine and the Aïn Jourdel material represents a primitive *Connochaetes*-like alcelaphine, then they should not be included in the same taxon. Given the rule of priority in taxonomy, the Aïn

Jourdel specimen should be re-instated as the type specimen of the species *Oreonagor tournoueri* (Thomas 1884), while the Aïn Boucherit material should be given a new name. For the present purpose the Aïn Boucherit material is not formally named, but for the sake of convenience it is referred to as “species A”. It should be noted that the specimen from Bouri 1, referred to by Vrba as *?Oreonagor/?Megalotragus* sp. (Vrba 1997: 155), should also be included in species A.

The very primitive *Connochaetes*-like morphology of *O. tournoueri* from Aïn Jourdel points to North Africa as the likely area of origin for the genus *Connochaetes*. Such primitive wildebeest-like fossils have not been found until now in East Africa. However, after c. 2.5 million years ago early members of the genus *Connochaetes* had spread to East and probably to southern Africa (Vrba 1997). *Megalotragus*-like alcelaphines may also have originated in North Africa, as suggested by the presence of Species A and another similar species, ‘*Gorgon*’ *mediterraneus* (Arambourg 1979; personal observation).

A further point of interest concerns the origin of an earlier phase of wildebeest-like alcelaphines, *i.e.* the ancestral populations that gave rise to the genera *Connochaetes* and *Megalotragus*. From the postcrania of species A, as described in this chapter, and from the illustrations of the postcrania of *O. tournoueri*, as given by Thomas (1884), it appears that the ancestors of both sets of material were hartebeest-like. This is also suggested by some hartebeest-like tendencies in the dentitions and postcrania of *C. taurinus* (Chapter 6), which implies that hartebeest-like morphology first evolved in early alcelaphines, which later gave rise to the genera *Connochaetes* and *Megalotragus*. In this sense the caprine-like derived morphologies seen in both genera can be interpreted as reversals, which refer back to the caprine origins of very early alcelaphines. As noted (Chapter 3), this re-appearance of previously lost morphologies may be an example of retained genetic material, a process similar to the retaining of fixed morphological characters of which the function is not evident any more (*vide* Turnbull 2002; Mayr 2001).

CONCLUSION

It can be concluded that the material referred to *O. tournoueri* from Aïn Boucherit belongs to a different taxon from the type material of *O. tournoueri* from Aïn Jourdel. The Aïn Jourdel material is a primitive *Connochaetes*-like alcelaphine, while the Aïn Boucherit is an underived *Megalotragus*-like alcelaphine. Given the taxonomic priority of the type specimen from Aïn Jourdel the material from Aïn Boucherit should be renamed and for the present purpose this material is referred to as “species A”. The material from Bouri 1 should also be included in species A.

The genus *Connochaetes* probably originated in North Africa, and not in one of the other arid centres of Africa. It also appears likely that the ancestors of wildebeest-like alcelaphines were hartebeest-like, as is evident in the primitive body proportions and other hartebeest-like characteristics of species A.

The well-dated fossil record of East Africa suggests that the genus *Connochaetes* arrived in that region not later than c. 2.5 million years ago. If the genus originated in North Africa, the appearance of early forms of *Connochaetes* in southern Africa is likely to postdate this time. *C. taurinus* is commonly present in the pre-Cornelian fossil localities of southern Africa (Vrba 1976; Brain 1981), suggesting that the temporal form, *C. taurinus prognu*, as found in North and East African localities, would also have been present in southern Africa at the time of around 1.0 million years ago. The question, whether these populations gave rise to the earliest ancestral forms of the black wildebeest, is further addressed in the next chapter.

CHAPTER 9. THE EVOLUTION OF THE BLACK WILDEBEEST, *CONNOCHAETES GNOU*

INTRODUCTION

In this chapter the fossil evidence for black wildebeest evolution is presented. It is shown how the morphological changes in the earliest fossil populations can be linked to a shift towards a fixed territorial breeding behaviour. In modern black wildebeest populations this kind of behaviour is dependant on open habitat that is visually unobstructed (Chapter 4) and is the mechanism that separates black wildebeest from sympatric blue wildebeest. It is argued that a shift in reproductive behaviour in ancestral black wildebeest marks a major genetic change. This genetic change was the speciation process of the black wildebeest from a blue wildebeest-like ancestor. The pattern in black wildebeest evolution conforms to the concept of Baldwinian co-evolution, which suggests that a behavioural innovations can become genetically fixed and the driving force of evolution (Oppenheimer 2004). It is further argued that morphological shifts in fossil black wildebeest, which followed the speciation process, were due to less fundamental genetic changes, such as drift, or micromutations. Evidence for genetic drift is well expressed in geographical space in peripheral populations in the Cape coastal zone, which were markedly smaller than contemporary black wildebeest populations of the interior.

Black wildebeest fossil localities from the interior of southern Africa and from the Cape coastal zone are discussed in Chapter 5. However, for the sake of convenience these localities are listed in geographic and in chronological order in Table 22.

The fossils from Cornelia-Uitzoek are considered to represent the earliest black wildebeest populations. However, it should be noted that Gentry considers a species described from Olduvai, *C. africanus*, to be the earliest fossil form of the black wildebeest (Gentry & Gentry 1978). This difference in opinion is discussed after considering the southern African fossil evidence for black wildebeest evolution.

The fossil record of the black wildebeest is presented by skeletal element in the natural anatomical sequence, as in Chapters 7 and 8. The morphology of the fossil specimens are

described and discussed with reference to the morphological characters given in Chapter 7. Measurements are used to complement the anatomical descriptions (*vide* Chapter 3) and to outline temporal patterns in more detail. An attempt is made to present the material in a chronological order and to separate the interior material from the coastal material, as far as is possible. Therefore, fossil black wildebeest skull material from the interior and the Cape coastal zone are discussed under separate headings. The fossil dentitions are treated in the same way, although not under separate chronological headings. The postcrania are presented only per skeletal element, because of the large temporal gaps in the fossil record of the Cape coastal zone.

Table 22. A chronological list of selected fossil assemblages from the interior of southern Africa and from the Cape coastal zone, which have produced fossil materials of black wildebeest.

GEOLOGICAL TIME	LAND MAMMAL AGE	INTERIOR ASSEMBLAGES	CAPE COASTAL ASSEMBLAGES
Holocene	Recent	Deelpan Maselspoort Kareepan	
Late Pleistocene	Florisian	Spitskop Mahemspan Sunnyside Pan	Elandsfontein Bone Circle Swartklip 1 Sea Harvest Klasies River
Middle Pleistocene	Florisian	Florisbad	Elandsfontein
End-Early Pleistocene	Cornelian	Cornelia-Uitzoek	Duinefontein 2 Elandsfontein

SKULL AND HORNCORES

Interior Cornelian

Description

The oldest fossils in southern Africa that can be recognised as ancestral to *C. gnou* are from the end-Early Pleistocene site of Cornelia-Uitzoek. There are a number of horn core specimens from the Van Hoepen collections. One is the type specimen of *C. gnou laticornutus* Van Hoepen 1932, which is considered to be a female (Gentry & Gentry 1978). A previously unnumbered specimen (COR 2838), a complete horn core pair and braincase presumably collected in the time of A.C. Hoffman, is referred to in Gentry & Gentry (1978: 365) and is evidently a male, because of its size and enlarged basal bosses (Figure 102). Complete material collected in the course of this study include a horn core pair without braincase, COR 1991, which is illustrated in Brink & Rossouw (2000; Appendix D), a hornless partial braincase with most of the frontals preserved, COR 2826, and an almost complete right horn core, COR 2624.

The sample of horn cores and partial crania from Cornelia-Uitzoek is large enough to provide an impression of intra-population variability. Sexual dimorphism appears to have been more pronounced than in living populations of blue wildebeest. The specimen COR 2838 exceeds the size of the largest male *C. taurinus* in the Florisbad modern comparative collection. The Cornelian horn cores are generally similar to *C. taurinus*, but they differ in having incipient basal bosses in the males, as can be seen in COR 2838 (Figure 102, char. 1). As noted by Gentry, basal bosses in female specimens from Cornelia-Uitzoek, such as the type, are smaller than those of the males and are similar in size to those of extant males of *C. taurinus* (Gentry & Gentry 1978). Variability in the basal bosses of males is evident in the more pronounced inflation of the basal area in COR 1991, but less so in COR 2838. When compared to *C. taurinus* there is a tendency for the Cornelian horns to be inclined more forward and to be less sharply recurved (*vide* Van Hoepen 1932b; Gentry & Gentry 1978; Figure 102). The latter is characteristic of primitive wildebeest (Gentry & Gentry 1978). The variability in curvature seems random and not determined by sex, unlike the basal boss development. The space in between the horn bases of the Cornelian specimens is larger than in extant *C. taurinus* and the frontal area tends to be more flattened than in *C. taurinus* (Figure 102, char. 2).

The horn insertions are not as posteriorly positioned as in *C. taurinus*. However, compared to *C. taurinus* the horn bases extend more posteriorly (Figure 102, char. 3) so that they approach the nuchal line and the occipital protuberance. The horn insertions are wider apart than in *C. taurinus* (Figure 102, char. 4), similar to the condition in *Connochaetes* sp. from Olduvai Beds I and II (Gentry & Gentry 1978). The occipital protuberance tends to be more prominent than in *C. taurinus* (Figure 102, char. 5). This feature and the wide horn insertions represent underived morphologies. A similar prominence in the occipital protuberance is found in the type specimen of *Oreonagor tournoueri*, which is a primitive wildebeest (Chapter 8).

In all specimens from Cornelia-Uitzoek the frontals' suture is largely or partly fused (Figure 102, char. 6). However, in COR 1991 the frontals' suture appears to be less fused than in COR 2838. Since the fusion of the frontals' suture represents an advanced state in *Connochaetes*, the lesser degree of fusion of the frontals' suture in COR 1991 is in contrast to the expansion of its horn bases, which are in a relatively advanced state.

COR 2838 and COR 2826 have antero-posteriorly shortened and dorso-ventrally flattened braincases compared to *C. taurinus* (Figure 102, char. 7). This is reflected by the shortened basioccipital. The basioccipital also has a flattened valley between the tubercula muscularia, which is like *C. gnou*. Although somewhat damaged the tubercula muscularia in COR 2838 appear to have been rather sharply demarcated resembling *C. gnou*. The spaces for the auditory bullae in COR 2838 are large, as in *C. taurinus*.

Discussion

Virtually all the skull characters that can be considered advanced are associated with agonistic behaviour in black wildebeest, as described in Chapter 4. These characters can be seen in various stages of development in the Cornelia-Uitzoek assemblage. The fact that these characters appear as a mosaic suggests that they are in a state of change, as might be expected in an evolving lineage.

The incompleteness of the fossil material prevents an evaluation of characters such as the size and protrusion of the orbits and the size of the paroccipital processes. Facial shortening can be

addressed indirectly by the lower dentitions, where the size of the M₂ and premolar shortening are used as proxies for facial shortening.

Interior Florisian

Description

There appears to be very little variability in the curvature of black wildebeest horn cores from Florisbad in spite of the time span represented by the spring material (Chapter 5). The horn core curvature of the Florisian form of *C. gnou* is intermediate between specimens from Cornelia-Uitzoek and the modern black wildebeest specimens. From a well-preserved horn core pair (FLO 6500) (Figures 102C & D) and from another virtually complete specimen, which has most of the braincase and horn cores preserved (FLO 6501), it is clear that, apart from the horn core curvature, almost all the characters of modern black wildebeest are present. The basal bosses are fully developed (Figure 102, char. 8), the horn bases have reached their extreme posterior position on the skull (Figure 102, char. 9), the frontals' suture is fully closed (Figure 102, char. 10), the forehead is flat or concave (Figure 102, char. 11), the braincase is flattened and shortened and the basioccipital is short with a flattened valley in between the tubercula muscularia. Poor preservation does not allow a direct assessment of the size of the auditory bullae and of the paroccipital processes. However, the morphologies associated with these two characters suggest that they too would have been in the modern state. It is only the curvature of the horns that are not yet fully modern (Figure 102, char. 12).

A horn core pair from Mahemspan has essentially the same morphology as the Florisbad specimen, but another one, now fragmented, is referred to by Gentry & Gentry (1978) as having a more advanced curvature than typical horn cores from Florisbad. If the ESR dates of Mahemspan are reliable, this variability would suggest that black wildebeest horn cores were in a stage of transition at the time of the Last Glacial Maximum.

Holocene black wildebeest horn cores, such those from the Holocene hyaena dens at Spitskop and from Deelpan, are modern in all respects.

Discussion

There is virtually no difference between the Florisian black wildebeest skulls and modern ones, except for the curvature of the horn cores. The curvature is not as downward and forward, as in modern examples. It seems that the curvature of the horn cores may have assumed its modern aspect as recently as the Last Glacial maximum. From the shape of the horns it is inferred that the social behaviour the Florisian black wildebeest was indistinguishable from the modern. If the Florisbad spring dates are reliable, the skull form of the black wildebeest seems to have changed very little over a period of time approaching 400 000 years.

Cape Cornelian

Description

The Elandsfontein horn cores (Klein & Cruz-Urbe 1991) and the newly described specimen from Duinefontein 2 (Klein *et al.* 1999) are in the same general stage of evolution as the specimens from Cornelia-Uitzoek. The horn cores tend to be more anteriorly inclined than *C. taurinus* and have incipient basal bosses. However, the Cape horn cores appear smaller, more compact and seem to have less recurving tips than those from Cornelia-Uitzoek. There are no preserved crania to evaluate their relationship with specimens from Cornelia-Uitzoek.

Discussion

Although the skull materials from Cape coastal localities are not as complete as those from the interior, they provide some impression of biogeographic differentiation between interior and coastal populations. The differences between the Cornelian black wildebeest horn cores from Elandsfontein and Duinefontein 2 and those from Cornelia-Uitzoek are on a similar scale to those observed between *M. priscus* from Elandsfontein and from Florisbad. In both cases the horn cores are somewhat shorter and more compact with less sharply recurved horn core tips.

The difference in horn shape between interior and coastal Cornelian black wildebeest has bearing on the question of whether the *M. priscus* from Elandsfontein is correctly associated with the Cornelian component of the fossil assemblage. Given that *M. euicornutus* is associated with the interior Cornelian and that *M. priscus* is likely to be a Florisian immigrant

(Chapter 6), it is more probable that the *M. priscus* from Elandsfontein forms part of the Middle Pleistocene Florisian component of the site. This question can be addressed further through renewed fieldwork at the site and with the application of new dating techniques.

Cape Florisian

Description

There are no Florisian black wildebeest horn cores available from Elandsfontein (Klein & Cruz-Urbe 1991; personal observation). Late Pleistocene skull fragments from Swartklip with incompletely preserved horn cores appear to represent fully modern crania of black wildebeest. Apart from the Swartklip specimens there are only fragmentary horn cores from other Florisian Cape coastal localities.

LOWER DENTITION

Interior

On morphological grounds it is virtually impossible to distinguish between the lower dentitions from Cornelia-Uitzoek and those from Florisbad or geologically younger sites. This suggests that the tendency towards smooth enamel surfaces and simplicity in occlusal outline appeared very early in Cornelian *C. gnou* or it may reflect that this morphology was already present in its assumed immediate ancestor, the southern populations of *C. taurinus prognu*. Given that the dentitions of *C. taurinus prognu* from Tighenif have smoother enamel surfaces and less complex occlusal morphology than living blue wildebeest, the latter explanation seems more probable. This would suggest that the tendency towards rugosity and complexity in occlusal enamel patterns is of recent origin in the blue wildebeest.

The lower dentitions from Cornelia-Uitzoek are large (Figure 103). Two complete wildebeest tooththrows from Cornelia-Uitzoek fall within the upper limit of the size variation of extant *C. taurinus* (Figure 103A). The same applies to a single lower jaw from Tighenif. In order to complement the small Cornelian sample of complete tooththrows, the M₂ was selected for further analysis, since it can be used as a proxy for jaw size and the size of the snout. In alcelaphines the occlusal length and width dimensions of the M₂ are not much affected by the stage of wear, in contrast to the M₃ and the M₁ (Brink *et al.* 1999). This is an advantage in

that the M_2 can be used for size comparisons regardless of the stage of wear. The Tighenif specimens ($n = 41$) are similar in size to the specimens from Cornelia-Uitzoek ($n = 12$), but both are larger than *C. taurinus* (Figure 104A). There is no statistical difference in the occlusal length ($F(1.5) = 3.14$; $p > 0.5$) and in the occlusal width ($F(1.49) = 2.06$; $p > 0.05$) of the M_2 between Cornelia-Uitzoek and Tighenif.

The premolar row of Cornelian *C. gnou* is shortened in relation to that of *C. taurinus*, but it is not as pronounced as in later forms (Figure 103B). The incipient stage of premolar row shortening suggests that this character is in the process of transition, comparable to the character states of the horn cores and skull base mentioned above.

Lower tooththrow dimensions from the Florisbad spring overlap with the modern sample (Figure 103A). A plot of the M_2 's from Florisbad shows overlap with Spitskop, Kareepan and with the modern sample (Figure 104A). This can be interpreted as an indication that from the Middle Pleistocene to the present there has been no reduction in size in lower jaw and, by implication, no reduction in snout dimensions (Figure 104B).

Cape coastal zone

The lower dentitions from the Swartklip 1 assemblage are morphologically and metrically indistinguishable from those of the interior Florisian and of modern *C. gnou* (Figure 103). This applies to absolute dental dimensions and also to premolar row shortening. This is in accordance with the presumed Late Pleistocene age of Swartklip 1. It is noteworthy that there is no evidence for size change in the lower dentitions given the biogeographically peripheral position of the Swartklip fossil population in relation to contemporary inland populations.

Discussion

The dimensions of the M_2 of Tighenif are similar to those of Cornelia-Uitzoek and this supports the impression gained from the skulls and horn cores that *C. gnou laticornutus* was similar in size to *C. taurinus prognu*. The difference in size of the M_2 between *C. taurinus prognu* and modern blue wildebeest indicates that in the intervening time period there was dental size reduction in *C. taurinus*. This supports the conclusion drawn from observations on

the skulls and horn cores that in the time after the Cornelian LMA the *C. taurinus* lineage also underwent morphological changes that can be interpreted to reflect genetic drift.

Size reduction in the M₂ reached its modern state at the time of the Florisian LMA, suggesting that no facial reduction occurred since this time. It appears that this is also valid for the Cape coastal populations, suggesting that biogeographic isolation did not have the effect of reducing the size of the face.

Premolar row shortening in the specimens from Cornelia-Uitzoek almost approaches the modern condition and this is in contrast to the incipient stage of reduction in the size of the M₂. It suggests that premolar shortening was in advance of facial size reduction.

POSTCRANIUM

Axis

The axes in the Cornelia-Uitzoek collections are comparable in length to *C. taurinus*, but are considerably more robust (Figure 105). The concavity on either side of the crista ventralis is more hollowed in axes from Cornelia-Uitzoek and in this respect they are more like *C. taurinus* than the extant *C. gnou*. In the four specimens available from Florisbad this feature is similar to extant *C. gnou* (Figure 105).

There is a decrease in stoutness of the axis, seen in the measurement SBV (the width of the body of the vertebra), from the Cornelian *C. gnou laticornutus* sample through the Florisian samples to the modern (Figure 105B). The specimens from Florisbad, Spitskop and Kareepan cluster near the upper limit of variation of living *C. gnou* (Figure 105B). The specimens cluster tightly enough to suggest that they represent a morphologically stable population over time. A single specimen from the Late Holocene site of Deelpan falls within modern limits of variation of *C. gnou*. Size reduction in ancestral *C. gnou* appears to have coincided with decreasing robustness as seen in the different slopes of the regressions lines in Figure 105B. That is, fossil populations had more robust axes than extant populations, suggesting that ancestral black wildebeest probably had heavier heads, horns and necks than the ancestral and modern blue wildebeest and modern black wildebeest.

Although the three Late Pleistocene specimens from Swartklip cluster within the modern comparative sample, the sample is too limited to confirm whether its small size is representative of the fossil population. The patterns observed for the width of the body of the axis in the various fossil assemblages seem to be mirrored largely by the plots of the cranial articular surface (Figure 105A & B)

Humerus

Although the proximal humerus is very distinctive (Chapter 7), it is fragile and seldom preserves in a complete state. Of all the diagnostic characters it is only the appearance of the longitudinal ridge in the fossa radialis that can be observed in the fossil record. In the two specimens from Cornelia-Uitzoek this character is not yet present, but it is variably expressed in Florisbad sample. This character is present in all later material.

The distal ends usually preserve well and, given that the distal width correlates with the length of the humerus ($r = 0.77$; $p = 0.001$), it is possible to use the distal ends for size comparisons between different fossil populations. Metrical comparisons were based on two sets of measurements, the width of the trochlea (BT) plotted against cranio-caudal depth of the medial part of the distal end (Dmd) and the width of the trochlea plotted against the distal width (Bd) (Figures 106 & 107). In the central interior the cranio-caudal depth and trochlea width of the distal humerus of *C. gnou* decrease from Cornelian to Florisian times (Figure 106A). The distal dimensions of two specimens from Cornelia-Uitzoek seem to represent a population larger in size than *C. taurinus*. One specimen falls inside the 95% limit of variation of *C. taurinus* and the other close to the lower limit of variation of Mahemspan *M. priscus*. The samples from Florisbad, Maselspoort, Kareepan and *C. gnou* cluster together and are only marginally larger than modern *C. gnou* (Figure 106A).

The Swartklip sample clusters in the lower half of the modern *C. gnou* sample, somewhat reduced in size compared to Florisian and Holocene samples from the interior.

When distal width is taken into account some relative changes in proportions of the distal humerus can be observed. In the Florisbad sample there is a slight proportional increase in distal width, compared to *C. taurinus*. In this respect the three specimens from Cornelia-

Uitzoek appear more like *C. taurinus* (Figure 107A). The relationship between BT and Dmd visible in the Florisbad material is also seen in a single specimen from Spitskop, in the mid-Holocene samples from Maselspoort and Kareepan and in the modern sample of *C. gnou*. In the late Florisian sample from Swartklip this trend is even more accentuated. Of all fossil and modern *C. gnou* the humeri of the populations represented by Swartklip had proportionally the widest distal ends, but the narrowest trochleae (Figure 107B).

In both sets of distal measurements (Figures 106 & 107) the material from Cornelia-Uitzoek is larger than that of *C. taurinus*. Florisbad, Kareepan and Maselspoort form a tight cluster towards the upper end of variation of extant *C. gnou*, but do not exceed it. This suggests that from the Florisian until the mid-Holocene there was little change in the size of the distal humerus in *C. gnou* and that size reduction probably occurred after the mid-Holocene.

The Late Pleistocene material from the Cape coastal zone is more reduced in size than contemporary populations from the interior. The progressive widening of the distal end of the humerus is of interest, as it is in part due to an increase in projection of the lateral epicondyle and an increase in projection of the attachment for the collateral ligament on the lateral distal end (*vide* Nickel *et al.* 1992). This is also seen in much larger format in *M. priscus*, and is presumed to be a response to greater stress on the elbow joint. It suggests that Swartklip populations of black wildebeest had smaller, but more compact upper forelimbs than living populations.

Radius

There is only one proximal radius specimen from Cornelia-Uitzoek. In this specimen the lateral part of the proximal articulation is less extended laterally and the incision for the lateral coronoid process of the ulna is deep, as in *C. taurinus*. Although this specimen suggests that *C. gnou laticornutus* was blue wildebeest-like in its morphology, it cannot be predicted what the trend in variability would have been in the fossil population from Cornelia-Uitzoek. In the fossil samples from Florisbad and in all later occurrences advanced black wildebeest-like morphology has been established (*vide* Chapter 7).

The few complete fossil specimens available limit the scope for comparisons. The proximal dimensions are used as proxies for complete measurements. Distal width seems to be a less satisfactory measurement, because of great variability in the way that the distal ulna attaches to the radius. The metrical results from the radii of fossil *C. gnou* assemblages from the interior broadly support the patterns observed for the humerus (Figure 108A). The Florisbad specimens and the mid-Holocene specimens from Kareepan and Maselspoort cluster near and beyond the upper extreme of modern *C. gnou*. The late Holocene specimens from Deelpan cluster within the upper range of variation of modern *C. gnou* (Figure 108A). The mid-Holocene samples show the pattern seen in the humerus, suggesting that the forelimb of *C. gnou* had not reached its present reduced size by the mid-Holocene.

The small sample of complete radii from Swartklip clusters within, but at the lower limits of variation of extant *C. gnou* (Figure 108B). This pattern is supported by a larger sample of proximal radii from Swartklip (Figure 108B). In contrast to the distal humerus the Swartklip radii are similar in proportions to other fossil samples and the modern sample of *C. gnou*.

Metacarpal

The sample from Cornelia-Uitzoek consists of three distal metacarpals. Two of these specimens show distal flare and dorso-ventral flattening in the shaft that tend towards the modern condition. In the interior Florisian and mid-Holocene samples the modern morphology seems to be established in all respects. Proximally the tuberositas ossis metacarpalis is reduced, while distally the shaft of the metacarpal has the distinctive distal flare and dorso-ventral flattening (*vide* Chapter 7). In the coastal samples the modern morphology of the metacarpal is fully expressed, even in the single Cornelian specimen from Elandsfontein (see below). Therefore, in the earliest ancestral populations of black wildebeest from the interior and from the Cape coastal zone modern morphology was appearing or already present.

Bivariate plots were made of length against shaft width (Figure 109A), length against distal breadth (Figure 109B), proximal depth against proximal width (Figure 110A) and smallest shaft depth against distal width (Figure 110B). Figure 109A gives an impression of size and robusticity, while Figure 109B reflects size and the extent of weight bearing response in the metacarpal. Proximal (Figure 110A) and distal (Figure 110B) measurements were added to

the analysis to allow the inclusion of incomplete specimens from Cornelia-Uitzoek and to enlarge the sample sizes.

In the interior the metacarpal reduces in size from the Cornelian LMA to the modern-day. Length dimensions indicate that the Florisbad sample clusters within the combined mid-Holocene sample, but that these materials are larger than modern *C. gnou* (Figures 109A & B), suggesting stasis in metacarpal size from the Florisian to the mid-Holocene. Therefore, the modern size of the metacarpal is reached only after the mid-Holocene, as can be seen in the material from Deelpan. This pattern is repeated in the proximal and distal plots (Figures 110A & B).

The relationship between metacarpal length and shaft width in Florisian and mid-Holocene samples from the interior is similar to that of modern *C. gnou*. However, distal width reduces proportionally with the increase in bone length in modern *C. gnou* (Figures 109A & 109B). In a similar way proximal depth decreases with an increase in proximal width in modern *C. gnou* (Figures 110A & B). In the bovid metacarpals distal width increases in response to loading. To a lesser extent the response is also seen in proximal width. This implies that the neck and head weight was reduced in black wildebeest after the mid-Holocene. This hypothesis may be tested once suitably preserved skull material becomes available from the mid-Holocene.

The Late Pleistocene samples from the Cape coastal zone are in all respects smaller than contemporary interior populations. The shaft and distal width dimensions of the Swartklip sample indicate that it was more robust than modern and contemporary Florisian populations from the interior (Figure 109A & B). The fact that the Swartklip material represents a restricted period of time in the Late Pleistocene provides the opportunity to evaluate the mixed Elandsfontein samples. In Figures 109 and 110 it is evident that there are at least three time periods represented; a Cornelian phase represented by the specimens clustering with *C. taurinus* and larger, a mid/late-Florisian component clustering with Florisbad and the mid-Holocene samples from the interior and a Late Florisian component represented by the Bone Circle material. The Bone Circle specimens cluster at the lower limit of variation of the Swartklip materials. The lack of temporal resolution in the Elandsfontein metacarpals precludes a more detailed discussion on the relationship between coastal and interior materials during the Cornelian LMA and the Florisian LMA.

Femur

Because the femur does not preserve as well as other limb elements, mainly shaft pieces are available for study. Therefore, only univariate metric comparisons based on shaft width (SD) were undertaken. The assumption that shaft width (SD) is proportional to bone length (GL) has been tested by a correlation analysis of femur length and shaft width of extant *C. gnou* (Figure 111A). A test of linear correlation (Pearson r) showed that this assumption is justified.

Figure 111B shows that there is no significant difference between samples of modern *C. gnou* and the combined mid-Holocene samples of Maselspoort and Kareepan. This suggests from the mid-Holocene there was no reduction in the size of the femora of fossil *C. gnou* from the interior. The Swartklip sample is also statistically indistinguishable from the modern *C. gnou* sample.

Tibia

There are only distal parts of the tibia available from Cornelia-Uitzoek and there are no characters in the distal tibia that allow distinction between black and blue wildebeest (*vide* Chapter 7). This precludes an evaluation of morphological change in early populations of ancestral black wildebeest. The two complete specimens from Florisbad appear modern in that the tibia is recurved in both dorsal and plantar views and that the proximal part of the shaft on the plantar side is hollowed. Other proximal pieces from Florisbad show the same morphology. All geologically younger specimens from the interior and from the Cape coastal zone show the modern morphology.

The metrical comparisons of the tibia are given in Figure 112 and in Figures 113A and B. All complete fossil specimens from Florisbad and geologically younger sites fall within the variation of modern *C. gnou* (Figure 112). This is unexpected, given the observations on the front limb. However, when dimensions of the distal tibia are considered (Figure 113A & B), it appears that the small sample sizes of the complete tibiae present a skewed impression of the variability in these fossil populations.

The distal tibiae from Cornelia-Uitzoek fall within the cluster of *C. taurinus*. This is in contrast to the M₂, the humerus and the metacarpal from Cornelia-Uitzoek, which appear larger than extant *C. taurinus*. The Florisbad specimens are markedly smaller than the Cornelia specimens. They overlap with the lower limit of variation of *C. taurinus*, but coincide with the upper limits of Maselspoort and Kareepan assemblages. The Florisbad specimens overlap slightly with the upper limit of variation of modern *C. gnou*. The Deelpan specimens cluster entirely within the modern sample (Figure 113A).

In Figure 113B a distal tibia from Klasies River plots within the lower range of variation of the Florisbad sample, within the combined mid-Holocene sample and within the sample of modern *C. gnou*. However, black wildebeest tali from Klasies River, which are discussed elsewhere (*vide* Brink *et al.* 1999; Appendix D), cluster with the Florisbad assemblages and are larger than the tali of modern *C. gnou*. Therefore, although the distal tibia and the talus articulate in the skeleton, the two elements responded differently in the course of black wildebeest evolution. The assemblage from Swartklip is markedly smaller than the mid-Holocene material from Kareepan and in some cases even smaller than modern specimens (Figure 113B).

Besides a reduction in size, there is a temporal trend in the distal tibia that suggests that the dorso-plantar depth of the distal tibia (Dd) decreases with increased distal width (Bd). The regression lines in Figures 113A and 113B illustrate this trend. This trend is evidently not a response to a general reduction in body size, since the smallest distal tibiae from Swartklip has a Dd/Bd relationship that resembles that of the Florisbad tibiae. This temporal trend may also suggest that the Late Pleistocene black wildebeest populations of the Cape coastal zone descended from interior Florisian populations.

Metatarsal

There are no unique external morphological characters in the metatarsals of modern *C. gnou* that distinguish them from *C. taurinus* (Chapter 7). However, there are metrical and proportional differences. The metatarsal is more common and better represented in the fossil collections than the metacarpal. This applies in particular to the material from Elandsfontein and from Sea Harvest.

Length (GL) and shaft width (SD) dimensions of fossil *C. gnou* are illustrated in Figures 114A and 114B. A reduction in robusticity and size in time can be observed in the material from Florisbad, Kareepan and Maselspoort. The Maselspoort/Kareepan sample is intermediate in size between extant *C. gnou* and Florisbad *C. gnou*. It appears that during the Florisian reduction in length of the metatarsal lagged behind that of the metacarpal. Also, reduction in metatarsal length was more gradual than in the metacarpal (Figures 109A & 114).

The patterns indicated above are essentially duplicated by proximal measurements (Figure 115). It is noteworthy that the single specimen from Cornelia falls within the 95% confidence limits of extant *C. taurinus*, but very close to the limits of the Florisbad cluster. This may represent the smaller end of a size spectrum in the Cornelia-Uitzoek specimens, or it may indicate that in the metatarsal the distinction between these assemblages was not well defined.

The linear relationship between metatarsal length and shaft and the relationship between proximal width and depth, as seen in modern *C. gnou*, appear to have been established by the Florisian LMA (Figures 114A & 115).

As in the case of the metacarpals, the metatarsals from Elandsfontein suggest three phases of fossil accumulation at the site; a Cornelian phase, an earlier Florisian phase and a late Florisian “Bone Circle” phase (Figure 114B). The Cornelian phase is represented by one specimen, which plots outside the Florisbad cluster (Figure 114B). The Florisian component coincides with the mid-Holocene sample from Maselspoort and Kareepan. The Bone Circle metatarsals are smaller and comparable in length with those from Swartklip, but have more slender shafts. The Swartklip specimens plot at the lower end of variation of *C. gnou*, but have robust shafts, more like the Florisbad metatarsals. The Sea Harvest specimens cluster with those of Swartklip.

In proximal dimensions the Elandsfontein Bone Circle specimens overlap with those from Swartklip. The Sea Harvest sample of proximal metatarsals coincides entirely with the Swartklip sample.

DISCUSSION

Introduction

The fossil record allows an appreciation of evolution in geological time, but also in geographical space. Although the temporal and geographical components of evolution are linked, these components are separated to aid the discussion.

Black wildebeest evolution in geological time

Temporal trends

The temporal trends in the black wildebeest fossil record are outlined and summarised in Figures 116 to 118. The focus is on the interior of southern Africa, because it has the oldest fossils, the longest and most continuous fossil record and because today and historically black wildebeest occurred as natural populations in the interior (Chapter 4). In outlining the temporal trends in black wildebeest evolution the revised chronology of fossil localities and assemblages, as given in Chapters 5 and 6, provides a temporal framework.

Due to the incompleteness of fossil preservation, certain measurements and combinations of measurements are taken as substitutes for others in a given skeletal element. These values give an approximation of size and robusticity in fossil black wildebeest (Figures 116 to 118).

The M_2 and toothrow/molar row are used as indicators of facial shortening and associated adaptations, as discussed in the text. For the axis the product of the length and width of the corpus (LCDe X SBV) is used. The axis can be taken as a proxy for neck dimensions. In the humerus the distal width and trochlea width (Bd X BT) give a better approximation of bone length (GL) ($r = 0.84$; $p = 0.0001$) than only Bd. For the radius bone length and breadth of the proximal articular facet (GL X BFp) ($r = 0.922$; $p = 0.00$) and proximal breadth and breadth of the proximal articular facet (Bp X BFp) ($r = 0.71$; $p = 0.001$) are given as proxies for bone size. There is a good sample of complete metacarpals (GL), which allows a consideration of length changes through time. However, the width dimensions of the shaft (SD) are included to allow an impression of stoutness (GL X SD). The width of the shaft (SD) is used as a substitute for the length of the femur (*vide* Figure 111). Distal width and distal depth (Bd X

Dd) are used in the tibia as a proxy for length (GL) ($r = 0.61$; $p = 0.006$). For the metatarsal, bone length and shaft width (GL X SD) are used in the same way as in the metacarpal. The proximal width and depth of the metatarsal was also tested (Bp X Dp), but was found not to be useful as a proxy for bone length ($r = 0.17$; $p > 0.05$).

The temporal trends in the fossil history of the black wildebeest can be summarised as follows:

- In the earliest black wildebeest from Cornelia-Uitzoek the horn bases are enlarged and incipiently inflated, while the skull base is dorso-ventrally flattened. In these populations the premolar row is already much reduced, which is a reflection of the changes to the horn bases and skull base.
- In the time between the Cornelian and the early Florisian the premolar row and the head (M_2) underwent relatively rapid change to reach their modern proportions and dimensions in the Florisian LMA, which remained unchanged until today.
- The neck (axis) and the humerus also reduced relatively rapidly in the time between the Cornelian and the early Florisian. During the Florisian there was no change in size in the axis, humerus and radius.
- The whole of the front limb underwent size reduction at the time of the mid-Holocene, a pattern that is more extremely expressed distally in the radius and metacarpal. The whole of the front limb reached its modern dimensions some time after the mid-Holocene.
- The pattern of change in the hind limb differs from that seen in the front limb. In the Cornelian specimens tibia size reduction preceded the humerus, being already of the size of extant *C. taurinus* or smaller.
- During the Florisian there was no size change in the tibia. There was a marked mid-Holocene size reduction in both the tibia and the metatarsal, as in the front limb.

The origin of the black wildebeest

The first question that can be addressed from the fossil record concerns the origin of the first populations of black wildebeest. It has been suggested that the black wildebeest originated from an early form of blue wildebeest (Gentry 1978; Brink 1993), which was probably a southern population of *C. taurinus prognu*. This suggestion can be tested by the data presented in this chapter.

If *C. taurinus prognu* is the last common ancestor of modern *C. taurinus* and modern *C. gnou*, one may expect to find primitive characters in *C. taurinus prognu*, which are shared with the earliest forms of *C. gnou*. In both *C. taurinus prognu* and *C. gnou laticornutus* the horns are not as sharply recurved as in modern *C. taurinus* or in *C. gnou* (Gentry & Gentry 1978; Geraads 1981). Other shared characters are the large size of *C. taurinus prognu* and *C. gnou laticornutus* and the tendency towards simplicity in enamel patterns in the molars and the smoothness of the enamel of the molars, as seen in the material of Tighenif. The M₂ of the *C. taurinus prognu* type material from Tighenif could be directly compared with the material from Cornelia-Uitzoek and shows that statistically the two fossil populations are not different. Apart from the M₂ it was not possible to compare the other skeletal elements of *C. taurinus prognu* with those of *C. gnou laticornutus* from Cornelia-Uitzoek, because the material was not available for study in the Natural History Museum in Paris. However, the size of the axis and of the distal humerus provide indirect evidence in support of the horn cores and the M₂ that ancestral black wildebeest were larger than modern blue wildebeest.

This evidence can be taken as support for the hypothesis that the earliest populations of black wildebeest evolved from southern populations of *C. taurinus prognu* and that these populations were larger in body size than extant *C. taurinus*. Gentry's (1978) hypothesis can now be presented as a phylogenetic diagramme (Figure 119).

It will be possible to test this hypothesis further through an analysis of the cranial and postcranial materials of *C. taurinus prognu* from Olduvai and when suitably complete and dated pre-Cornelian materials from southern Africa become available.

Evolutionary patterns

The temporal patterns in Figures 116 to 119 can be summarised as consisting of an initial shift in cranial morphology, followed by longer periods of almost no morphological change and punctuated by times of rapid change. This pattern has been termed “punctuated equilibria” (Eldredge & Gould 1972; Chapter 3), which can be described as “rapid rearrangement of constraints, followed by periods of stability” (Ruse 1992).

It appears that the fossil material from Cornelia-Uitzoek represents a time of rapid change, which can be assumed to reflect the process of macromutation, when a new species, *C. gnou*, appeared in the fossil record. The diagnostic cranial characteristics of black wildebeest were in an early stage of evolution. From the variability in the expression of these characters, such as the inflation of the basal areas of the horns, the size of the basal boss and the degree of fusion of the frontals’ suture, it can be deduced that the process was dynamic and that changes occurred rapidly. The abrupt appearance of such novelties, seen in the material from Cornelia-Uitzoek, can be interpreted as the sudden phenotypic expression of mutations to homeobox genes (Schwartz 1999; Chapter 4). Since such changes can happen in sympatric populations, there is no need to invoke biogeographic isolation to explain the appearance of the first ancestral populations of black wildebeest. The black wildebeest fossil record of the interior conforms to Goldschmidt’s prediction that speciation occurs rapidly through macromutations (Goldschmidt 1940).

Micromutation, on the other hand, is thought to occur within a species and can lead to variation, but not necessarily to speciation (Goldschmidt 1940; Schwartz 1999; Chapter 3). Morphological change in the post-Cornelian fossil history of the black wildebeest can be ascribed to micromutations, or drift. The Florisian LMA, mainly represented by the materials from Florisbad and Spitskop in Figures 116 to 118, covers a time of some 400 000 years. In the interior this time in black wildebeest evolution is characterised by only minor changes in the shape and size of both cranial and postcranial elements. The period of relative stability in the morphology of fossil black wildebeest is matched by the stability in the taxonomic composition of the Florisian large mammal faunas of the interior. The long period of equilibrium in the interior Florisian ecosystem spans most of the Middle Pleistocene and Late Pleistocene (Chapter 6).

During the mid-Holocene in the relatively short time represented by the materials from Kareepan and Maselspoort there was a general reduction in body size in all skeletal elements, excluding the cranial elements. This represents an evolutionary punctuation in the course of black wildebeest evolution in that size reduction occurred in virtually the whole body and far exceeded the degree of morphological change seen throughout the Florisian LMA. Although the mid-Holocene was a time of rapid size reduction, the time between approximately the Last Glacial and the mid-Holocene shows that size reduction of the hind limb preceded that of the front limb. In this sense changes in the various skeletal elements were not in phase and followed a mosaic pattern. There is good evidence for palaeo-environmental change during the mid-Holocene in central southern Africa, when wetter and a more predominantly summer rainfall conditions followed on the drier early Holocene (Scott & Nyakale 2002). There may be some relationship between the changes in black wildebeest body size and habitat changes due to the mid-Holocene palaeo-climatic change. However, the absence of similar responses to the forcing effects of Middle Pleistocene palaeo-climatic events on black wildebeest evolution argues against such an explanation. Alternatively, anthropogenic effects may have had some influence on the mid-Holocene evolutionary punctuation in the fossil record of the black wildebeest. The mid-Holocene coincides with rapid expansion of Later Stone Age populations in southern Africa (Deacon & Deacon 1999), and factors like changes in fire regimes may have become significant in selection.

The Deelpan samples provide the best evidence that black wildebeest reached its modern size some time after the mid-Holocene.

Territorial behavioural in the earliest black wildebeest

There are three sets of uniquely derived morphologies that can be observed in the earliest black wildebeest fossils:

1. incipiently derived caprine-like horns and associated horn base morphologies
2. modified posterior skulls to accommodate the above morphologies
3. reduced premolar rows, which reflect the re-organisation of the posterior part of the skull.

These morphologies are interrelated and are directly associated with the unique territorial breeding behaviour of black wildebeest (Chapter 4). The presence of these morphologies is an indication that the earliest ancestral black wildebeest populations, as represented by the Cornelia-Uitzoek material, had already undergone a shift towards a more fixed kind of territorial breeding behaviour. To test this assumption the data summarised in Figures 116 to 119 were condensed as ratio diagrams (Figure 120). The aim of this presentation is to show the relative chronology of morphological changes in black wildebeest skeletal elements by using the modern blue wildebeest as a reference. In Figure 120 the proportions of the lower premolar row can be taken as a proxy for changes in the skull, as explained in Chapter 7. Therefore, the shortening of the premolar row reflects the changes in the flattening and reorganisation of the posterior part of the skull and, consequently, reflects the appearance of specialised territorial behaviour in ancestral black wildebeest. Because premolar row shortening was already far advanced in the Cornelia-Uitzoek material in comparison with the other skeletal elements (Figure 120), it confirms the impression gained from direct observations on the skull that there was a shift towards more territorial behaviour in the earliest populations of black wildebeest and that these changes preceded other morphological changes as seen in the other parts of the body. The specialised territorial behaviour of black wildebeest is the primary reason for reproductive isolation from the blue wildebeest when ranges overlap. From the evidence presented here it can be taken that by the time of the formation of the fossil assemblages at Cornelia-Uitzoek black wildebeest had already undergone a shift towards more specialised territorial behaviour. This would have caused reproductive isolation from sympatric blue wildebeest, suggesting that these populations would have been specifically distinct from contemporary blue wildebeest.

A feature that is more indirectly associated with territorial behaviour in *C. gnou* is the general decrease in size of the snout in relation to the posterior parts of the skull, which suggests a reduction in olfactory ability in *C. gnou*. Proxy evidence for the appearance of these features is reduction in tooth row and in M_2 dimensions. However, these features followed on premolar reduction and, therefore, it can be assumed that the reduction in olfactory ability was a consequence of initial changes related to a more specialised territorial behaviour.

If morphologies related to territorial behaviour appeared early in the fossil record, one may predict that adaptations linked to vision, which is equally linked to territorial behaviour

(Chapter 7), would have appeared early and synchronously with the changes in the skull and with the early reduction of the premolar row. However, the region of the orbits is not sufficiently preserved in the fossil specimens from Cornelia-Uitzoek to test this prediction.

It has been shown that small changes in the developmental rate of certain organs can cause major phenotypic reorganisation, which is a process known as heterochrony (Gould 1977, 1992). The appearance of morphologies associated with territorial breeding behaviour can be viewed as an example of such phenotypic reorganisation. Morphologies associated with territoriality in black wildebeest are also reflected in their early ontogenetic appearance. For example, the early fusion of the frontals' suture in Cornelian *C. gnou* is paralleled in its early fusion in juveniles of living black wildebeest (personal observation). The early ontogenetic fusion in the frontals' suture reflects the importance of the structure and the fact that activities related to territorial behaviour in adult life, such as head bashing and horn clashing, starts at a young age in black wildebeest (S. Vrahimis pers. comm.). The presence of the fused condition of the frontals' suture in the earliest ancestral fossil black wildebeest is a parallel to the early ontogenetic development of the character in modern forms of *C. gnou* and highlights its evolutionary importance. This parallel between ontogeny and phylogeny in black wildebeest gives further support to the argument that territoriality in breeding behaviour was closely linked to the process of speciation.

It has been demonstrated that territorial breeding behaviour in black wildebeest is directly dependant on open, visually unobstructed habitat (Chapter 4). Therefore it can be deduced that open-structured habitat must have been sufficiently available in the Cornelian palaeo-environment to allow territorial behaviour in early black wildebeest. This assumption is supported by the presence of a significant grassland component in the Cornelian palaeo-environment and by the trend in palaeo-environmental change towards openness. In Figure 27 there is still a remnant component of closed and woodland habitat in the ungulate fauna from Cornelia-Uitzoek, but in the Florisbad fauna this element has disappeared entirely, so that only a grazing component and an aquatic component remains. Eventually, in the Holocene there is only an open grassland component. Therefore, the appearance of an endemic character in southern African ungulate faunas can be related to changes in the habitat structure of the grasslands over the last million years (Chapter 6), in which the trend was from lightly wooded grasslands to entirely open grasslands. It is likely that in the first ancestral black wildebeest a

shift in breeding behaviour coincided with, or was a response to, the appearance of such open, visually unobstructed habitat.

The phylogenetic significance of caprine characteristics in black wildebeest

Virtually all the uniquely derived characters of black wildebeest, the osteological characters and those seen in the soft tissue, seem to have evolved in parallel to caprines. The appearance of caprine-like characteristics in black wildebeest is highly significant for understanding its evolution, since they refer back to a common ancestry between the tribes Caprini and Alcelaphini (*vide* Gentry 2000). These characteristics of black wildebeest are examples of the persistence of blueprint morphology. The caprine blueprint, which is inherent in all wildebeest-like alcelaphines, re-appeared once it was triggered by the shift in breeding behaviour in the process of speciation. The propensity of the genus *Connochaetes* to develop caprine characteristics can be described as parallelphyly, which is defined as the independent acquisition of the same character by descendants from a common ancestor (Mayr 2001: 67). Parallelphyly can be distinguished from polyphyly, or convergence, where the same characters are independently acquired in unrelated groups.

The acquisition of caprine characteristics by black wildebeest has bearing on the method of cladistic analysis, which disregards homoplastic characters in constructing phylogenies (Wiley *et al.* 1991). Since most cases of homoplasy are caused by parallelphyly (Mayr 2001), it is predicted that in assigning polarity states to alcelaphine materials it would be very difficult to separate convergent characters from parallelphylic characters, unless the caprine origins of the Alcelaphini is taken into account. In contrast, the application of the morphological blueprint approach allows an understanding of bovid evolution without the need to conduct a conventional cladistic analysis. The value of the cladistic method as a way of initially organising large bodies of data is recognised, but where possible such analyses should be complemented by a consideration of a wider range of characters including behaviour. It is further advisable that cladistic analyses should consider the ancestral genotype and its phenotypic potential (Mayr 2001). This can be achieved by applying a morphological blueprint approach.

The evolution of the black wildebeest is a good example of the re-appearance of ancestral morphologies embedded in the genome of the organism. The inherent, but latent, caprine

genetic predisposition, or blueprint, of the black wildebeest can be viewed as a constraint, which has governed its evolution (*vide* Chapter 3).

Black wildebeest evolution in geographic space

Introduction

A display of the metric data of the postcranial elements is presented in Figures 121 and 122. The x-axes represent an approximate geological time scale, while the y-axes are the measurements chosen to illustrate changes in body size and proportions. Because the skeletal elements are given independently and not in relation to the blue wildebeest, the values are not logarithmically transformed. The diagrams on the left in the figures show the data from the interior, while the diagrams on the right have the data from the Cape ecozone. They highlight the geographical differences between materials from the interior and contemporary materials from the Cape coastal zone, as discussed below.

*The fossil record of *C. gnou* in the Cape coastal zone*

The horn core and postcranial materials from the Cape coastal zone usually differ from contemporary materials in the interior in being smaller and more compact. This can be seen in the horn cores from Elandsfontein and Duinefontein 2, and less clearly in the fragmentary late Florisian horn materials from Swartklip.

The dentitions are the exception in that the late Florisian dentitions from Swartklip are not different from those of the interior Florisian or from modern populations. This is consistent with the pattern of change in dentitions from the interior, which suggests that since the early Florisian there was no change in black wildebeest dentitions. This applies both to dental size and premolar proportions.

Pre-Florisian black wildebeest postcrania from the Cape coastal zone show a pattern similar to that of the horn cores. The few pre-Florisian metacarpals from Elandsfontein (Figures 109B, & 110B) indicate that they were more robust than contemporary interior specimens. However, it is only from the late Florisian that a better impression of geographic differences emerges. There is a marked reduction in size relative to contemporary interior materials. The trend is somewhat less expressed in the axis and humerus, but pronounced in the other skeletal

elements (Figures 121 & 122). The single distal tibia from the Klasies River old collection supports the evidence provided by the talus (Brink *et al.* 1999) that Florisian size reduction in the Cape coastal zone probably did not start until the Last Interglacial. It is noteworthy that the metacarpals of Sea Harvest are somewhat larger on average than the Swartklip assemblage, but that they do not differ significantly from these specimens ($F(1.12)=0.03$; $p=0.87$). The Elandsfontein Bone Circle assemblage is significantly smaller than the Swartklip assemblage ($F(1.13)= 5.89$; $p<0.05$). If the trend of body size reduction may be taken to reflect the passage of time, then it is likely that Sea Harvest would be equal in age to Swartklip, or somewhat older, but that the Elandsfontein Bone Circle material postdates the Swartklip assemblage. Elandsfontein Bone Circle metatarsals are the smallest of the coastal samples, confirming the pattern seen in the metacarpals.

In the late Florisian postcranial materials from the Cape coastal zone there was a reduction in body size and a mosaic change in skeletal proportions compared to interior populations. Late Florisian coastal populations seemed to have become increasingly stocky and robust, reducing in size at a much faster rate than contemporary populations of the interior. Pending more accurate radiometric dates for Swartklip and other coastal sites, it seems that this pronounced reduction in size must have occurred within a space of 70 – 80 000 years. These changes seem to be entirely unrelated to the Late Pleistocene temperature changes to which Klein (1986) has related changes in the body size of the carnivores.

It is of interest to note that although there was a size reduction in late Florisian coastal populations the body proportions resemble those from interior Florisian and mid-Holocene and not modern populations (Figure 123). This supports the suggestion that late Florisian coastal populations descended from interior Florisian populations (Brink 1993). It also suggests that after the mid-Holocene size reduction of interior black wildebeest populations was a response to different selective forces than those causing selection in the Last Glacial populations of the Cape coastal zone.

The evidence from Klasies River suggests that the Florisian differentiation between interior and coastal black wildebeest probably started towards the end of the Last Interglacial, some 80 – 90 000 years ago, and accelerated during the Late Pleistocene to culminate in very small-bodied populations, seen in the Elandsfontein Bone Circle materials. Cape coastal black

wildebeest evidently reached the maximum extent of size reduction immediately before their extinction in the Cape coastal zone. The extinction coincided with a decline in suitable coastal habitat, due to the rise in postglacial sea levels and to the increase of the coastal fynbos at the expense of grassland habitat (Deacon 1983; Klein 1983).

Dispersal and vicariance in black wildebeest evolution

The biogeographic concept of vicariance can be defined as genetic changes occurring in populations that became reproductively isolated from other similar populations due to their separation in geographic space (Chapter 3). This definition implies that dispersal from a point of origin, the parent population, is followed by genetic changes in the daughter populations and that these changes occur incrementally through natural selection. If one attempts to invoke vicariance to explain black wildebeest speciation, the requirement of a preceding dispersal of ancestral populations is satisfied by the well-documented presence of ancestral blue wildebeest in southern African (Vrba 1975, 1997). These populations would have been similar to *C. taurinus progna*, which had a virtually pan-African distribution (Chapter 8). However, contrary to the prediction the fossil evidence does not suggest biogeographic isolation or an incremental speciation process. The speciation of the black wildebeest can be understood in the first place as reflecting a behavioural shift, a ‘Baldwinian’ speciation event (see above). The fossil evidence shows that the speciation of the black wildebeest coincided with a rapid phenotypic re-organisation, associated with or driven by a shift in territorial breeding behaviour. The first ancestral black wildebeest would have been behaviourally distinct from contemporary blue wildebeest populations. This behavioural shift, which is linked to the appearance of permanently open, Highveld-type grasslands in central southern Africa, would have governed mate selection and would have been the basis for reproductive isolation of these populations. It can be concluded that the process of speciation of the first black wildebeest from a blue wildebeest-like ancestor was not due to biogeographic isolation and subsequent genetic drift, but rather to a behavioural shift linked to a change in habitat structure.

However, there was post-speciation genetic drift in the biogeographically peripheral fossil populations of the Cape coastal zone. This genetic differentiation is evident in the late

Florisian Cape coastal populations being markedly smaller than contemporary interior populations. During the course of the Late Pleistocene this diminution in body size was progressive (Figures 121 & 122). For morphology to be expressed consistently in the phenotype there has to be a genetic basis (Chapter 3). In order to maintain the distinctive genetic basis, as is evident in Figures 121 and 122, a cessation of gene flow between the interior and coastal populations is required. This implies that Cape coastal populations of late Florisian black wildebeest were biogeographically isolated from the interior. Therefore, the changes in body size seen in late Florisian black wildebeest populations from the Cape coastal zone can be interpreted as an example of vicariance.

The presence during the late Florisian of biogeographically isolated black wildebeest populations in the Cape coastal zone raises two questions. The first concerns the presence of black wildebeest on the Cape coast, when it is commonly known today that the predominant vegetation of the Cape coastal zone, the fynbos, does not offer suitable grazing. The closed nature of the fynbos vegetation will also offer difficulties in allowing male black wildebeest forming breeding territories. The answer to this question lies in the evidence for the dispersal during the Last Glacial of not only black wildebeest, but virtually the whole suite of Florisian grazers from the interior into the Cape coastal zone (Klein 1972, 1983). During glacials lowered sea levels exposed the continental margin to provide additional habitat (Van Andel 1989). These coastal environments would have mimicked the open grasslands of the interior (Klein 1972, 1983). Consequently Last Glacial fossil assemblages from the Cape coastal zone, which contain black wildebeest, also contain a suite of grazing ungulates that normally would be associated with the plains of the interior (Chapter 6). In certain debates on dispersal and vicariance a biogeographic barrier is postulated (Chapter 3). The Cape Fold Mountains provide a form of barrier between the interior and the Cape coastal zone. Even if the Cape Fold Mountains were not an impenetrable barrier, it would have impeded the natural movement of grazing ungulates between the interior and the coast. Furthermore, the great distance between the two areas would have added to the effect of the Cape Fold Mountains as a biogeographic barrier (Ford 1955).

The second question is whether there is evidence for vicariance in coastal black wildebeest in the time before the Last Glacial. From the morphology of the black wildebeest horn cores from Elandsfontein and Duinefontein 2 it is apparent that very soon after the Cornelian

speciation event ancestral black wildebeest populations dispersed into the Cape coastal zone. This dispersal event would have occurred during a glacial period, because interglacial high sea levels do not allow sufficient habitat for grazing plains living animals. Furthermore, the fossil evidence indicates that there was at least one post-Cornelian presence of black wildebeest in the Cape coastal zone before the Late Pleistocene. On this basis it can be concluded that dispersals of interior plains living grazing ungulates occurred more than once during glacials that preceded the Last Glacial. Therefore, vicariance in coastal populations would have been a common phenomenon.

If the general temporal trend in black wildebeest evolution can be described as a process of size reduction, then it is of interest that Cape coastal populations of the Last Glacial were more advanced than contemporary interior populations. The acceleration in evolution in the Cape coastal zone fits the biogeographic model, which Geist (1971) constructed for Canadian bighorn sheep. This model predicts that evolution in bighorn sheep accelerates when biogeographically peripheral populations expand their ranges to occupy new territories after a glacial. Given that the Cape coastal zone is peripheral to the interior, which is the centre of origin of the black wildebeest, there is a parallel between Geist's mountain sheep and black wildebeest in that evolution was accelerated in biogeographically distal populations.

The black wildebeest is only one of a range of grazing ungulates that occupied the glacially exposed continental platform in the Cape coastal zone. Other taxa include the local forms of the extinct Florisian grazers, a local form of the plains zebra (*E. quagga quagga*), the southern springbok (*A. marsupialis australis*), the local form of the blesbok, the bontebok (*D. pygargus pygargus*) and possibly the recently-extinct blue antelope (*Hippotragus leucophaeus*). These forms cannot survive in the fynbos today and only the bontebok survived the postglacial changes. Bontebok survived in the southern Cape in limited numbers, which is probably due to its adaptability (Chapter 6). It can be concluded that over the last million years the large mammal component of the glacial ecosystems of the Cape coastal zone reflects periods of repeated range expansion of grazing plains-living ungulates from the interior (dispersal) and subsequent biogeographic isolation in the Cape coastal zone (vicariance) (*vide* Chapter 3; Figure 124).

General discussion

Bergman's 'Rule'

Bergman's 'rule' predicts that animals in colder environments will reduce the surface area of the body and increase their body volume in order to maintain basal metabolism more efficiently (*vide* Moen 1973). If this 'rule' applies, then one may expect an increase in body size during colder, glacial conditions. Although it has been suggested that some species, such as carnivores and hyraxes from the Cape coastal zone, show evidence of body size increase during glacials (Klein 1986; Klein & Cruz-Urbe 1996), this prediction has not been tested in bovinds. The present study provides an opportunity to test whether Bergman's 'rule' can be applied to fossil ruminants in South Africa.

Fossil black wildebeest from interior Last Glacial assemblages, such as Spitskop and Mahemspan, show no increase in size, but rather tend to fall into a general Florisian body size category. However, the assemblages from Sea Harvest, Swartklip and Elandsfontein Bone Circle, which are generally considered to be Last Glacial in age, show a marked decrease in body size. This is the opposite of what would have been expected from Bergman's 'rule'. This reduction in size in fossil black wildebeest from the Cape coastal zone is more likely to be explained by the hypothesis that evolution is accelerated in biogeographically distal populations or by the nutrient status of the substrate and quality of grazing. The glacially exposed continental shelf around southern Africa, which is now submerged, was the main habitat of coastal populations of *C. gnou* during Last Glacial. The soils in that environment are sands derived from the rocks of the Cape Supergroup, which would have been relatively nutrient-poor and low in productivity (Deacon 1983). It would have been harsh marginal habitat for grazing ruminants and it can be envisaged that factors other than temperature would have controlled body size. Therefore, Bergman's 'rule' seems not to apply in the case of the black wildebeest.

The effects of population bottlenecks in the morphology of extant C. gnou

The only fossil material of *C. gnou*, which postdates the mid-Holocene size reduction, is the small assemblage from Deelpa. The axis, humerus, radius, metacarpal and tibia of black wildebeest from Deelpa fall within the 95% confidence limits of the modern reference sample used in this study. Therefore, there is no evidence for osteomorphological or size

modifications in post-1930's black wildebeest. Even if the present populations of black wildebeest were bred from a few hundred individuals (Vrahimis in press), a relatively small founder population can produce genetically sound offspring. This point is illustrated by a small population of feral cattle, the Chillingham breed, which now comprises 49 animals and lives in a park in northern England. This population, which is thought to have experienced no immigration for at least 300 years, remains viable in spite of being almost genetically uniform (Visscher *et al.* 2001). In the absence of obvious genetic problems in the modern comparative sample, one may assume that the population bottlenecks of the late 19th and early 20th century have had no serious impact on the genetic viability of modern black wildebeest.

It should be noted that the work of Corbet & Robinson (1991) and Corbet *et al.* (1994) indicate that the genetic variability of black wildebeest is considerably less than that of blue wildebeest. They ascribe this to the early 20th century population bottlenecks in black wildebeest. However, an alternative explanation is that the genetic data reflect the size of the founder population(s) of the earliest ancestral black wildebeest. This possibility needs to be tested by genetic analysis of pre-bottleneck black wildebeest specimens. Consequently, samples of sub-fossil black wildebeest specimens from Maselspoort, Kareepan, Deelpan and the Holocene hyaena dens from Spitskop have been submitted for genetic analysis. This study is in progress (P. Bloomer pers. comm.).

In the light of the above the modern black wildebeest populations appear not to be threatened by reduced genetic diversity, but rather it is under serious threat of extinction from hybridisation with blue wildebeest in game reserves and game farms in central southern Africa.

Genetic evidence for the evolution of the black wildebeest

The genetic evidence provided by Harley (1988), Corbet & Robinson (1991) and Corbet *et al.* (1994) suggests that the evolutionary split between black and blue wildebeest postdates one million years. This accords with the fossil evidence presented in this study.

The evolutionary position of C. africanus

The fossil skull from Olduvai, which was given the name *C. africanus* (Hopwood, 1934), exhibits size reduction and a narrowing of the frontal space in between the horn bases that

suggested that it might be an early form of *C. gnou* (Gentry & Gentry 1978). The type specimen of *C. africanus*, of uncertain provenance in the Olduvai sequence, is presently kept in the Natural History Museum, London. The author was able to examine the type specimen and to confirm the observations of Gentry.

The issue of *C. africanus* as a potential ancestor of the black wildebeest is problematical. It is in conflict with the fact that all of the fossil evidence of black wildebeest, besides the type specimen of *C. africanus*, is found in southern Africa. It also does not accord with the proposition that the origin of the black wildebeest was related to territorial breeding behaviour in open tree-less habitat in southern Africa.

Vrba (1997: 158) considers fossil wildebeest specimens from Bouri (Middle Awash, *c.* 0.6 million years old) to resemble *C. taurinus prognus* from Olduvai Beds II-IV, but also *C. africanus* in respect of a ridge on the basal part of the horn core. This points to some variability within ancestral populations of *C. taurinus*, which may explain the morphology of *C. africanus*. Since the type specimen of *C. africanus* is the only fossil referred to this taxon so far, it would be sensible to expand the fossil sample before serious consideration can be given to the suggestion that this fossil represents an ancestor of the black wildebeest.

CHAPTER 10. CONCLUSION

INTRODUCTION

The aim of this study was to investigate the palaeontological evidence for the evolution of the large mammal biota in the central interior of southern Africa. This evidence is drawn from two major sites, Cornelia and Florisbad and some additional sites. The central interior includes the shrub and temperate grasslands of the Nama Karoo and Highveld and contains a large mammal fauna dominated by plains game. Historically it was the home to vast herds of zebra, wildebeest, blesbok and springbok. This biota was made up of local endemics and more recent immigrants. It is equivalent to, but distinct from similar biotas in centres of semi-arid grasslands in East and North Africa. Palaeontological studies give a direct insight into the emergence of the modern biota. It is evident that the biota has changed through time with extinction, immigration and with the evolution of recent endemics. Noteworthy among the latter is the black wildebeest and this study focuses on the evolution of this species as an exemplar of change in the biota.

The hypothesis that there was a close relationship between the appearance of open, Highveld-type grasslands and the evolution of the black wildebeest seems to be supported by the evidence presented in this study.

ALCELAPHINE MORPHOLOGICAL GROUPS

The roots of the tribe Alcelaphini can be traced back to the Middle Miocene, although in the fossil record it becomes more visible towards the end of the Miocene. The evolutionary radiation of the earliest alcelaphines seems to be closely linked to that of caprines and both these groups have an antilopine ancestry (Gentry 2000). This evolutionary origin can be seen in the morphology of modern and fossil southern African Alcelaphini. In this study a morphological approach is applied that allows the identification of a morphological blueprint, which can be loosely equated with the concept of a 'Bauplan'. It represents the essence of the morphology of an organism or parts of it. In the course of this study two morphological groups in the Alcelaphini could be identified, (1) *Connochaetes* spp. and *M. priscus* and (2) *A.*

buselaphus and *D. pygargus*. The wildebeest group is characterised by the persistence and the re-appearance of caprine morphological characteristics. This basic morphological division is also evident in the body proportions of these taxa, with wildebeest having caprine-like body proportions and hartebeest having antilopine-like body proportions. This grouping of taxa (Figure 86) differs from the classification of Vrba, which is based on a cladistic analysis (Vrba 1997).

PARALLELISM IN *MEGALOTRAGUS PRISCUS* AND *CONNOCHAETES GNOU*

The wildebeest-like character of *M. priscus* is evident in most of its skeletal elements, but it is more pronounced in the horn curvature, the dentitions and in the front limb elements. Of particular note is the presence of a unique morphological character in the distal tibia. The plantar articular facet for the os malleolare is enlarged to the extent that it dominates the articulation. This may be a marker shared by all *Megalotragus*-like alcelaphines. It can be concluded that *M. priscus* is not a large hartebeest, as formerly assumed on the basis of parallel cranial characters, but rather that it is a large wildebeest-like alcelaphine. In those skeletal elements in which it is more derived and wildebeest-like, it resembles *C. gnou*, more than *C. taurinus*, suggesting parallel evolution in *M. priscus* and *C. gnou*. It is speculated that the basis for this parallelism was some element of territoriality in the behaviour of *M. priscus*, which would manifest in aggressive intraspecific interactions. The aurochs-like forward horn shape and bovine body plan (Figure 85) accord with this suggestion.

THE EVOLUTIONARY SIGNIFICANCE OF CAPRINE MORPHOLOGIES IN ANCESTRAL BLACK WILDEBEEST

The shift to a more specialised kind of territoriality in early the black wildebeest reflects the appearance of a caprine behaviour pattern. Virtually all the diagnostic morphologies in ancestral black wildebeest, which distinguished it from blue wildebeest, can be related to caprine-like agonistic behaviour. This is of evolutionary significance, as it suggests there is a latent and phenotypically unexpressed caprine tendency embedded in the genome of wildebeest. This refers back to the Miocene common ancestry of the tribes Alcelaphini and

Caprini. Caprine morphology was activated by a shift to more caprine-like behaviour in ancestral black wildebeest. The tendency of once-lost characteristics to re-appear in closely related forms is known as parallelphyly (Mayr 2001).

A further evolutionary implication of the re-appearance of caprine characteristics in black wildebeest concerns the method of phylogenetic systematics (cladistics). The basis of the cladistic methodology is the ordering of organisms hierarchically according to synapomorphies, but not to consider homoplasies. If parallelphyly is a common phenomenon in that apomorphic characters can be lost and re-appear repeatedly in the evolution of closely related forms, as suggested by this study, it implies that the presence of shared derived characters cannot necessarily be taken to imply monophyly in closely related forms.

THE ORIGIN OF THE GENERA *CONNOCHAETES* AND *MEGALOTRAGUS*

The alcelaphine fossils from North Africa examined in the course of this study point to North Africa as the likely area of origin of the genera *Connochaetes* and *Megalotragus*. This conclusion is tentative and rests on morphology and the assumed geological age of the materials from Aïn Jourdel and Aïn Boucherit, Algeria.

The species *Oreonagor tournoueri* from Aïn Jourdel is commonly seen as a likely ancestor of the genus *Connochaetes* (Gentry 1978). Subsequently Arambourg (1979) referred materials from Aïn Boucherit to this taxon and used the material as a neotype and neosyntypes to redescribe the species. However, it is shown in this study that the Aïn Boucherit material represents an underived form of *Megalotragus*-like alcelaphine, while the Aïn Jourdel material represents a primitive *Connochaetes*-like alcelaphine. Therefore, they should not be included in the same taxon. Given the rule of priority in taxonomy it is suggested here that the original type specimen from Aïn Jourdel should be re-instated as the type specimen of the species *Oreonagor tournoueri* (Thomas, 1884), while the Aïn Boucherit material should be given a new name. For the sake of convenience the Aïn Boucherit material is referred to as 'species A'. The fact that two separate sets of fossil material have been referred to the same taxon, one representing a primitive form of *Connochaetes* and the other an underived form of *Megalotragus*, has caused confusion in literature. On the basis of the 'neotype' from Aïn

Boucherit the material from Bouri 1, Middle Awash, has been referred tentatively to the taxon *?Oreonagor/?Megalotragus* sp. (Vrba 1997). The Bouri 1 specimen should also be included in species A.

The very primitive *Connochaetes*-like morphology of *O. tournoueri* from Ain Jourdel points to North Africa as the likely area of origin for the genus *Connochaetes*. Until now such primitive wildebeest-like fossils have not been found in East Africa. However, after c. 2.5 million years ago early members of the genus *Connochaetes* had spread to East and probably to southern Africa (Vrba 1997). The underived *Megalotragus*-like morphology of species A and the presence of another similar species, '*Gorgon*' *mediterraneus* (Arambourg 1979; personal observation) suggest that the genus *Megalotragus* may also have originated in North Africa. There is no fossil evidence for *Megalotragus*-like Alcelaphini in East Africa before c. 2.7 million years ago (Harris 1991; Vrba 1997).

A further point of interest concerns the origin of an earlier phase of wildebeest-like alcelaphines, the ancestral populations that gave rise to the genera *Connochaetes* and *Megalotragus*. The postcrania of species A and the illustrations of the postcrania of *O. tournoueri* from Ain Jourdel (Thomas 1884) suggest that the ancestors of both sets of material were hartebeest-like. This and the remnant hartebeest-like tendencies in the dentitions and postcrania of *C. taurinus* imply that hartebeest-like morphology first evolved in early alcelaphines, which later gave rise to the genera *Connochaetes* and *Megalotragus*. In this sense the caprine-like derived morphologies of the genera *Connochaetes* and *Megalotragus* represent the re-appearance of previously lost morphology and refer back to the caprine origins of the earliest alcelaphines.

THE EVOLUTION OF DISTINCTIVE LARGE MAMMAL FAUNAS IN SOUTHERN AFRICA

The fossil assemblages from Cornelia-Uitzoek and Florisbad are representative of the time period of approximately the past 1.0 million years. The modern large mammal faunas of southern Africa are the end product of the evolutionary process reflected by these two assemblages. They are the type assemblages of the Cornelian and Florisian Land Mammal

Ages (LMA) and provide the temporal frame for understanding large mammal evolution in central southern Africa. Before this study these localities were essentially undated. To address this problem the ESR and OSL dating techniques were applied to Florisbad to other localities in central southern Africa. Cornelia-Uitzoek is dated by means of correlation with East African localities, primarily Olduvai. These results and new data on the palaeo-ecology of large mammal species provide an opportunity for a revised definition of the Cornelian LMA and the Florisian LMA. This revision serves as background and as chronological framework for assessing the fossil history of the black wildebeest.

During the last approximately 1.0 million years there is a trend in faunal turnover in the interior of southern Africa that suggests that the grassland habitat became more open in structure. In this time the endemic character of the southern African large mammal faunas evolved essentially through immigration, extinction and *in loco* evolution. In the faunal assemblages from Cornelia-Uitzoek there is an archaic component, which includes *Hipparion steytleri*, *H. cornelianum*, the suids *Kolpochoerus limnetes*, *Metridiochoerus compactus*, and *Phacochoerus modestus* and *Hippopotamus gorgops*. There is a remnant of a woodland habitat and a closed habitat component in the Cornelian fauna (Figure 27). A derived component consists of endemic southern African taxa, such as the earliest form of the black wildebeest, *C. gnou laticornutus*, the post-Olduvai Bed IV/ pre-Florisian form of *Damaliscus niro*, and an early morphotype of *A. bondi*. These forms can be distinguished from their Florisian descendants in their less derived morphologies. The incipiently endemic character of the fauna from Cornelia-Uitzoek reflects an early stage in the evolution of distinctiveness in southern African large mammal faunas.

The Florisian LMA is defined on the absence of archaic Cornelian taxa and on the presence of number of extinct taxa, which are *Equus capensis*, *E. lylei*, *Homoiceras antiquus*, *Megalotragus priscus*, *Damaliscus niro*, *Antidorcas bondi* and the new southern African caprine species. Some of these extinct forms are descendants of Cornelian precursors, such as *E. capensis*, *H. antiquus*, *D. niro* and *A. bondi*. The latter two species are more derived than the ancestral Cornelian forms and can be easily distinguished on morphological grounds. The palaeo-ecological trend towards open grasslands is complete in the Florisian faunas of the interior. The presence of endemic forms with a local evolutionary history, such as *C. gnou* and *A. bondi*, is complemented by the appearance in the fossil record of new species. The

alcelaphines, *A. buselaphus* and *D. pygargus*, the lechwe, *K. leche*, the modern hippopotamus, *H. amphibius* and probably *E. lylei* are examples of such new arrivals. These taxa have no Cornelian forerunners and seem not to have evolved locally. It is likely that *M. priscus* also was an immigrant species. The Florisian LMA spans the time from c. 700 000 to 10 000 years ago.

The trend in large mammal evolution, which reflects the appearance of open habitat, culminated in the Florisian LMA. The Florisian is characterised by extant and extinct grazing ungulates interacting in a highly productive open grassland ecosystem and by an aquatic large mammal component, reminiscent of the modern Okavango (Brink & Lee-Thorp 1992; Chapter 6). This component was associated with the existence of numerous perennial lakes. Today these lakes survive as semi-arid pans. For the duration of the Florisian LMA, between approximately 700 000 and 10 000 years ago, there was a period of stability in faunal turnover. This stability coincided with morphological stasis in the black wildebeest. At the end of the Pleistocene the Florisian ecosystem was disrupted by extreme aridification in the interior of southern Africa, which led to the disappearance of the Okavango-like lake system and the extinction of six grazing ungulates and the aquatic taxa. The modern Nama Karoo and Highveld are an arid remnant of the Florisian LMA, while some of the aquatic forms survive in the Okavango region as Florisian relicts. However, post-Florisian morphological change in black wildebeest only started in the mid-Holocene and was not in phase with terminal Pleistocene aridification and extinction. Black wildebeest reduced to its modern size in the late Holocene.

There was a geographic expansion of the Cornelian and Florisian ecosystems into the Cape coastal zone. During glacials the eustatic exposure of the continental platform provided additional habitat for interior plains game. This allowed the large mammal faunas of the interior to expand their ranges and to disperse into the Cape coastal zone. These dispersals resulted in reproductive isolation of the daughter populations in the Cape from the parent populations of the interior. For the Late Pleistocene this process of vicariance can be traced in considerable detail. The process, marked by an accelerated reduction in size and changes in body proportions in coastal fossil black wildebeest populations, produced populations of markedly smaller body size compared to contemporaneous interior populations. During earlier glacials in the Cornelian and Florisian the expansion of inland populations into the Cape

coastal zone seems also to have occurred repeatedly and applied to almost all the taxa commonly associated with the interior.

OPEN GRASSLANDS AND TERRITORIAL BEHAVIOUR IN BLACK WILDEBEEST: A MODEL FOR THE EVOLUTION OF THE BLACK WILDEBEEST

It appears that black wildebeest evolved from a blue wildebeest ancestor soon after 1.0 million years ago on the interior plateau of southern Africa. Today this area has an open habitat structure. Black wildebeest is restricted to open grasslands not by trophic factors, as it shares essentially the same feeding niche with blue wildebeest, but by its territorial breeding behaviour. This behaviour, which demands visually unobstructed habitat, is the basis for the reproductive isolation of sympatric black wildebeest and blue wildebeest in that black wildebeest select mates in a different way than blue wildebeest. Depending on the environmental circumstances blue wildebeest can be territorial or not. Because of its flexible social behaviour, it can occur in open or wooded grasslands. Black wildebeest is not behaviourally or ecologically more fit to survive in open grasslands than blue wildebeest, but is restricted to such habitat by its breeding behaviour.

The fossil evidence for black wildebeest evolution indicates a temporal pattern in which there is an initial shift in cranial morphology, followed by longer periods of almost no morphological change and punctuated by times of rapid change. The changes in the cranial anatomy of the earliest black wildebeest fossils from Cornelia-Uitzoek reflect the specialised morphologies associated with territorial breeding behaviour of the modern black wildebeest. This implies an early shift towards specialised territorial breeding behaviour. In modern populations this kind of behaviour is the mechanism underlying reproductive isolation in sympatric populations of black wildebeest and blue wildebeest. It can be assumed that this would have applied equally to the earliest Cornelian black wildebeest and contemporary blue wildebeest populations and that a shift in territorial breeding behaviour marked the speciation of the black wildebeest from a blue wildebeest ancestor. This process initiated genetic changes that resulted in a major phenotypic re-organisation that produced the modern black wildebeest. It can be concluded that the territorial breeding behaviour of modern black

wildebeest was already fully functional in the first ancestral black wildebeest populations, as seen in the fossils from Cornelia-Uitzoek.

This leads to the deduction that there was no palaeo-ecological need for black wildebeest to have evolved, except that the environment presented an opportunity. This opportunity, the formation of permanently open-structured habitat in sufficient abundance, was exploited when ancestral black wildebeest assumed a behavioural shift towards greater territoriality. This behavioural shift was not an innovation, but only an extreme of the behavioural spectrum of the ancestor that became fixed. This model can be described as a form of co-evolution, where behaviour drives evolution. In the case of the black wildebeest the process of speciation was accompanied by a shift towards caprine-like social behaviour. This shift in behaviour appears to have activated a morphological response that was latent in the genotype of the ancestral form. One extreme of an existing behavioural pattern of the ancestral form (the blue wildebeest) was favoured, because the physical environment (open habitat) allowed it. It is proposed that a shift towards a more specialised territorial breeding behaviour in southern populations of *C. taurinus prognus* was the determinant factor in the speciation of the black wildebeest.

THE POST-SPECIATION EVOLUTIONARY HISTORY OF THE BLACK WILDEBEEST

After the speciation event there were times of equilibrium and times of accelerated change in body size and proportions. These changes reflect smaller scale genetic shifts, also referred to as micromutations or drift. The process accords with an evolutionary pattern described as punctuated equilibria. In the time following the speciation of the black wildebeest from a blue wildebeest ancestor there was a mosaic pattern in temporal changes in the various skeletal elements in that they were not in phase. The front limb experienced marked and apparently rapid diminution until the Florisian, after which a period of stasis followed until the mid-Holocene. After the mid-Holocene there was a final phase of reduction in the forelimb before it reached its present dimensions. In the hind limb reduction was more continuous, but there is again evidence for a period of equilibrium, which lasted throughout the Florisian to the mid-Holocene. The final phase of body size reduction occurred in the mid-Holocene.

Ancestral black wildebeest populations dispersed into the Cape coastal zone soon after the Cornelian speciation event. Dispersals seem to be closely related to the glacial exposure of the now submerged continental platform to the south and west of the mountains of the Cape. Body size reduction was accelerated in the Cape coastal zone, but particularly during the later part of the Florisian LMA. Body size reduction increased in tempo soon after the Last Interglacial and reached its maximum during the terminal Pleistocene. This process reflects vicariance in the Last Glacial coastal environment, where accelerated rates of evolution through genetic drift in geographically isolated populations resulted in a reduction in body size, but not in speciation.

CONCLUDING STATEMENT

The evolution of the black wildebeest from a blue wildebeest ancestor was associated and probably driven by a shift in breeding behaviour characterised by increased levels of aggression. This behaviour resembles to some extent the intra-specific aggression of advanced forms of sheep and led to the re-appearance of genetically latent caprine morphology in the phenome of ancestral black wildebeest. Therefore, the evolution of the black wildebeest can be seen as a return to a caprine blueprint that was stimulated by a shift in breeding behaviour. A parallel of this process can be seen in a newly discovered caprine from montane areas in southern Africa. Alcelaphine-like dental adaptations evolved in parallel to those of the black wildebeest (Appendix C). Both these evolutionary processes reflect the Miocene common ancestry of the tribes Caprini and Alcelaphini and emphasise the importance of morphological blueprints for understanding evolution.

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APPENDIX A. OSTEOLOGICAL ILLUSTRATIONS¹ AND FIGURES²

¹ All scale bars indicate cm units

² Graphic projections are given in mm units

Figure 1. The three arid centres of Africa with past interconnecting corridors.

Figure 2. A temporal model of black wildebeest evolution, as suggested by Gentry & Gentry (1978). The model illustrates changes in the shape of the horn cores over time. The specimens represented are a modern specimen, NMB-F 84 (A), a Florisbad specimen, FLO 6500 (B), and a specimen from Cornelia-Uitzoek, COR 2838 (C)

Figure 3. A map of southern Africa illustrating the different biomes (after Low & Rebelo 1996).

Figure 4. Maps of southern Africa illustrating the historic distribution of the black wildebeest and blue wildebeest (after Skinner & Smithers 1992). The southern limit of the range of the blue wildebeest as inferred from historic records and fossil finds is shown as a line.

Figure 5. A map of southern Africa showing the fossil localities as discussed in the text. The insert shows a temporal ordering of the fossil localities (based on data presented in Chapters 5 and 6).

Figure 6. A map showing the positions of the Deelpan A & D fossil brown hyaena burrows.

Figure 7. Map of the Maselspoort fossil site.

Figure 8. Composite views of the Maselspoort mid-Holocene bone occurrence.

Figure 9. A map of the Karepan fossil locality.

Figure 10. A map of the Spitskop donga system and fossil localities.

Figure 11. A map of Mahemspan showing the approximate position of Van Hoepen's excavation.

Figure 12. A map of Sunnyside Pan and the position of the Pleistocene hyaena burrow.

Figure 13. The geographic position and local geology of Florisbad. (After Loock & Grobler 1988).

Figure 14. Plan of the Florisbad spring mound indicating the positions of the excavations, including the three test pits.

Figure 15. A model illustrating the depositional history of the Florisbad fossil bearing deposits. It shows the distinction between the two kinds of fossil context; mainly carnivore-accumulated materials from the spring vent structures (B1) and the remains of human habitation on intact land horizons (B2).

Figure 16. The distribution of pans in the vicinity of Florisbad, illustrating the Okavango-like aquatic habitat characteristic of the Flosian Land Mammal Age in the interior of southern Africa. (After Grobler & Loock 1988).

Figure 17. Plot of augur drill sections through the Florisbad spring mound (after Brink 1987).

Figure 18. Correlation of the profile of the Florisbad spring section (A & C) with the third test pit (B). The third test pit was used as the reference section in the ESR/OSL dating exercise (Grün *et al.* 1996) The localities of these sections on the Florisbad spring mound are given in Figure 14. The spring section is modified after Kuman & Clarke (1986), while radiocarbon results given in C are from Scott & Nyakale 2001.

Figure 19. ESR and OSL age estimates on fossil teeth and sediments from the third testpit at Florisbad (after Grün *et al.* 1996).

Figure 20. ESR age estimates on fossil teeth from the Florisbad Spring (after Grün *et al.* 1996) .

Figure 21. A north-facing panoramic view of the fossil-bearing deposits of Cornelia-Uitzoek (A). The arrow points from the position of the current excavation (B & C), which was started in 1998.

Figure 22. A north-facing diagrammatic section of the fossil-bearing Quaternary deposits of Cornelia-Uitzoek within a basin of Permian Ecca shale (modified after Butzer 1974).

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Figure 23. North-facing vertical plot of vertebrate fossils from the new excavations at Cornelia-Uitzoek (A), enlarged and superimposed on an inverted south-facing section of the 1998 test excavation (B), illustrating the intrusive nature of the bone occurrence.

Figure 24. A plot of the vertebrate fossils from the new excavations at Cornelia-Uitzoek. The 1998 test cutting is indicated in the north-western corner of the exposure.

Figure 25. A large bovid rib and the basal horncores of *Megalotragus eucornutus*.

Figure 26. Map indicating the geographic position of fossil localities from North Africa.

Figure 27. An ecological characterisation of ungulate faunas from Cornelia-Uitzoek, from the Florisbad spring and from Kareepan. These assemblages represent respectively the Cornelian LMA, the Florisian LMA and modern faunas of the central interior of southern Africa. The mixed feeder, *T. oryx*, and the fine feeder, *R. campestris*, are not included.

Figure 28. A revised biochronology for the last million years in southern Africa. The Cornelian LMA and the Florisian LMA are shown in relation to a geological time scale. The fossil localities from the interior of southern Africa and from the Cape coastal zone are ordered in accord with this temporal frame.

Figure 29. Dorsal and left lateral views of skulls of a male *C. gnou* (NMB-F 84) (left) and a male *C. taurinus* (NMB-F 56) (right). The numbers refer to the characters listed in the text, pages 95 – 96.

Figure 30. A comparison of premaxilla width between *C. gnou* (n = 10) and *C. taurinus* (n = 10). A t-test shows that there is no statistical difference between the means of the two samples (p=0.98).

Figure 31. The skull and horn cores of *M. priscus* from Erfkroon: frontal view (A), right lateral view (B) and an enlarged right lateral view of the braincase (C).

Figure 32. Basal horn core dimensions of *M. priscus*, illustrating the two palaeopopulations.

Figure 33. Right lateral views of lower jaws of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The lower jaw of *M. priscus* (C. 2472) is from Mahemspan.

Figure 34. An arrangement of the *M. priscus* brain case and horn cores from Erfkroon, an upper jaw from Mahemspan and a complete lower jaw from Mahemspan. This arrangement is the basis for the reconstruction of the skull of *M. priscus*, given in Figure 35.

Figure 35. A reconstruction of the skull of *M. priscus*, as would have been found in populations around the Modder River.

Figure 36. Occlusal views of the right M² of *Aepyceros melampus* (A), a caprine/early alcelaphine from the Middle Miocene locality of Fort Ternan (B), *Damalacra* sp. from Langebaanweg (C), an advanced alcelaphine from the Shungura Formation Omo (D) and *A. buselaphus* (E). Specimens B to D are after Gentry (1980) and illustrate increasingly derived alcelaphine characteristics, while *A. melampus* (NMB-F 119) is morphologically very similar to the Fort Ternan specimen. The numbers refer to the characters listed in the text, page 111.

Figure 37. Occlusal views of the left upper dentitions of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 111 – 112.

Figure 38. Buccal views of the M³ of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). An additional molar of *C. gnou* (F) is included to show the variability in the distally projecting basal part of the metastyle. The numbers refer to the characters listed in the text, pages 111 – 112.

Figure 39. In A occlusal views are given of the left M₂ of (i) *Aepyceros melampus* (NMB-F 119), (ii) an early alcelaphine from the Middle Miocene site of Fort Ternan (*Kubanotragus tanyceras*), (iii) *Damalacra* sp. from Langebaanweg, (iv) an advanced alcelaphine from the Shungura Formation Omo and (v) *A. buselaphus* (A) (partly after Gentry 1980). Specimens B to F are respectively *D. pygargus*, *A. buselaphus*, *M. priscus*, *C. taurinus* and *C. gnou*. The numbers refer to the characters listed in the text, pages 114 – 115.

Figure 40. The length of the premolar row against that of the toothrow (A) and a comparison of the means and ranges of toothrow and premolar ratios (B) of extant Alcelaphini and *M. priscus*.

Figure 41. Height of mandibular articulation above the occlusal surface in *C. gnou* and in *C. taurinus*. The premolar row (indicated in red) in *C. gnou* is shorter than in *C. taurinus*. This is a function of a distal shift in occlusal pressure, which was caused by a re-arrangement of the major chewing muscles due to the lowered position of the mandibular articulation in relation to the occlusal plane. The lowered mandibular articulation reflects changes to the posterior part of the skull in *C. gnou*.

Figure 42. Mandibular depth at M₂/M₃ in relation to premolar shortening. The regression line representing *Connochaetes* spp and *M. priscus* (A) suggest that there is no functional relationship between these variables. When *A. buselaphus* and *D. pygargus* are included (B) there is an apparent positive relationship between the variables. This reflects the effect of body size, which masks the absence of a true functional relationship between the two variables.

Figure 43. Axis: ventral views of male and female extant Alcelaphini and of *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *C. taurinus* (C), *M. priscus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 120 – 121.

Figure 44. Axis: left lateral views of male and female extant Alcelaphini and of *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *C. taurinus* (C), *M. priscus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 121 – 122.

Figure 45. Breadth (SBV) against length (LCDe) of the axis of extant Alcelaphini and *M. priscus*.

Figure 46. Ventral (A) and cranial (B) views of the axis of *M. priscus*. The number refers to the character listed in the text, page 121.

Figure 47. Cranial articular width (BFcr) against length of the corpus and the dens (LCDe) of the axis in extant Alcelaphini and *M. priscus*. This illustrates the difference between hartebeest-like and wildebeest-like alcelaphines.

Figure 48. Dorsal views of the humeri of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 122 – 124.

Figure 49. Lateral views of the humeri of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 122 – 124.

Figure 50. Humerus: distal width (Bd) against greatest length (GL) (A), and trochlea width (BT) against the cranio-caudal depth of the medial part of the distal humerus (Dmd) of extant Alcelaphini and *M. priscus*.

Figure 51. Dorsal views of the radii of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 125 – 126.

Figure 52. Lateral views of the radii of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 125 – 126.

Figure 53. Radius: proximal views of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D), *C. gnou* (E) and *C. gnou* (F). The numbers refer to the characters listed in the text, pages 125 – 126.

Figure 54. Distal views of the radii of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 125 – 126.

Figure 55. Proximal width (Bp) against the total length (GL) of the radii of extant Alcelaphini and *M. priscus*.

Figure 56. Ratios of proximal depth (Dp) over proximal width (Bp) of the radii of extant Alcelaphini and *M. priscus*. This illustrates the greater dorso-volar depth of the radius *A. buselaphus* and *D. pygargus*.

Figure 57. Dorsal views of the metacarpals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 127 – 129.

Figure 58. Proximal views of the metacarpals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 127 – 129.

Figure 59. Volar views of the metacarpals of extant Alcelaphini and *M. priscus*. *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 127 – 129.

Figure 60. Lateral views of the metacarpals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 127 – 129.

Figure 61. Metacarpal shaft width (SD) against length (GL) of extant Alcelaphini and *M. priscus*.

Figure 62. Proximal depth (Dp) against proximal width (Bp) of the metacarpals of extant Alcelaphini and *M. priscus* (A) and their ratios (B).

Figure 63. The ratio of distal width (Bd) over distal depth (Dd) of the metacarpals of extant Alcelaphini and *M. priscus*.

Figure 64. The depth of the peripheral part of the medial condyle (Ddp) against the depth of the achsial part of the medial condyle (Dda) of the metacarpals of extant Alcelaphini and *M. priscus*. The regression line represents the combined samples of *C. taurinus* and *C. gnou*.

Figure 65. Dorsal views of the femora of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 130 – 131.

Figure 66. Lateral views of the femora of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 130 – 131.

Figure 67. Plantar views of the femora of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 130 – 131.

Figure 68. Distal views of the femora of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 130 – 131.

Figure 69. Femur shaft width (SD) against length (GL) (A) and distal width (Bd) against length (GL) (B) in extant Alcelaphini and *M. priscus*.

Figure 70. The depth of the lateral condyle (Dld) against the depth of the medial condyle (Dmd) of the metacarpal in extant Alcelaphini and *M. priscus*. The regression line represents the combined samples of *C. taurinus* and *C. gnou*.

Figure 71. Dorsal views of the tibiae of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 132 – 134.

Figure 72. Plantar views of the tibiae of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 132 – 134.

Figure 73. Lateral views of the tibiae of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 132 – 134.

Figure 74. Distal views of the tibiae of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The dorsal side is towards the top of the page. The numbers refer to the characters listed in the text, pages 132 – 134.

Figure 75. Distal width (Bd) of the tibia against length (GL) in extant Alcelaphini and *M. priscus*. The regression line represents the *C. gnou* sample.

Figure 76. The distal depth (Dd) of the tibia against its distal width (Bd) in extant Alcelaphini and *M. priscus*.

Figure 77. Dorsal views of the metatarsals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 135 – 136.

Figure 78. Plantar views of the metatarsals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 135 – 136.

Figure 79. Proximal views of the metatarsals of extant Alcelaphini and *M. priscus*: *D. pygargus* (A), *A. buselaphus* (B), *M. priscus* (C), *C. taurinus* (D) and *C. gnou* (E). The numbers refer to the characters listed in the text, pages 135 – 136.

Figure 80. Shaft width (SD) against length (GL) of the metatarsal in extant Alcelaphini and *M. priscus* (A) and the ratios of SD/GL (B). The regression lines in A show the linear relationships of these variable in *C. gnou* and *C. taurinus*.

Figure 81. Proximal width (Bp) against proximal depth (Dp) of the metatarsals in extant Alcelaphini and *M. priscus*. The regression lines show the linear relationships of these variables in these taxa.

Figure 82. Distal width (Bd) against greatest length (GL) of the metatarsal in extant Alcelaphini and *M. priscus*. The regression line represents the combined samples of *C. taurinus* and *C. gnou*.

Figure 83. Depth of the peripheral part of the medial condyle (Ddp) against depth of the axial part of the medial condyle (Dda) of the metatarsal in extant Alcelaphini and *M. priscus* (A). There is no statistical difference in the ratios of Ddp/Dda among the various taxa (B).

Figure 84. Ratio diagrams of means of limb lengths of Alcelaphini, Antilopini and Caprini. In A the similarity in bodyplans of Antilopini (*Gazella dorcas* & *Antidorcas marsupialis*) and Alcelaphini (*A. melampus*, *A. buselaphus* and *D. pygargus*) is illustrated, but contrasted with the body plan of a primitive sheep, *Ammotragus lervia*. In B the primitive alcelaphine antilopine body plan, as illustrated by *G. dorcas*, is contrasted with the advanced caprine-like bodyplans of *Connochaetes* spp. and *M. priscus*. Data for Antilopini are taken from Peters (1989) and Peters & Brink (1992), while data for *A. melampus* (n = 3) and *O. aries* (n= 4) are from the Florisbad comparative collections of modern mammals.

Figure 85. A skeletal reconstruction of *M. priscus* (B & C) based on the data presented in this chapter. The body plan of *C. taurinus*, after Kingdon (1982), is given as reference (A).

Figure 86. A summary of the alcelaphine phylogeny (A), as proposed by Vrba (1997), and a proposed alternative (B), based on the morphological comparisons provided in this chapter.

Figure 87. Temporal ranges of fossil members of the wildebeest group, given in the context of the southern African Land Mammal Age scheme and according to a geological time scale. The temporal ranges are based on Gentry & Gentry (1978), Gentry (1978), Geraads (1981), Harris (1988, 1991), Vrba (1997) and data provided in this study.

Figure 88. The original type specimen of "*Antilope*" *ournoueri* from Ain Jourdel - frontal view (A), enlarged postero-frontal view (B) and a left lateral view (C). The numbers refer to the characters listed in the text, pages 149 – 150.

Figure 89. The neotype of *Oreonagor tournoueri* from Aïn Boucherit; frontal view (A), posterior view (B), forwardly tilted frontal view (C), right lateral view (D) and postero-frontal view (E). Views C to E are enlarged. The numbers refer to the characters listed in the text, pages 152 – 154.

Figure 90. Frontal views of the skulls of *C. taurinus* (A), the type of *Oreonagor tournoueri* (Thomas 1884) (B), the neotype of *O. tournoueri* (C) and of *M. priscus* from Erfkroon (D).

Figure 91. Lateral views of the skulls of *C. taurinus* (A), of the type of *Oreonagor tournoueri* (Thomas 1884) (B), of the neotype of *O. tournoueri* (C) and of the reconstructed skull of *M. priscus* from Erfkroon (D).

Figure 92. Occlusal view of the neosyntype upper jaw 1966-5-37 of *Oreonagor tournoueri* from Ain Boucherit (A) and occlusal and buccal views an upper jaw fragment 1954-8-17 (B). The numbers refer to the characters listed in the text, pages 156 – 157.

Figure 93. Buccal views of the alcelaphine upper third molars from An Boucherit, referred to *Oreonagor tournoueri*; 1953-22-171 (A), 1953-8-243 (B), 1954-8-7 (C) and an unnumbered specimen (D). The specimens are presented so that they appear to be from the left side of the jaw. The number refers to the character listed in the text, page 157.

Figure 94. Lower dentitions assigned to *Oreonagor tournoueri* from Ain Boucherit; right lateral and occlusal views of the neosyntype lower jaw 1966-5-133 (A), an occlusal view of the neosyntype lower jaw fragment 1954-8-16 (B), an enlargement of the second molar of 1954-8-16 (C) and a line drawing of 1954-8-113 (D). The numbers refer to the characters listed in the text, pages 158 – 159.

Figure 95. Dorsal (A) and lateral (B) views of a right humerus, 19543-8-218, from Aïn Boucherit. The numbers refer to the characters listed in the text, pages 159 – 160.

Figure 96. Metacarpals from An Boucherit: dorsal views of 1953-22-118 (A) and 1954-8-219 (B) and a proximal view of 1953-8-207 (C). The numbers refer to the characters listed in the text, page 161.

Figure 97. Ratio diagram (A) of the metacarpals of extant Alcelaphini and those referred to *Oreonagor tournoueri* from Ain Boucherit and a plot (B) of depth of the achsial part of the medial condyle (Dda) against the distal width (Bd) of the metacarpal of extant Alcelaphini and those referred to *O. tournoueri* from Ain Boucherit. The upper regression line indicates *A. buselaphus*, while the lower indicates the combined samples of *C. taurinus* and *C. gnou*.

Figure 98. Femoral pieces assigned to *Oreonagor tournoueri* from Ain Boucherit: medial (A) and distal views (B) of a distal piece (1953-22-108) and a plantar view of a shaft piece (C). The number refers to the character listed in the text, page 162.

Figure 99. Trochlea width (BT) against the dorso-plantar depth of the medial part of the trochlea (Dmd) of the femur, 1953-22-108, from Ain Boucherit.

Figure 100. Distal views of tibiae referred to *Oreonagor tournoueri* from Aïn Boucherit: 1953-22-113 (A), 1954-15-36 (B) and 1960-5-154 (C). The remarkable *Megalotragus*-like enlargement of the plantar articulation facet for the os malleolare in the Aïn Boucherit material is illustrated. Comparative distal views of the tibiae of *A. buselaphus* (D), *M. priscus* (E), *C. taurinus* (F) and *C. gnou* (G) are given. The numbers refer to the characters listed in the text, page 163.

Figure 101. Ratio diagram of the limb elements from Ain Boucherit referred to *O. tournoueri*, showing its primitive body proportions.

Figure 102. Frontal and lateral views of the horn cores of *C. gnou laticornutus* from Cornelia-Uitzoek (A & B) and *C. gnou antiquus* from Florisbad (C & D). The numbers refer to the characters listed in the text, pages 169 – 171.

Figure 103. Dental dimensions of fossil *C. gnou*: length of the molar row against length of the toothrow (A) and ratios of toothrow/premolar row illustrating premolar shortening (B).

Figure 104. Length and breadth dimensions of the M₂ (A) and a plot illustrating temporal change in the M₂ of fossil *C. gnou* (B).

Figure 105. The breadth of the facies cranialis (BFcr) of the axis against the length of the corpus and the dens (LCDe) (A) and the smallest width of the corpus (SBV) against LCDe (B).

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Figure 106. Breadth of the trochlea (BT) of the humerus against distal medial depth (Dmd) of interior fossil assemblages (A) and the same plot without *M. priscus*, but including Swartklip 1 (B). The regression line represents the modern sample of *C. gnou*.

Figure 107. Breadth of the trochlea (BT) of the humerus against distal width (Bd) for interior fossil assemblages (A) and the same plot without *M. priscus*, but including Swartklip (B). The regression line represents the modern sample of *C. gnou*.

Figure 108. Breadth of the proximal articulation facet (BFp) of the radius against length (GL) (A) and of BFp against proximal breadth (Bp) (B).

Figure 109. Shaft width (SD) of the metacarpal against total length (GL) (A) and distal width (Bd) against GL (B). The upper regression line represents the combined mid-Holocene sample and the lower the modern *C. gnou* sample.

Figure 110. Proximal depth (Dp) of the metacarpal against the proximal width (Bp) (A) and the smallest depth of the shaft (DD) against the distal breadth (Bd) (B). The upper regression line represents the combined mid-Holocene samples and the lower the modern *C. gnou* sample.

Figure 111. Femur: a regression analysis of the total length measurements (GL) and shaft width measurements (SD) of modern *C. gnou* (A) and a comparison of SD measurements among modern and fossil wildebeest (B).

Figure 112. Distal width (Bd) of the tibia against the total length (GL) of fossil and extant wildebeest.

Figure 113. Distal depth (Dd) of the tibia against its distal width (Bd) for extant and fossil *C. gnou* from the interior of southern Africa (A), and from the Cape coast (B). The regression lines show the linear relationship between the two variables in fossil and modern *C. gnou* and in *C. taurinus*.

Figure 114. Greatest length (GL) of the metatarsal against shaft width (SD) of *C. gnou* from interior (A) and from coastal localities (B). The regression lines show the linear relationship between the two variables in fossil and modern *C. gnou*.

Figure 115. Proximal width (Bp) of the metatarsal against proximal depth (Dp) (A) and of distal width (Bd) and distal shaft depth (DD) of *C. gnou* from the interior and from coastal localities. The regression lines in A show the relationship between the two variables in fossil and modern *C. gnou*.

Figure 116. Box and whisker plots (mean, std error and std deviation) illustrating temporal changes in fossil populations of *C. gnou* from the interior of southern Africa: length of the M₂ (A), shortening of the premolar row (B), the axis (C), the distal humerus (D).

Figure 117. Box and whisker plots (mean, std error and std deviation) illustrating temporal changes in fossil populations of *C. gnou* from the interior of southern Africa: radius length (A), proximal radius (B), metacarpal length (C) and the distal metacarpal (D).

Figure 118. Box and whisker plots (mean, std error and std deviation) illustrating temporal changes in fossil populations from the interior of southern Africa: femur shaft (A), distal tibia (B) and metatarsal length (C).

Figure 119. Temporal pattern in wildebeest horn cores, illustrating the evolutionary sequence of the black wildebeest.

Figure 120. Comparative ratio diagrams of skeletal elements of fossil *C. gnou*.

Figure 121. Temporal and spatial patterning in the fossil elements of *C. gnou*: the axis, humerus and radius.

Figure 122. Temporal and spatial patterning in the fossil elements of *C. gnou*: the metacarpal, tibia and metatarsal.

Figure 123. Ratio diagrams of limb elements of interior and coastal Florisian black wildebeest.

Figure 124. A biogeographic model illustrating vicariance in black wildebeest and in other plains-living grazing ungulates.

APPENDIX B: TABLES OF MEASUREMENTS*

*** All measurements are in mm.**

Table 23. Width of the premaxilla in *C. taurinus* and *C. gnou*

Taxon	Accession no	Sex	
<i>C. gnou</i>	.		
	NMB-F84	M	74.2
	NMB-F6029	M	70.0
	NMB-F89	M	68.2
	NMB-F12057	M	76.4
	NMB-F85	M	69.2
	NMB-F9484	M	76.5
	NMB-F9393	F	65.5
	NMB-F8741	F	63.3
	NMB-F9387	F	65.0
	NMB-F8707	F	64.0
<i>C. taurinus</i>	NMB-F57	M	77.2
	NMB-F73	M	74.0
	-	M	73.5
	-	M	68.2
	NMB-F49	M	70.0
	NMB-F56	M	76.5
	NMB-F60	F	64.0
	NMB-F12088	F	63.0
	NMB-F64	F	62.9
	NMB-F12066	F	62.5

Table 24. Measurements of the lower jaw

Taxon	Accession no.	Sex	Tooth-row	P-row	M-row	L M ₂	B M ₂	Depth of mandible at M ₂
<i>C. taurinus</i>								
	NMB-F 8732	M		110.4	29.8	79.7	23.5 12.4	-
	NMB-F 9356	F		110.7	29.6	81.8	26.4 12.6	61.4
	A 1039			118.0	34.4	84.0	26.6 12.4	64.5
	NMB-F 9357	M		112.0	35.5	77.7	27.8 13.2	-
	A 2840			110.0	31.9	78.7	24.6 13.1	61.5
	-			119.0	33.2	86.1	26.9 13.0	63.5
	A 1438			111.3	26.1	85.0	25.6 12.9	58.9
	NMB-F 9310	M		111.2	30.2	81.0	25.9 12.3	65.8
	A 1441a			106.0	28.9	76.8	25.4 14.0	56.2
	A 1441b			110.5	32.8	77.9	26.9 11.8	62.4
	-			112.7	28.3	81.6	26.0 12.4	67.1
	-			110.5	34.0	79.2	26.1 11.6	63.3
<i>C. gnou</i>								
	NMB-F 6011			88.5	20.8	67.3	20.3 11.5	53.5
	A 12 15			88.5	20.3	68.3	20.4 12.0	49.0
	A 1596			93.4	22.0	70.8	21.9 12.2	50.2
	NMB-F 9411			92.4	22.2	71.8	22.4 10.5	53.8
	NMB-F 9413			90.2	19.1	70.3	22.4 11.4	52.0
	NMB-F 9408			88.1	19.4	69.0	21.8 10.8	49.0
	-			92.0	19.5	71.5	21.5 11.3	55.0
	-			93.6	21.9	70.5	21.8 10.5	56.3
	-			92.5	21.6	72.2	21.8 11.5	58.5
	A 1600			91.5	21.2	70.6	21.3 12.1	52.2
	A 2945			96.0	22.5	71.1	23.3 12.5	47.7
	A 1601		\	95.0	24.2	70.7	21.6 12.1	52.1
	NMB-F 9391	F		93.3	20.7	72.3	22.5 11.0	51.0
	NMB-F 9358	M		103.7	25.4	76.7	25.0 11.0	59.5
	NMB-F 8742			98.3	23.2	73.1	22.0 10.0	53.9
	-			95.5	22.3	73.8	23.2 10.8	58.0
	NMB-F 9870	M		102.5	23.0	78.5	24.5 10.4	53.4
	NMB-F 7447	M		94.5	22.2	71.2	23.0 10.9	52.9
	NMB-F 6029	F		94.8	22.2	72.0	23.1 11.1	-
<i>A. buselaphus</i>								
	NMB-F 8740			96.1	30.0	65.3	21.1 11.7	49.4
	NMB-F 6022			88.7	24.7	67.5	21.2 11	46.4

-	110.3	36.7	71.7	22.9	10.8	48.5
-	95.5	30.8	62.9	18.4	11.3	47.4
-	95.8	28.0	67.0	20.7	10.7	48.7
NMB-F 7434	99.1	31.3	66.5	20.6	10.6	45.1
<i>D. pygargus</i>						
NMB-F 9403	82.9	25.0	57.1	19.2	9.6	40.7
A. 2942	81.0	24.8	58.5	18.0	8.0	41.2
A. 2836	76.4	19.7	56.3	17.6	9.8	39.8
A. 1347	84.6	21.3	64.0	18.4	8.9	39.4
-	83.6	25.5	60.3	18.1	9.0	43.3
-	88.1	28.6	59.8	18.9	8.4	43.9
-	84.2	25.5	59.0	18.8	8.3	41.0
-	76.8	22.8	52.8	16.8	9.0	43.3
-	79.2	21.8	57.5	18.4	9.5	41.6
-	79.1	22.2	55.5	16.4	9.7	39.2
-	82.8	24.7	57.9	17.7	9.3	38.9
Florisbad spring						
FLO 1019	-	-	73.3	24.6	10.5	-
FLO 1040	-	-	74.5	24.8	9.9	56.0
FLO 1022	92.1	23.4	68.4	20.0	10.9	55.8
FLO 1051	88.9	19.5	68.2	20.7	11.5	-
FLO 1043	97.0	21.8	75.5	23.1	12.0	-
FLO 1028	-	-	79.2	25.0	10.8	-
FLO 1041	-	-	-	22.8	9.8	-
FLO 4744	97.4	22.3	76.9	23.0	11.9	53.1
FLO 4240	102.2	25.0	76.0	23.5	12.7	-
FLO 4238	-	-	71.1	22.0	11.9	-
FLO 1025	102.5	23.8	76.8	24.6	11.4	53.3
FLO 1027	93.0	20.5	70.5	19.3	11.5	-
FLO 1020	92.1	22.2	69.5	19.0	-	-
FLO 4236	95.0	19.5	74.0	23.0	12.3	-
FLO 4235	91.4	21.7	70.4	21.0	12.2	-
FLO 375	89.0	19.3	68.3	22.4	11.1	-
FLO 4427	92.8	22.6	70.5	21.3	12.0	-
Cornelia-Uitzoek (<i>M. eucornutus</i>)						
COR 551	130.6	33.1	96.5	32.6	12.5	-
COR 142	-	-	-	31.0	11.5	-
Cornelia-Uitzoek (<i>C. .gnou laticornutus</i>)						
COR 84	-	-	-	27.5	13.2	-
COR 565	-	-	-	27.9	13.4	-

	COR 566	-	-	-	29.5	13.5	-
	COR 564	-	-	-	26.5	12.6	-
	COR 563	-	-	-	28.5	14.9	-
	COR 562	-	-	-	27.4	13.6	-
	COR 1271	115.0	28.5	86.2	27.0	15.4	-
	COR 932	-	-	-	27.8	14.7	-
	COR 552	112.4	27.1	85.2	26.5	14.5	-
Mahemspan <i>(M. priscus)</i>							
	C. 2472	125.3	25.3	101.3	31.9	15.5	68.9
	C.2325	126.5	25.3	97.7	30.4	15.2	76.0
	C. 1793	129.0	27.6	99.8	30.1	14.4	69.3
	C. 1584	138.8	30.0	107.7	32.2	16.3	82.0
	C. 1411	127.5	25.9	-	31.2	14.8	-
	C. 2451	134.2	30.6	97.7	30.8	14.2	-
	C. 1864	132.3	25.4	-	33.5	15.0	-
	C. 2535	-	-	-	32.4	15.2	-
	C. 2540	-	-	-	31.9	15.5	-
Mahemspan <i>(Connochaetes spp.)</i>							
	C. 2423	96.0	21.5	73.3	23.5	12.2	-
	C. 2378	-	-	77.8	25.2	12.0	-
	C. 2257	-	-	79.0	23.3	12.5	-
	C. 405/1	-	-	78.0	24.1	11.1	-
	NO NO	-	-	-	25.0	11.8	-
	C. 1840	-	-	-	24.4	12.5	-
	C. 1845	-	-	75.0	24.9	11.1	-
	C. 2047	-	-	-	24.0	13.6	-
	-	-	-	-	-	-	-
Swartklip							
	-	-	-	-	-	-	-
	ZW 2023	85.6	24.0	61.6	-	-	-
	ZW 5742	93.5	18.8	74.7	-	-	-
	ZW 1460	89.2	21.6	67.6	-	-	-
	ZW 2600	97.4	23.4	74.0	-	-	-
	-	-	-	-	-	-	-
Spitskop							
	-	-	-	-	-	-	-
	PK-B 85	-	-	77.1	24.8	11.1	-
	PK-B 9/1	94.7	-	73.3	23.3	11.0	45.0
	PK-B 25	-	-	-	27.2	12.3	-
	PK-A 55	-	-	-	28.1	14.0	-
	-	-	-	-	-	-	-
Kareepan							
	-	-	-	-	-	-	-
	BH 126	-	-	-	22.0	12.0	-
	BH 3076	-	-	-	24.3	11.4	-
	BH 3104	-	-	-	21.8	10.9	-
	BH 3253	-	-	-	21.1	12.2	-
	BH 269	-	-	-	23.0	11.4	-

Aïn Boucherit

1966-5-1-133	90.8	25.2	65.6	21.0	10.4	43.2
1954-13-8	89.4	22.2	67	21.5	11.3	42.7
1954-8-16	-	-	70.5	23.3	10.2	44.2
1953-22-162	87.5	20.8	67.5	21.0	11.5	42.6
1953-22-221	-	-	-	21.5	10.0	-
1954-8-177	-	-	-	21.2	9.9	46.5
195?-13-9	-	-	-	22.6	9.5	41.5
1953-22-190	-	-	-	22.3	10.6	-
1953-22-178	-	-	-	25.1	11.4	-
1954-8-113	-	-	-	21.6	10.6	-

Tighenif

1953-13-282	119.4	28.5	81.0	27.0	13.8	-
(?M. priscus) 1955-13-358	130.4	32.0	95.3	30.0	13.9	-
(?M. priscus) 1956-12-29	121.7	-	96.2	28.3	13.8	-
1956-127-127	-	28.0	81.8	23.1	14.2	-
(?M. priscus) 1955-13-894	140.4	33.5	-	32.5	13.0	63.0
-	-	-	-	29.0	14.3	-
1954-7-247	-	-	-	29.0	13.1	-
-	-	-	-	27.0	13.1	-
-	-	-	-	25.0	13.2	-
-	-	-	-	28.9	14.3	-
-	-	-	-	27.5	12.4	-
-	-	-	-	31.2	13.5	-
-	-	-	-	28.7	13.9	-
1955-13-544	-	-	-	27.7	15.5	-
-	-	-	-	26.7	14.8	-
1955-13-1171	-	-	-	28.0	14.5	-
-	-	-	-	29.3	13.2	-
-	-	-	-	28.2	15.2	-
-	-	-	-	26.5	13.3	-
1955-12-929	-	-	-	28.4	13	-
-	-	-	-	30.0	14.1	-
-	-	-	-	29.6	13.2	-
-	-	-	-	28.1	13.4	-
1955-13-87	-	-	-	29.8	13.4	-
1935-13-670	-	-	-	29.1	13.5	-
-	-	-	-	30.0	12.9	-

-	-	-	-	28.2	13.1	-
1955-13-1162	-	-	-	29.8	12.6	-
-	-	-	-	28.7	-	-
-	-	-	-	27.5	13.7	-
1955-13-384	-	-	-	28.9	13.0	-
-	-	-	-	26.7	13.4	-
-	-	-	-	29.7	13.7	-
1955-13-1175	-	-	-	30.1	14.3	-
-	-	-	-	29.9	13.3	-
1955-13-628	-	-	-	29.9	13.6	-
-	-	-	-	28.3	13.2	-
-	-	-	-	30.3	13.5	-
-	-	-	-	30.7	13.7	-
-	-	-	-	29.3	13.7	-
-	-	-	-	28.3	12.8	-
-	-	-	-	28.1	12.8	-
-	-	-	-	28.0	14.3	-
-	-	-	-	27.2	12.9	-

Table 25. Measurements of the axis

Taxon	Accession no.	Sex	LCde	LAPa	BFcr	BFed	SBV	H
<i>C. taurinus</i>								
	SAM36108		99.2	86.4	72.8	42.2	43.3	114.5
	NMB9352		104.8	87.0	82.2	42.8	45.7	114.0
	NMB9356		96.2	84.5	80.4	41.4	43.6	103.0
	NMB8737		108.6	112.0	92.0	46.4	48.4	129.0
	AZ563	F	100.7	93.0	81.4	45.2	42.8	-
<i>C. gnou</i>								
	SAM39121		81.6	71.0	65.7	36.9	42.6	87.5
	SAM39318		84.8	72.2	65.9	34.6	41.9	93.0
	SAM39233		84.2	68.9	67.6	36.5	42.1	87.0
	SAM38249		75.7	63.8	63.5	35.0	40.5	86.0
	SAM36660		87.5	78.0	72.9	39.5	43.5	104.0
	SAM36675		86.4	77.4	74.2	40.7	41.5	106.0
	SAM38783		82.6	72.5	67.8	37.8	43.4	91.5
	SAM37090		84.7	75.9	66.0	37.6	41.0	95.0
	SAM35619		83.0	68.0	63.6	35.0	40.8	86.7
	SAM35853		85.7	72.0	71.8	40.5	42.0	97.5
	SAM36710		80.9	61.7	67.0	36.0	43.4	85.0
	NMB-F8708		96.1	91.1	72.3	42.1	46.4	109.6
	NMB-F9779		87.5	78.7	68.5	36.3	43.9	-
	NMB-F8742		88.5	76.1	72.4	38.9	50.0	102.5
	NMB-F8741		85.4	67.8	64.1	31.5	38.5	87.0
	NMB-F7439		75.8	71.2	66.5	34.6	40.9	94.0
	NMB-F8736		80.1	71.0	67.6	36.1	40.4	98.5
	NMB-F9358		78.3	80.3	73.2	34.6	44.9	105.0
	NMB-F7447		82.4	71.1	70.9	36.3	41.7	99.0
<i>A. buselaphus</i>								
	NMB-F7437		94.1	82.3	68.2	35.0	34.1	82.0
	NMB-F9956		93.0	80.5	72.6	35.5	36.0	86.0
	NMB-F6022		97.4	79.8	70.9	37.4	37.1	82.5
	NMB-F8715		99.8	81.4	70.8	38.3	35.5	91.0
	NMB-F8740		100.5	81.9	73.5	39.8	37.7	97.5
	NMB-F9417		108.3	108.5	76.8	46.4	45.1	110.0
	TMP AZ20	F	90.0	-	70.0	33.5	34.0	80.0
	TMP AZ64	F	93.0	-	67.0	33.5	36.5	84.0
	SAM 3620	F	99.0	-	71.0	38.5	38.0	93.0
	SAM 3877	F	103.0	-	71.0	38.0	37.0	89.0
	TMP AZ44	M	101.0	-	72.0	37.5	36.5	96.0
<i>D. pygargus</i>								
	NMB-F9963		-	-	55.5	-	-	-
	NMB-F7446		76.3	65.2	53.7	26.7	29.8	69.0

	NMB-F9346		77.4	69.8	53.6	26.8	26.9	68.5
	NMB-F12220	M	77.5	66.0	51.2	26.5	27.6	67.0
	NMB-F944	F	72.1	69.4	53.8	29.2	27	70.0
	NMB-F6028	M	77.6	65.7	56.0	27.6	25.7	75.0
	NMB-F6007		76.0	65.0	54.1	26.0	25.8	71.0
Mahemspan								
<i>(Connochaetes spp.)</i>								
	C. 1951		104.0	-	84.3	42.5	53.5	-
	C. 2516		94.6	-	83.2	42.0	58.0	-
	-		100.5	-	80.7	42.0	49.0	-
	C. 1805		-	-	86.6	-	50.0	-
Mahemspan								
<i>(Connochaetes spp.)</i>								
	C. 2368a		116.5	-	102.5	52.7	64.7	-
	C. 2406		128.4	-	113.7	59.0	63.3	-
	C. 2222		113.0	-	98.6	50.5	56.0	-
	C.2221		125.2	-	103.0	-	59.5	-
	C. 2337		116.2	-	95.2	47.0	-	-
	C. 1869		-	-	99.6	-	-	-
	C. 2351		-	-	106.0	-	-	-
	C. 2272a		-	-	110.2	-	-	-
Cornelia-Uitzoek								
<i>(C. gnou laticornutus)</i>								
	COR 602		109.5	-	86.2	45.5	54.7	-
	COR 601		107.0	-	86.3	42.0	54.0	-
	COR 600		112.0	-	86.3	47.6	50.2	-
Florisbad spring								
	-		91.4	-	78.8	37.8	48.7	-
	FLO 2086		85.0	-	75.2	-	49.0	-
	FLO 2123		86.6	-	75.0	-	50.3	-
	FLO 2095		84.3	-	72.2	37.1	47.5	-
Spitskop								
	PK-A 78		90.5	-	76.0	41.7	45.3	-
	PK-A 33		94.9	83.8	77.9	48.1	44.2	-
	PK-A		95.0	-	79.2	50.0	-	-
	PK-A 17		-	-	82.5	-	-	-
Kareepan								
	BH 1952		85.7	-	76.7	46.5	47.7	-
	BH 1950		83.0	-	71.9	-	48.5	-
	BH 284		91.6	-	78.0	40.0	46.0	-
	BH 554		84.8	-	70.4	38.2	41.9	-

Deelpan

DP-A 31	88.9	-	77.3	37.0	43.0	-
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Swartklip

ZW 2858	84.9	-	-	-	41.4	-
ZW 1515	79.0	-	-	-	43.7	-
ZW 2134	91.5	-	-	-	43.8	-

Table 26. Measurements of the humerus.

Taxon	Accession no.	SEX	GL	BT	Bd	Dmd	SD
<i>C. taurinus</i>							
	TMAZ563	F	242.0	60.4	62.1	60.7	34.5
	SAM36064	F	256.5	59.0	60.0	56.4	33.0
	SAM36108	F	262.0	60.2	65.6	61.5	34.9
	NMB9352	F	250.0	55.7	60.2	62.2	-
	NMB9356	M	273.0	64.5	70.6	66.6	-
	NMB8737	M	265.0	59.0	62.2	62.3	-
<i>C. gnou</i>							
	SAM39122	F	210.4	51.6	-	52.0	27.2
	SAM39311	F	-	50.4	51.1	52.2	-
	SAM39231	F	207.3	51.0	54.9	50.8	26.4
	SAM38249	F	198.2	48.0	50.8	48.2	24.4
	SAM36660	M	220.6	52.5	53.4	53.8	27.5
	SAM36675	M	220.0	52.7	59.4	53.3	26.6
	SAM38783	F	209.5	51.6	-	53.8	26.9
	SAM37090	F	218.0	51.9	-	54.0	26.8
	SAM35619	F	210.8	49.3	50.8	52.0	23.9
	SAM35853	M	226.5	53.5	53.8	55.0	28.0
	SAM36239	F	218.5	51.7	54.0	53.0	26.5
	SAM36710	F	204.2	51.0	53.0	52.0	28.4
	NMB8708	M	234.0	56.0	60.7	57.5	29.7
	NMB9779	M	232.0	53.2	60.9	56.6	30.4
	NMB8742	M	227.6	54.6	62.8	54.1	29.9
	NMB8741	F	210.0	50.3	53.8	49.8	25.8
	NMB7439	M	210.0	47.9	49.8	51.7	25.4
	NMB8736	M	218.5	51.7	54.7	53.3	26.9
	NMB7447	M	223.5	53.9	57.3	54.9	28.0
	NMB9358	M	248.5	58.0	59.1	59.3	29.7
<i>A. buselaphus</i>							
	NMB7437	F	232.0	48.2	51.6	50.6	-
	NMB9956	M	244.0	50.7	51.7	53.6	-
	NMB8739	F	244.5	49.5	54.4	52.2	-
	NMB8715	F	228.0	47.0	49.1	49.9	-
	NMB8740	F	248.5	51.3	54.3	54.2	-
	NMB9417	F	252.0	52.5	55.0	55.1	-
	NMB9930	F	234.0	48.2	50.0	51.5	-
	TMAZ2085	F	227.0	48.0	51.0	51.5	-
	TMAZ645	F	230.0	48.0	49.5	50.5	-
	SAM39820	F	230.0	49.0	53.5	52.5	-
	SAM38773	F	236.0	50.0	55.0	54.0	-

	SAM36206	F	237.0	51.0	54.0	52.0	-
	MNB7006	M	232.0	49.0	54.5	52.5	-
	TMAZ449	M	240.0	48.0	53.5	51.0	-
<i>D. pygargus</i>	NMB9963	F	185.0	38.4	38.6	40.2	-
	NMB7446	F	180.0	37.7	40.5	38.0	-
	NMB9346	F	186.0	38.7	40.2	40.3	-
Mahemspan (<i>M. priscus</i>)	C. 2334		295.0	71.0	79.8	76.7	40.7
	C. 2384		-	73.0	82.0	77.4	42.2
	C. 1903		-	74.2	86.2	75.3	42.8
	C.2166		-	79.5	-	78.8	44.2
	C. 1802		-	74.7	84.3	75.2	41.4
	C. 2127		302.0	77.2	86.7	79.7	45.3
	C. 2019		-	78.8	89.2	78.2	-
	C. 1423		-	78.3	82.8	77.2	42.1
	C. 1602		-	74.0	81.0	75.5	-
	C. 1810		-	73.6	85.7	-	48.0
	C. 2508		-	77.8	86.0	80.7	46.3
	C. 2465		-	73.8	87.5	77.2	48.0
	C. 1884		-	73.7	80.3	75.0	39.1
	C. 2189		295.0	74.2	84.2	75.0	43.5
Florisbad	FLO3833		-	57.0	61.1	58.4	32.5
	FLO1931		-	55.7	60.5	57.8	-
	FLO3834		-	54.9	60.0	59.5	-
	FLO1940		-	55.6	59.7	-	-
	FLO1937		-	51.8	55.6	53.0	29.8
	FLO1850		-	58.4	-	-	-
	FLO1935A		-	53.5	-	55.7	-
	FLO1935B		-	53.6	57.2	53.8	-
	FLO1935C		-	52.3	54.6	55.0	-
	FLO1935D		-	55.7	55.8	56.1	-
	FLO1939B		-	51.5	58.6	54.0	-
	FLO3835		-	51.8	55.9	50.3	29.0
	-		-	52.4	56.5	57.0	30.5
	-		-	58.0	61.2	-	-
Swartklip	KB8596		-	48.8	54.8	49.7	-
	KM31219		-	49.4	56.6	50.5	-
	LP3700		-	50.4	55.0	49.4	-
	LP3706		-	51.4	57.0	51.0	-
	LP3707		-	52.0	-	54.4	-
	LP3708		-	46.0	51.0	47.8	-
	ZW5539		-	49.8	56.2	-	-

ZW2346	-	48.7	56.0	51.6	-
ZW3284	-	48.6	57.0	52.9	-
ZW2813	-	47.9	56.8	49.8	-
ZW5481	-	48.1	57.9	51.0	-
ZW5543	-	47.4	56.0	50.0	-
ZW315	-	48.9	57.3	52.1	-
ZW2063	-	49.3	54.7	49.8	-
ZW2350	-	48.9	56.6	52.6	-
ZW2066	-	46.0	52.0	-	-
ZW5017	-	48.0	55.3	50.8	-
ZW2068	-	48.0	54.7	-	-
ZW544	-	50.4	56.3	53.3	-
ZW3733	-	46.5	54.8	48	-
ZW5532	-	46.8	53.0	50.2	-
ZW5433	-	49.7	59.6	51.3	-
ZW2811	-	53.7	-	53.3	-
ZW2355	-	46.9	52.7	47.6	-
ZW2349	-	45.8	43.0	47.2	-
Cornelia- Uitzoek (C. gnou laticornutus)					
COR983/1	-	60.5	65.9	-	-
COR550	-	61.9	70.0	66.3	-
COR1279	-	68.2	74.5	72.7	-
Kareepan					
BH1012	-	50.7	56.5	52.4	28.3
BH1001	-	56.0	58.8	-	30.2
BH1008	-	51.8	59.8	55.0	55.6
BH1010	-	-	66.3	58.4	31.7
BH1004	-	54.4	61.0	57.5	29.3
BH1005	-	57.1	62.5	60.0	31.2
BH1015	-	55.9	63.5	60.7	-
BH999	-	54.2	60.7	55.7	29.1
BH1020	-	53.3	59.9	56.0	29.3
BH1016	-	51.8	54.7	56.6	27.3
BH1014	-	52.4	56.8	52.8	-
BH997	-	50.8	54.4	51.0	26.0
BH100	-	52.8	59.7	-	29.0
BH253	-	55.8	62.5	58.0	30.6
BH254	-	57.1	63.0	-	31.3
Deelpan					
DPD12	-	48.8	51.4	50.5	-
DPD40	-	51.5	56.5	54.7	27.2
DPA32	229.1	52.7	58.0	54.2	29.8

Maselspoort

-	-	-	52.1	56.5	54.4	27.4
-	-	-	55.5	60.5	60.7	30.9
-	-	-	52.5	60.5	58.0	30.7
-	-	-	52.5	58.9	57.0	29.1
-	-	-	53.5	58.0	55.8	28.1
-	-	-	52.6	57.8	56.3	27.9
-	-	-	50.3	53.5	51.4	-

Ain Boucherit

1954-8	218.0	213.0	48.5	51.4	49.5	26.6
1953-22	112.0	221.6	46.0	50.0	49.4	27.0
1953-22	59.0	-	46.4	47.3	-	23.0
1954-22	59.0	-	47.4	50.9	51.8	-
1953-22	114.0	-	45.5	-	46.0	23.6
1966-5	40.0	-	46.6	50.1	-	-

Table 27. Measurements of the radius.

Taxon	Accession no.	Sex	GL	BFp	Bp	Dp	Bd
<i>C. taurinus</i>							
	TMAZ563		304.3	59.8	70.4	32.7	59.9
	M		312.0	59.2	67.4	31.0	58.2
	SAM36108		319.0	60.5	70.6	32.6	60.1
	NMB9352		309.6	60.1	69.0	33.2	59.0
	NMB9356		337.0	64.0	77.9	36.8	68.7
	NMB8737		343.0	61.7	68.7	33.0	60.2
<i>C. gnou</i>							
	SAM39121		259.3	50.3	57.5	28.3	49.0
	SAM39318		273.3	48.9	55.1	29.2	-
	SAM39233		262.4	50.0	57.6	29.3	47.3
	SAM38249		245.2	47.5	54.2	27.5	46.5
	SAM36660		269.0	51.5	58.1	31.2	50
	SAM36675		267.8	51.5	58.0	28.6	54.6
	SAM38783		256.0	51.3	59.2	28.4	46.6
	SAM37090		266.0	51.0	58.4	28.1	45
	SAM35619		246.5	48.5	56.4	27.7	47.9
	SAM35853		287.2	51.0	59.5	31.6	52.2
	SAM36239		268.6	50.5	55.7	28.4	48.4
	SAM36710		255.5	50.6	57.2	27.1	50.0
	NMB8708		282.0	56.4	66.1	29.4	53.3
	NMB9779		284.0	56.1	65.0	31.7	52.8
	NMB8742		274.9	55.1	62.0	30.3	52.1
	NMB8741		265.5	48.3	56.4	27.4	46.2
	NMB7439		248.0	48.1	54.3	29.4	44.8
	NMB8736		258.7	49.8	59.9	29.5	49.7
	NMB7447		269.8	52.6	59.7	30.8	52.4
<i>A. buselaphus</i>							
	NMB7437		301.8	49.6	54.3	29.4	45.7
	NMB9956		313.0	50.5	57.8	30.4	48.7
	NMB8739		308.8	49.6	55.8	29.0	50.8
	NMB8715		306.0	47.5	53.1	28.1	47.0
	NMB8740		310.0	50.7	56.3	30.4	51.7
	NMB9417		325.0	56.0	63.1	33.6	52.0
	NMB9930		302.0	49.5	55.6	29.0	47.3
	SAM39820	F	295.0	49.0	54.5	29.5	45.0
	TMAZ2085	F	295.0	47.0	53.0	27.5	47.5
	TMAZ645	F	297.0	49.0	56.0	29.5	46.0
	SAM36206	F	299.0	49.5	55.5	30.0	47.5
	SAM38773	F	305.0	50.0	55.5	30.5	48.5
	TMAZ449	M	295.0	49.0	55.0	28.0	49.5

	MNB70006	M	310.0	50.0	55.5	29.0	46.0
<i>D. pygargus</i>							
	NMB9963		230.0	38.4	41.8	22.3	35.6
	NMB7446		222.0	37.3	41.5	23.0	35.0
	NMB9346		238.0	38.0	41.4	22.3	36.4
	NMBF6007	F	223.6	37.0	39.8	22.6	36.0
	NMBF9444	F	229.0	36.7	40.5	22.4	35.8
Mahemspan (<i>M. priscus</i>)							
	C.2147		394.0	77.2	94.3	45.3	77.0
	C.2283		364.0	73.8	87.1	42.5	71.0
	C.1389		381.0	74.7	86.2	45.7	72.1
	C.2373		360.0	75.7	87.7	44.8	-
	C.1871		390.0	74.8	-	44.0	-
	C.2321		365.0	75.5	85.7	44.5	70.7
	C.2367		382.0	75.4	82.5	42.5	-
	C.2413		375.0	73.4	85.0	42.3	71.3
	C.1396		384.0	72.8	85.7	42.9	71.1
Mahemspan (<i>C. taurinus</i>)							
	BM1935A		327.0	66.7	74.0	35.8	54.7
	C.1985		325.0	67.5	74.4	37.2	-
Florisbad spring							
	FLO1990		284.6	56.4	65.0	31.8	53.8
	FLO3845		288.1	56.0	-	31.9	56.7
	FLO1995		289.0	59.2	68.6	31.8	56.9
	FLO1991		283.9	54.0	62.0	31.1	54.0
	FLO3668		-	52.1	61.0	28.2	-
	FLO1972		-	56.3	64.7	31.8	-
	FLO3750		-	53.2	60.7	29.5	-
	-		-	-	-	-	55.5
	FLO1990		285.0	56.2	65.0	31.0	53.8
	-		-	-	-	-	54.0
	-		-	58.0	66.1	32.2	-
Swartklip							
	ZW3305		262.5	49.3	57.2	26.5	44.8
	ZW523		257.4	48.3	55.2	26.5	44.8
	ZW6723		256.0	-	47.0	25.0	45.6
	ZW5475		262.6	50.3	56.6	26.6	44.7
	ZW3970		-	48.5	54.6	27.1	-
	ZW2334		-	47.7	53.2	25.2	-
	ZW6609		-	51.2	56.4	27.3	-
	ZW1989		-	47.0	53.0	25.3	-

	ZW3096	-	50.7	56.7	-	-
	ZW5814	-	45.9	51.8	24.9	-
	ZW3306	-	49.3	56.0	26.3	-
	BM1850	-	48.6	54.2	-	-
Cornelia-Uitzoek						
<i>(C. gnou laticornutus)</i>						
	1935B	-	62.1	69.9	35.1	-
	1935C	-	-	-	36.4	-
Sunnyside						
	1935D	378.0	75.2	-	41.3	65.4
	SS6	371.0	-	-	43.0	72.0
	SS11	385.0	-	-	46.1	79.3
	KM31219	-	-	-	-	54.5
Deelpan						
	LP3700	287.0	55.6	61.3	31.8	46.5
	LP3707	279.0	51.5	60.2	28.7	52.5
	LP3707	270.0	51.7	58.0	28.0	46.8
	DP-D13	-	46.1	53.6	27.0	-
Kareepan						
	BH1056	-	55.5	62.5	32.0	-
	BH1064	-	55.5	62.4	28.5	-
	BH1066	-	59.5	67.4	35.0	-
	BH85	-	56.0	64.1	31.7	-
	BH693	265.0	51.0	58.9	28.8	49.5
	BH536	289.3	54.7	-	30.6	51.5
	BH234	-	54.5	61.8	32.2	-
	BH220	-	57.1	63.0	32.5	-
	BH653	-	-	-	-	49.8
	BH255	295	-	-	-	-
	BH1078	296.2	57.2	64.1	32.4	53.6
	BH1074	289.5	57.0	63.0	30.2	53.0
	BH1077	284.5	58.3	65.5	31.5	55.5
	BH1075	283.5	57.9	65.7	31.7	57.3
	BH1076	282.5	-	-	-	-
	BH1070	296.7	55.5	64.2	30.9	55.0
	BH1071	260.0	51.3	57.6	28.6	45.0
	BH1072	260.0	50.6	57.0	27.4	48.9
	BH1073	294.0	56.3	-	-	-
	BH1068	-	57.8	65.5	31.6	-
	BH1065	-	56.1	-	30.7	-
	BH1054	-	60.6	67.8	34.7	-
	BH1060	-	56.4	64.1	31.7	-

BH1055	-	55.5	62.7	31.8	-
BH1057	-	57.2	64.2	32.3	-
BH1067	-	54.7	61.6	29.7	-
BH1069	-	54.3	58.9	29.0	-
BH1063	-	54.9	63.1	29.7	-

Maselspoort

MP34	280.0	54.7	59.0	31.0	51.4
MP35	282.5	56.3	64.0	32.8	51.0
MP36	292.0	54.2	58.0	30.4	51.3
MP37	285.0	53.5	59.8	32.4	-
MP38	273.5	52.7	58.6	29.5	47.0
MP39	272.3	53.1	58.1	28.5	52.7

Ain Boucherit

1954-8-128	241	38.7	43.7	22.6	-
1954-13-36	-	42.0	48.1	23.7	-
1953-22-55	-	38.9	42.6	21.1	-

Table 28. Measurements of the metacarpal.

Taxon	Accession no.	Sex	GL	Bp	Dp	SD	DD	Bd	Dd	Dda_	Ddp
<i>C. taurinus</i>											
	NMB9352		223.0	47.6	27.9	27.7	21.7	49.7	28.8	26.5	20.8
	NMB9356		237.0	51.5	32.4	30.0	22.5	56.6	33.0	29.2	22.6
	NMB8737		247.5	48.2	31.0	27.7	21.5	52.7	29.9	27.6	22.8
	SAM36061		229.8	45.8	29.0	24.8	19.0	47.2	29.4	-	-
	TM563		226.4	46.5	29.0	28.2	19.5	50.3	27.7	26.5	-
	SAM36101		240.4	45.8	30.7	25.6	19.9	49.0	30.5	-	-
<i>C. gnou</i>											
	SAM38981		201.8	43.4	27.9	24.2	18.5	44.6	27.3	-	-
	SAM39122		191.5	39.4	26.4	22.4	16.0	43.3	26	-	-
	SAM39311		195.8	40.7	-	22.2	17.4	42.0	25	-	-
	SAM39233		186.0	40.6	26.8	21.7	16.7	42.8	26.2	-	-
	SAM38249		181.7	39.4	26.0	20.7	15.7	41.0	24.6	-	-
	SAM36660		196.1	41.2	28.1	22.9	17.0	43.6	26.1	-	-
	SAM36675		190.0	43.4	30.4	22.7	16.5	46.8	27.2	-	-
	SAM38783		191.4	39.7	25.0	22.0	16.1	43.3	25.6	-	-
	SAM37090		190.1	40.2	27.0	22.2	16.1	43.4	26.6	-	-
	SAM35619		183.0	39.4	27.7	21.0	16.5	42.7	25.0	-	-
	SAM35853		200.9	43.4	28.2	22.6	17.2	44.8	26.7	-	-
	SAM36239		200.5	42.0	27.0	20.9	-	43.5	26.5	-	-
	SAM36710		185.0	40.0	27.4	22.8	15.5	42.6	26.1	-	-
	NMB8708		206.9	44.0	29.8	23.3	17.8	45.6	28.0	25.1	20.2
	NMB9779		204.4	44.0	27.2	24.3	17.2	46.7	28.6	25.3	20.5
	NMB8742		202.5	42.5	27.4	24.4	18.3	44.7	28.9	25.4	20.5
	NMB8741		195.2	36.9	26.3	21.6	15.8	41.5	24.0	21.6	17.7
	NMB7439		186.7	40.1	25.3	20.7	15.6	41.6	25.0	22.3	17.9
	NMB8736		196.8	42.5	27.0	21.9	15.4	43.9	26.1	23.9	17.9
	NMB9358		209.7	44.7	29.3	24.3	18.0	46.8	28.7	26.0	21.1
	NMB7447		195.7	42.8	28.0	21.8	15.6	45.0	26.1	24.7	19.7
<i>A. buselaphus</i>											
	NMB8715		255.0	39.0	24.3	22.0	15.0	40.8	26.8	24.5	21.0
	NMB8740		258.0	43.6	27.0	25.5	19.4	45.6	28.6	26.0	22.5
	NMB9417		258.0	43.0	27.0	25.5	18.6	45.4	30.4	27.5	23.7
	NMB9930		242.0	40.4	25.6	22.0	17.0	43.5	27.6	26.1	22.0
	NMB7437		243.0	38.3	25.6	21.2	16.7	41.3	27.4	25.4	21.0
	NMB9956		257.0	41.0	27.0	23.1	17.3	42.9	28.9	25.8	21.2
	NMB8739		260.0	43.0	26.5	23.7	17.9	44.0	28.8	26.6	21.6
	SAM36206	F	247.0	41.5	28.5	25.6	17.4	42.5	27.5	-	-
	SAM39820	F	248.0	40.0	27.5	21.6	17.0	41.5	28.0	-	-
	SAM39820	F	252.0	42.5	27.0	-	19.5	42.5	28.0	-	-
	TMAZ2085	F	255.0	40.5	25.0	21.5	16.0	41.0	25.5	-	-

	TMAZ645	F	260.0	41.5	28.5	23.1	18.0	43.0	29.0	-	-
	SAM38773	M	243.0	42.0	27.0	21.8	16.9	42.5	27.5	-	-
	MNB70006	M	253.0	39.0	26.0	22.0	15.6	40.0	27.5	-	-
<i>D. pygargus</i>	NMB9963		209.1	31.1	20.7	16.0	14.0	31.0	21.0	19.3	16.5
	NMB7446		200.0	30.6	19.5	17.1	13.9	31.0	20.2	19.0	16.0
	NMB9346		210.0	32.0	20.6	17.7	13.7	32.0	21.3	19.4	17.1
	NMB12254		211.2	32.4	20.9	17.9	14.6	31.8	22.3	20.5	18.3
	NMB12245		204.7	30.6	21.3	18.0	14.0	32.1	21.2	19.4	17.5
	NMB7438	M	210.4	30.7	21.0	17.0	13.8	32.1	21.8	19.0	17.0
	NMB12246		216.0	31.7	21.5	18.5	14.9	32.0	-	20.0	18.2
	NMB12260		216.0	32.7	22.1	19.3	14.3	33.0	-	20.4	18.0
Florisbad spring	FLO3825		219.9	48.0	31.4	27.0	20.8	48.8	29.1	26.4	23.5
	FLO4098		-	-	-	-	-	49.9	29.8	26.1	23.0
	FLO3824		206.2	44.0	29.3	27.5	18.4	48.2	27.3	24.5	21.0
	FLO1974		201.2	46.2	31.4	28.7	19.4	48.9	28.0	25.5	22.7
	FLO3828		204.7	44.4	28.7	26.8	19.6	47.4	27.8	25.0	21.2
	FLO1866		-	41.4	28.0	26.7	18.3	-	-	-	-
	FLO1910		-	41.5	28.3	-	-	-	-	-	-
	FLO1895		-	44.5	30.2	-	-	-	-	-	-
	FLO3907		-	45.2	30.0	-	-	-	-	-	-
	FLO3908		-	44.2	28.7	-	-	-	-	-	-
	FLO3919		-	-	-	-	-	49.6	28	25.4	21.7
	FLO1879		-	-	-	-	-	46.5	26.6	25	-
	FLO3918		-	-	-	-	19.0	47.0	-	-	-
	C.1446		208.2	43.2	30.3	-	18.5	49.7	-	26.5	22.8
	-		203.4	42.2	28.5	26.3	18.0	49.0	-	24.5	21.4
	-		-	46.2	31.0	28.6	20.1	-	-	-	-
	-		-	41.6	27.4	-	-	-	-	-	-
	-		-	-	-	-	19.0	45.0	-	24.5	21.6
Mahemspan											
(<i>C. taurinus</i>)	C.2026		231.0	49.3	34.6	28.6	20.4	54.6	31.4	28.5	25.0
	C.2475		-	-	-	-	18.9	48.6	28.3	24.8	20.0
Mahemspan											
(<i>M. priscus</i>)	C.2131		258.7	65.7	40.3	37.0	25.4	71.0	35.5	33.0	29.3
	C.2453		254.2	63.5	35.6	37.0	24.7	69.5	-	-	28.7
	C.1424		248.8	61.7	37.3	35.0	23.0	65.3	35.7	32.8	28.5
	C.1886		266.0	65.5	31.7	40.0	26.3	68.0	39.0	34.7	29.2
	C.1945		250.0	59.3	37.5	39.4	-	66.0	-	-	-
	C.1422		252.5	58.5	35.2	36.6	22.7	65.0	-	31.5	-
	C.2286		258.2	61.8	37.5	-	24.9	66.3	36.2	33.8	29.0
	C.1939		246.0	59.6	35.7	-	24.0	62.0	-	-	26.7

C.1361	263.6	65.1	38.0	40.0	26.0	69.8	-	32.5	27.2	
C.2219	252.2	63.6	36.8	38.7	25.6	69.0	-	32.8	28.4	
C.2357	252.3	61.6	35.0	36.2	23.7	65.9	36.0	32.5	27.7	
C.1968	242.0	25.8	-	32.7	-	63.0	-	-	-	
C.1917	262.9	67.4	42.0	41.2	29.7	71.8	-	35.9	32.2	
C.1969	262.0	65.0	37.3	40.8	27.8	67.1	-	-	-	
C.1384	259.0	62.2	36.0	36.5	-	66.7	-	-	-	
Vlakkraal										
<i>(M. priscus)</i>										
C.1446	265.8	58.8	37.0	35.8	23.6	63.8	35.6	31.6	28.6	
Cornelia-Uitzoek										
<i>(C. gnou laticornutus)</i>										
COR542	-	-	-	-	19.6	54.9	29.1	27.8	23.0	
COR541	-	-	-	-	19.2	51.7	28.7	25.4	21.0	
COR1512	-	-	-	-	25.0	55.2	-	-	-	
Elandsfontein b/c										
BM1935A	-	39.0	26.0	-	-	-	-	-	-	
1935B	-	38.1	25.1	-	-	-	-	-	-	
1935C	-	-	-	-	15.7	40.0	25.1	18.9	17.5	
1935D	-	-	-	-	16.4	39.0	-	19.0	-	
H13/1	-	-	-	-	16.5	39.0	24.3	18.0	17.4	
I5/7.8/5	-	-	-	-	16.0	39.5	23.5	18.6	17.8	
KM31219	-	-	-	-	16.7	39.8	24.8	19.2	18.4	
Elandsfontein										
LP3700	225.5	41.3	28.9	24.9	18.1	45.5	27.6	21.2	20.4	
EFT20084	213.0	41.2	28.7	24.7	17.6	46.0	27.3	20.5	19.5	
LP3707	218.0	41.1	28.3	24.4	18.3	45.5	28.3	21.3	-	
EFT391	204.3	46.3	30.9	38.7	19.7	52.4	29.6	-	-	
EFT11302	-	52.3	33.0	-	-	-	-	-	-	
EFT14285	-	-	-	-	-	47.5	28.0	-	-	
EFT5663	-	-	-	-	-	45.6	-	-	-	
EFT12276	-	44.3	30.0	-	-	-	-	-	-	
EFT12510	-	43.5	29.1	25.1	-	-	-	-	-	
EFT10705	-	-	-	-	-	44.6	25.5	-	-	
EFT14666	-	-	-	-	-	49.1	26.5	-	-	
EFT15463	-	-	-	-	-	43.6	25.6	-	-	
EFT413	185.6	40.4	26.8	22.6	17.2	42.1	26.2	-	-	
EFT414	188.2	39.0	26.1	21.0	16.6	40.2	24.1	-	-	
EFT11915	-	36.4	25.7	-	-	-	-	-	-	
EFT20247	-	39.8	27.0	-	-	-	-	-	-	
EFT11914	-	-	-	-	-	40.4	23.6	-	-	
EFT13916	-	-	-	-	-	41.7	25.7	-	-	
EFT12898	-	-	-	-	-	40.4	24.2	-	-	
Klasies River										
16A(1527)	-	-	-	-	-	38.0	25.3	-	-	

	1E16/17	-	-	-	-	-	38.3	25.5	-	-
	1/17aMCA	-	40.3	27.1	-	-	-	-	-	-
Swartklip										
	ZW5609	186.0	40.4	27.3	23.4	16.7	42.4	25.0	-	-
	ZW5753	191.1	39.0	26.4	21.8	17.0	40.8	23.9	-	-
	ZW6684	187.2	-	-	-	-	40.6	24.2	-	-
	ZW2523	192.0	41.6	27.7	-	18.1	44.2	24.6	-	-
	ZW6157	190.7	41.6	-	-	-	42.3	23.8	-	-
	ZW3219	191.3	40.0	26.3	23.3	18.8	42.7	24.7	-	-
	ZW1658	191.1	42.0	26.2	22.7	17.0	43.3	23.3	-	-
	ZW6688	185.9	38.6	24.9	20.7	16.4	39.1	22.8	-	-
	ZW1619	185.3	41.5	28.0	24.7	17.9	44.2	26.0	-	-
	ZW2699	191.3	40.4	25.3	22.4	16.0	40.5	23.9	-	-
	ZW1622	180.4	37.4	24.3	21.6	16.3	40.0	21.6	-	-
	ZW3242	185.0	40.5	27.2	23.3	15.9	-	-	-	-
	ZW3315	188.3	37.5	23.6	21.6	17.0	39.3	23.8	-	-
	ZW2100	197.0	42.8	28.0	24.0	18.2	45.5	25.8	-	-
	ZW2103	197.0	43.0	28.0	25.5	19.2	45.4	27	-	-
	ZW1722	186.1	37.0	24.4	21.1	16.9	39.5	22.5	-	-
	ZW5469	196.1	40.4	26.4	25.0	18.0	42.6	24.4	-	-
	ZW2466	194.1	44.8	27.9	23.8	17.6	45.0	26.0	-	-
	ZW5297	191.5	39.3	25.2	23.1	17.6	41.3	24.3	-	-
	ZW542	195.8	42.5	27.2	23.5	17.4	44.9	24.1	-	-
	ZW3314	191.2	38.6	25.7	21.8	15.5	40.4	24.1	-	-
	ZW5610	185.3	40.0	25.4	21.3	17.1	41.7	24.6	-	-
	ZW1610	186.3	40.5	26.2	23.5	-	42.7	24.4	-	-
Sunnyside (<i>C. taurinus</i>)										
	SS23	217.3	47.9	31.0	27.4	20.8	52.0	30.3	27.6	23.1
	SS24	218.5	47.2	32.5	27.5	20.5	52.2	30.0	27.1	23.0
	SWS26	-	48.5	31.3	26.6	-	-	-	-	-
Sunnyside (<i>M. priscus</i>)										
	SS17	245.3	59.5	35.5	33.7	23.0	65.1	36.5	32.2	28.8
Deelpan										
	DP-D51	212.0	42.2	28.7	23.3	18.3	45.7	27.9	24.9	21.5
	DP-D?	196.0	37.4	26.9	20.8	15.6	41.0	34.4	22.4	18.0
	DP-D283	196.2	41.0	27.3	21.7	16.0	40.3	25.9	23.2	19.9
Kareepan										
	BH523	216.1	45.3	-	27.3	18.8	48.5	-	24.4	20.4
	BH517	206.9	42.8	28.3	25.4	18.1	46.8	27.6	25.0	21.9
	BH236	-	-	-	23.0	-	45.0	26.9	23.7	20.7
	BH178	202.7	42.0	-	25.4	18.8	45.7	-	-	-
	BH391	214.2	45.2	30.8	25.0	18.9	47.0	28.0	26.0	21.5
	BH1274	205.3	-	-	25.2	18.5	46.0	-	-	-
	BH1265	213.8	45.8	30.9	26.9	19.3	49.0	-	-	-
	BH1291	205.9	42.5	27.5	25.2	18.8	46.5	-	-	-
	BH1258	212.4	47.5	30.1	25.0	19.7	48.7	29.8	27.5	22.2
	BH1256	214.9	46.1	30.6	25.8	18.6	49.2	28.9	26.4	-

BH1254	212.0	45.0	29.4	28.2	20.2	50.5	28.2	26.2	22.5
BH1247	202.0	-	28.5	24.0	17.9	44.8	26.8	23.8	20.1
BH1259	205.3	44.6	30.0	24.9	18.3	46.1	26.5	24.6	20.3
BH1248	208.0	44.4	31.0	27.5	18.3	49.0	28.2	25.7	21.6
BH1243	209.0	44.8	29.7	27.0	19.4	50.1	30.5	28.0	-
BH1257	212.7	44.6	-	25.0	18.8	46.3	27.7	24.6	21.7
BH1249	206.0	-	-	-	17.2	45.0	-	-	-
BH1262	203.5	45.9	30.9	26.2	16.7	49.0	-	-	-
BH1246	204.7	-	-	26.2	18.7	48.7	29.8	25.5	22.3
BH1246	204.7	-	-	26.2	18.7	48.7	29.8	25.5	22.3
BH1255	216.2	46.6	30.3	27.4	18.9	51.0	29.3	26.6	22.5
BH1260	196.5	41.3	27.8	24.6	17.6	44.5	-	23.3	20.0
BH1252	206.5	45.5	29.4	26.5	18.8	49.2	28.5	25.7	-
BH1253	207.8	-	30.5	27.4	18.1	47.9	27.1	24.2	20.5
BH1261	207	44.3	-	24.6	17.9	45.9	26.8	24.7	20.5
BH1263	207.5	42.7	28.5	23.6	18.0	46.4	-	-	-
BH1244	199.7	-	-	27.8	19.2	47.8	29.0	26.3	21.6
BH1251	194.5	39.9	26.5	22.6	16.2	43.1	25.7	23.5	19.6
Maselspoort									
-	202.3	41.4	27.0	24.1	16.4	43.5	26.4	24.6	20.1
-	200.8	43.2	-	25.9	18.0	45.1	27.3	26.0	22.0
-	211.1	44.6	30.0	25.6	19.2	46.4	27.8	25.5	21.1
MP40	199.8	44.4	28.8	24.7	17.6	46.5	27.5	25.7	21.0
MP43	204.3	45.7	29.9	26.9	17.9	45.5	26.0	24.6	20.5
MP44	207.3	43.2	29.5	25.7	18.0	46.5	28.0	25.0	21.2
Ain Boucherit									
1954-8	242.5	40.7	27.2	22.2	17.8	40.0	25.9	23.3	21.5
1953-22	242.7	37.0	25.7	21.4	16.9	40.8	-	24.0	21.5
1954-8	241.0	39.7	27.2	22.5	18.3	41.0	-	24.2	21.7
1954-8	-	40.6	-	22.3	18.4	-	-	-	-
1954-8	-	-	-	-	-	42.5	-	24.8	20.6

Table 29. Measurements of the femur.

Taxon	Accession no.	Sex	GL	Bp	SD	BT	Bd	Dld	Dmd
<i>C. taurinus</i>									
	TMAZ563		309.6	103.8	31.3	41.8	78.3	80.3	102.7
	TMAZ1272		326.2	108.8	31.0	44.7	82.7	86.7	107.8
	SAM36064		315.0	93.0	33.2	40.0	71.5	82.0	101.6
	SAM36108		320.0	105.2	35.0	-	79.0	85.2	109.3
	NMB9352		314.5	103.9	32.4	45.2	77.0	81.4	104.9
	NMB9356		343.0	118.0	33.3	46.5	88.7	93.9	121.4
	NMB8737		335.0	103.6	34.2	45.8	76.3	83.3	109.2
<i>C. gnou</i>									
	SAM39121		262.3	81.9	25.5	40.7	67.7	71.5	91.8
	SAM39318		270.5	87.4	27.6	40.6	69.6	71.0	90.6
	SAM39233		261.4	84.4	25.6	38.4	66.1	70.5	92.9
	SAM38249		242.5	81.6	23.1	37.9	62.4	66.5	88.0
	SAM36660		278.2	82.6	28.2	39.7	70.4	72.4	91.2
	SAM36675		271.0	89.3	26.6	40.5	69.2	70.6	91.0
	SAM38783		255.6	85.0	26.5	40.2	67.6	72.2	93.1
	SAM37090		265.5	90.1	26.8	41.8	70.2	72.4	94.6
	SAM35619		251.6	79.8	24.4	36.6	66.4	71.0	87.6
	SAM35853		282.2	87.6	28.6	41.7	73.0	74.0	93.4
	SAM36239		263.4	82.0	26.8	39.6	63.8	72.5	91.2
	SAM36710		260.9	88.3	27.3	41.2	69.6	70.4	92.8
	NMB8708		292.0	94.0	30.5	42.5	76.5	77.0	98.4
	NMB9779		284.0	90.4	29.2	41.4	73.8	76.8	97.1
	NMB8742		285.5	91.3	29.5	40.2	70.0	74.9	95.4
	NMB8741		257.0	80.1	24.4	36.3	61.9	71.6	91.6
	NMB7439		256.5	79.1	25.0	41.4	69.5	67.0	88.1
	NMB8736		265.5	80.7	24.7	40.0	64.9	72.2	90.5
	NMB9358		300.5	95.6	29.5	43.6	73.6	81.7	104.4
	NMB7447		273.0	88.0	27.0	44.4	69.1	75.0	98.8
<i>A. buselaphus</i>									
	NMB7437		285.0	80.7	23.7	34.7	63.0	73.0	88.1
	NMB8739		290.0	80.5	25.7	38.4	61.1	72.4	90.4
	NMB6022		275.0	77.3	24.4	-	64.4	-	-
	NMB8715		286.5	79.5	24.6	36.2	62.4	72.8	88.8
	NMB9417		300.0	93.0	28.0	36.3	67.1	77.0	93.4
	NMB9930		278.0	76.1	24.7	35	61.4	72.9	88.6
	TMAZ2085	F	270.0	74.0	26.0	33.5	60.0	70.0	83.0
	SAM39820	F	275.0	77.0	25.0	32.5	59	71.0	87.0
	TMAZ645	F	283.0	78.0	23.5	32.0	62.0	71.0	84.0
	SAM36206	F	290.0	82.0	27.0	35.0	61.0	71.0	86.0
	SAM38773	F	290.0	82.0	26.0	37.5	63.0	71.0	87.0
	MNB70006	M	276.0	79.0	24.0	35.0	61.0	72.0	85.0
	TMAZ449	M	285.0	78.0	25.0	32.5	63.0	70.0	83.0

<i>D. pygargus</i>								
	NMB9963	225.0	59.4	21.1	29.5	51.3	56.8	68.0
	NMB7446	215.0	61.5	21.3	26.1	48.3	54.6	65.7
	NMB9346	224.0	63.6	20.9	27.6	48.0	57.3	69.7
Mahemspan								
(<i>M. priscus</i>)								
	C.2403	393.0	-	41.5	57.0	104.0	107.3	135.0
	C.2220	425.0	-	46.3	-	-	-	-
	C.2171	413.0	-	44.4	55.5	-	-	-
	C.2718	408.0	-	47.1	-	-	-	-
	C.1956	-	-	42.2	-	-	-	-
	C.2248	-	-	39.8	-	-	-	-
	C.2457	-	-	43.3	-	-	-	-
	C.2441	-	-	43.0	-	-	-	-
	C.1385	-	-	38.7	-	-	-	-
Maselspoort								
	MP52	-	-	29.3	-	-	76.0	-
	MP58	-	-	27.8	-	-	-	-
Kareepan								
	BH1147	-	-	29.8	-	-	-	-
	BH1148	-	-	26.7	-	-	-	-
	BH1146	-	-	28.3	-	-	-	-
	BH1149	254.0	75.0	25.4	-	-	-	-
Florisbad spring								
	FLO2139	-	-	-	-	69.0	-	93.6
Swartklip								
	ZW1795	266.8	79.0	27.2	34.4	-	61.6	82.5
	ZW2822	-	-	28.3	-	-	-	-
	ZW5128	-	-	27.7	-	-	-	72.0
	ZW1572	-	81.2	27.0	-	-	-	-
	ZW3003	-	-	27.0	-	-	-	-
	ZW3969	-	-	27.9	-	-	-	-
	ZW2076	-	-	30.3	-	-	-	-
	ZW285	-	79.5	27.3	-	-	-	-
	ZW1575	-	-	-	-	67.8	70.8	-
	ZW2830	-	-	-	-	-	69.0	-
Erfkroon								
(<i>M. priscus</i>)								
	EFK2	398.0	134.8	45.0	57.8	98.0	106.0	132.8
Ain Boucherit								
	1953-22-120	300.0	-	27.0	-	-	-	-
	1953-22-108	-	-	-	33.6	-	-	85.7

Table 30. Measurements of the tibia.

Taxon	Accession no.	Sex	GL	Bp	Dp	Bd	Dd
<i>C .taurinus</i>	TMAZ563		338.4	81.0	78.9	52.8	40.9
	TMAZ1272		364.8	85.1	79.4	53.0	39.8
	SAM36064		350.0	80.0	76.5	52.0	39.1
	SAM36108		349.0	85.9	77.0	53.0	40.8
	NMB9352		340.0	80.2	73.0	53.9	41.7
	NMB9356		373.5	91.2	86.0	58.7	45.1
	NMB8737		386.0	82.3	77.0	51.6	39.4
<i>C. gnou</i>	SAM39121		296.6	71.3	66.4	45.4	34.2
	SAM39318		316.0	73.2	67.4	42.8	35.6
	SAM39233		297.7	70.8	65.4	41.7	33.7
	SAM38249		282.4	68.0	63.6	41.6	32.8
	SAM36660		319.0	75.0	70.0	43.0	36.0
	SAM36675		314.0	74.0	68.8	46.0	37.2
	SAM38783		290.6	72.8	68.2	42.0	36.0
	SAM37090		307.4	73.8	70.0	43.8	36.8
	SAM35619		282.5	69.2	67.0	42.4	34.7
	SAM35835		326.0	73.4	69.6	44.3	34.0
	SAM36239		305.0	70.0	67.3	40.3	33.7
	SAM36710		296.0	71.8	67.0	44.2	35.5
	NMB8708		335.0	79.4	73.5	49.3	38.0
	NMB9779		322.0	76.4	73.8	48.6	37.4
	NMB8742		317.5	75.9	71.0	47.7	35.3
	NMB8741		306.5	67.7	64.5	41.3	33.1
	NMB7439		290.0	72.8	65.0	44.1	34.0
	NMB8736		296.5	73.6	67.0	46.0	35.8
NMB7447		312.5	76.4	67.5	45.7	34.2	
<i>A. buselaphus</i>	NMB7437		332.0	68.1	67.5	44.0	35.9
	NMB8739		340.0	68.3	69.0	45.6	36.9
	NMB6022		330.0	67.4	67.0	44.3	37.1
	NMB8715		336.0	68.7	65.0	44.4	34.4
	NMB9417		355.0	73.1	73.0	48.0	37.6
	NMB9930		328.5	67.4	65.0	45.2	-
	TMAZ2085	F	317.0	67.0	68.0	40.5	33.5
	SAM39820	F	324.0	66.0	68.0	43.0	34.0
	SAM36206	F	332.0	67.0	67.0	45.5	35.5
	SAM38773	F	333.0	68.0	68.0	46.0	36.5
	TMAZ645	F	334.0	66.0	67.0	43.5	36.5
	TMAZ449	M	323.0	66.0	69.0	44.5	35.0
	MNB70006	M	336.0	68.0	66.0	43.0	34.0

<i>D. pygargus</i>	NMB9963	272.0	54.2	52.0	33.2	27.2
	NMB7446	260.0	53.8	50.0	32.4	26.8
	NMB9346	272.0	52.2	51.0	34.0	27.4
	NMB6028	275.0	53.9	51.0	33.1	27.3
Mahemspan						
(<i>M. priscus</i>)						
	C.1597	-	-	-	69.4	51
	C.1371	-	-	-	71.4	51.6
	C.1395	-	-	-	73.0	49.5
	C.2271	-	-	-	69.3	49.8
	C.2386	-	-	-	67.2	48.8
	C.1841	423	106.5	67.4	69.4	51.2
	-	-	-	-	68.3	49.3
	C.2525	-	-	-	68.0	51.2
	C.2236	-	-	-	61.2	-
	C.1906	-	-	-	65.0	43.5
	C.1963	-	-	-	71.1	51.0
	C.2509	-	-	-	71.8	52.5
	C.2514	-	-	-	68.0	51.8
	C.2394	-	-	-	68.5	52.9
	C.2170	-	-	-	75.5	53.5
	C.2134	-	-	-	74.0	50.8
	C.1809	-	-	-	65.3	48.9
	C.2445	-	-	-	70.7	47.9
	C.2072	-	-	-	69.5	49.0
	C.1992	-	-	-	73.5	-
Florisbad spring						
(<i>M. priscus</i>)						
	FLO1982	449.0	106.0	98.0	67.3	53.0
	FLO3931	-	-	-	65.9	50.5
Spitskop						
Sunnyside						
	SS	-	-	-	75.5	53.6
Cornelia-Uitzoek						
(<i>C. gnou laticornutus</i>)						
	COR535	-	-	-	-	41.1
	BM1850	-	-	-	53.1	40.3
	BM1935A	-	-	-	53.3	40.1
	1935B	-	-	-	53.4	39.3
Florisbad spring						
	FLO1983	-	79.6	73.2	49.8	37.8
	FLO2023	-	80.3	74.9	-	-
	FLO1919	-	-	-	48.8	39.6
	FLO1983	341.0	79.5	73.9	48.5	37.7
	FLO2010	-	-	-	50.2	38.6
	FLO2015	-	-	-	50.0	37.9
	FLO2016	-	-	-	50.2	37.1

	FLO3627	-	-	-	50.8	38.2
	FLO1997	-	-	-	50.2	37.1
	-	-	-	-	49.4	37.0
	FLO2000	-	-	-	47.8	36.0
	FLO3909	-	-	-	47.8	36.0
	FLO3909	-	-	-	47.0	34.5
	FLO3625	-	-	-	47.7	36.4
	-	334.0	-	-	47.5	35.0
	-	-	-	-	50.7	42.0
Spitskop (C. gnou)						
	1935C	-	-	-	50.3	37.3
	1935D	-	-	-	49.2	37.4
Spitskop (M. priscus)						
	PK-B13	-	-	-	72.5	51.5
Maselspoort						
	1939B	326.0	73.2	65.5	48.1	38.3
	KB8596	-	-	-	44.8	37.0
	KM31219	-	-	-	42.3	34.5
Kareepan						
	LP3700	338.0	-	-	48.1	37.0
	LP3706	-	-	-	45.5	34.5
	LP3707	-	-	-	45.0	35.2
	LP3708	-	-	-	47.0	-
	BH978	-	-	-	49.3	36.8
	BH947	-	-	-	45.9	35.0
	BH981	-	-	-	45.9	34.9
	BH985	-	-	-	48.3	37.0
	BH984	-	-	-	45.7	35.0
	BH971	-	-	-	43.5	34.3
	BH963	-	-	-	49.3	40.5
	BH965	-	-	-	49.0	38.5
	BH975	-	-	-	47.5	35.7
	BH970	-	-	-	44.5	35.5
	BH968	-	-	-	49.2	37.5
	BH966	-	-	-	46.9	-
	BH518	-	-	-	49.2	38.5
Deelpan						
	DP-D331	-	-	-	43.3	33.5
	DP33	323.0	70.5	68.0	46.2	36.1
Klasies River						
	1/15+4	-	-	-	47.3	34.8
Swartklip						
	ZW1623	293.0	-	-	42.2	32.7

ZW3239	315.2	-	-	44.8	35.5
ZW2763	-	-	-	41.6	31.2
ZW2393	-	-	-	44.0	34.2
ZW912	-	-	-	42.7	32.4
ZW5602	-	-	-	40.4	31.1
ZW5958	-	-	-	43.3	34.0
ZW2389	-	-	-	41.2	29.4
ZW1792	-	-	-	42.4	31.1
ZW279	-	-	-	45.4	33.1
ZW3000	-	-	-	42.8	34.2
ZW6152	-	-	-	42.0	33.1
ZW1626	-	-	-	42.1	31.9
ZW6612	-	-	-	39.8	31.0
ZW3606	-	-	-	45.1	36.6
ZW6222a	-	-	-	41.8	35.5
ZW5959	-	-	-	44.9	33.7
ZW6068	-	-	-	42.2	31.5
ZW839	-	-	-	41.6	32.5
ZW6348	-	-	-	38.8	32.0
ZW6207	-	-	-	41.5	31.1
ZW2753	-	-	-	45.0	36.6
ZW2392	-	-	-	43.0	33.3
ZW5533	-	-	-	43.8	34.3
ZW6307	-	-	-	41.4	32.6
ZW3612	-	-	-	42.0	33.0
ZW6607	-	-	-	43.6	35.0
ZW3349	-	-	-	45.0	34.6
ZW6596	-	-	-	40.5	30.1
ZW5825	-	-	-	44.4	34.6
ZW1624	-	-	-	41.5	32.9
ZW2754	-	69.0	64.5	-	-
Ain Boucherit					
1954-15-36	-	-	-	42.6	33.8
1949-5-4	-	-	-	41.8	33.8
1953-22-113	-	-	-	45.4	37.5
1966-5-154	-	-	-	42.2	34.6
1953-22-19	-	-	-	35.0	28.5

Table 31. Measurements of the metatarsal.

Taxon	Accession no.	Sex	GL	Bp	Dp	SD	DD	Bd	Dd	Dda	Ddp
<i>C. taurinus</i>											
	TMAZ563		245.5	41.8	44.3	24.4	21.2	46.5	29.0	-	-
	TMAZ1272		253.4	41.7	44.7	24.8	22.6	46.6	29.5	-	-
	SAM36064		249.5	39.0	44.5	21.0	20.8	44.0	29.0	-	-
	SAM36108		258.4	41.8	44.4	22.2	22.2	45.4	30.2	-	-
	NMB9352		245.0	38.6	39.0	24.4	22.1	46.5	29.2	25.6	21.0
	NMB9356		259.0	43.6	43.3	25.8	24.2	51.7	-	28.6	23.2
	NMB8737		266.0	40.4	40.0	24.6	23.4	47.8	-	28.1	21.6
<i>C. gnou</i>											
	SAM38989		223.8	37.4	40.6	19.5	18.6	41.4	26.3	-	-
	SAM39121		214.1	36.0	39.4	19.1	16.8	38.8	25.0	-	-
	SAM39318		224.6	36.5	39.4	20.0	18.4	38.7	25.0	-	-
	SAM39233		207.5	36.0	41.8	18.7	17.8	38.5	25.8	-	-
	SAM38249		203.0	34.3	40.0	17.2	16.9	37.4	24.4	-	-
	SAM36660		225.8	37.2	41.4	20.0	18.2	38.6	25.1	-	-
	SAM36675		211.8	38.4	41.0	19.1	17.6	41.2	26.4	-	-
	SAM38783		211.9	35.4	38.8	18.5	18.0	39.0	24.9	-	-
	SAM37090		212.4	35.9	41.7	19.4	18.1	40.5	26.1	-	-
	SAM35619		210.5	33.9	39.0	16.4	17.0	38.8	25.0	-	-
	SAM35835		231.2	38.0	38.4	19.7	17.9	39.8	26.0	-	-
	SAM36239		232.5	35.2	39.0	19.0	17.6	37.7	26.3	-	-
	SAM36710		225.8	36.2	39.4	20.0	17.5	39.1	25.5	-	-
	NMB8708		237.0	39.5	38.8	20.0	19.3	41.6	-	24.6	18.7
	NMB9779		233.2	39.7	37.7	20.3	19.3	42.7	-	24.1	18.7
	NMB8742		229.2	36.5	36.1	20.9	19.3	41.8	-	24.1	18
	NMB8741		219.7	33.6	33.1	18.0	16.9	37.7	-	21.8	17.8
	NMB7439		212.8	33.2	33.2	17.6	16.7	36.6	-	22.2	16.9
	NMB8736		221.3	36.0	36.4	18.7	17.5	40.0	-	23.6	19.6
	NMB9358		241.0	37.0	38.1	20.6	19.4	41.9	-	25.5	21.2
	NMB7447		222.5	36.1	36.2	18.8	17.1	40.2	-	23.3	19.1
<i>A. buselaphus</i>											
	NMB7437		253.0	34.2	35.0	18.9	17.5	38.9	-	23.6	18.5
	NMB8739		270.0	35.6	35.7	20.9	21.0	40.1	-	25.6	20.3
	NMB6022		254.5	33.7	34.7	19.8	19.2	38.6	-	24.0	18.5
	NMB8715		266.0	33.8	34.5	19.3	18.1	39.4	-	24.0	18.6
	NMB9417		272.5	37.8	37.7	22.5	20.0	42.9	-	25.7	20.4
	NMB9930		255.0	35.7	34.0	19.3	18.6	41.3	-	25.5	20.0
	SAM39820	F	255.0	34.5	34.5	19.8	19.3	39.0	26.5	-	-
	SAM36206	F	256.0	35.0	36.5	23.9	19.7	40.5	26.5	-	-
	TMAZ645	F	264.0	35.0	35.0	18.8	17.7	39.5	26.5	-	-
	TMAZ2085	F	265.0	34.0	36.5	21.5	20.0	41.0	25.5	-	-
	SAM38773	F	265.0	34.5	36.5	21.3	19.9	41.0	26.5	-	-
	TMAZ449	M	252.0	35.0	35.5	18.6	17.7	40.0	28.0	-	-
	MNB7006	M	263.0	34.5	33.5	19.5	18.8	38.8	26.0	-	-

<i>D. pygargus</i>	NMB9963	222.0	25.5	27.9	14.7	16.0	30.0	-	18.3	15.0
	NMB7446	210.0	26.0	26.9	14.7	15.5	29.2	-	17.2	13.3
	NMB9346	221.0	27.5	28.4	15.4	15.2	30.5	-	18.3	15.7
	NMB6028	224.0	27.1	27.2	14.6	15.0	30.9	-	19.0	15.3
Mahemspan										
<i>(M. priscus)</i>										
	C.2330	319.0	53.7	58.0	29.5	28.1	57.4	35.7	31.8	27.1
	C.2348	330.0	55.9	60.6	31.1	31.2	60.2	36.0	32.6	27.7
	C.1989	349.0	-	-	-	31.4	66	37.2	33.9	27.2
	C.1249	321.0	56.0	-	33.2	27.7	61.1	35.7	31.9	26.9
	C.2156	305.0	54.7	56.9	33.0	28.9	59.4	35	31.6	25.2
	C.1806	321.0	-	-	30.9	-	59.0	34.5	29.1	31.7
	C.1808	330.0	55.0	57.4	32.3	30.4	62.4	34.2	30.7	26.1
	C.2430	329.0	55.5	57.7	28.0	-	64.0	-	-	-
	C.2304	326.0	51.4	56.8	32.5	29.7	58.9	-	30.1	27.4
	C.2500	313.0	-	-	31.6	-	58.2	-	34.7	27.2
	C.1830	337.0	-	-	31.5	30.4	66.3	-	35.8	29.2
	C.1979	329.0	51.0	-	35.6	33.5	63.6	-	-	-
	C.1901	320.0	54.9	57.2	31.1	-	-	-	-	-
Florisbad spring										
<i>(M. priscus)</i>										
	FLO4790	327.0	48.9	-	30.4	27.2	58.0	-	-	-
	FLO1919	-	-	-	-	-	56.5	34.4	31.0	26.9
	FLO4791	-	52.2	58.8	32.4	-	-	-	-	-
	FLO1890	325.0	54.2	56.3	31.5	29.0	61.6	35.3	32.4	27.4
Sunnyside										
<i>(M. priscus)</i>										
	SS12	335.0	57.4	59.7	32.1	28.0	64.5	39.0	34.4	29.0
Cornelia-Uitzoek										
	COR540	-	-	-	-	-	51.6	30.6	27.3	23.8
	COR207	-	43.3	46.0	-	-	-	-	-	-
Florisbad spring										
<i>(C. gnou)</i>										
	FLO1920	234.3	42.6	45.0	25.0	21.5	46.0	28.6	-	-
	FLO3827	233.6	41.2	42.2	23.8	20.6	44.2	27.4	-	-
	FLO1885	229.9	40.7	40.8	24.8	20.7	45.2	28.5	-	-
	FLO1992	234.4	39.4	40.2	25.0	21.2	45.0	28.6	-	-
	FLO3823	238.0	40.0	43.8	25.5	21.4	46.2	27.9	-	-
	BM1850	236.0	39.2	42.5	24.3	21.6	43.4	27.2	-	-
	BM1935A	228.2	-	-	-	21.0	43.8	26.7	-	-
	1935B	236.7	41.0	45.0	25.4	21.0	45.7	28.2	-	-
	1935C	235.4	41.6	41.1	24.6	21.0	46.0	28.0	-	-
	1935D	-	38.3	41.4	26.0	-	-	-	-	-
	1939B	-	38.0	43.7	-	-	-	-	-	-
	KB8596	-	38.6	42.6	-	-	-	-	-	-
	KM31219	-	43.1	43.6	-	26.0	-	-	-	-

	NO NO	238.0	40.0	43.2	25.2	22.0	45.5	28.0	25.9	21.0
Spitskop <i>(C. taurinus)</i>										
	LP3700	-	-	-	-	24.2	-	-	-	-
Maselspoort										
	LP3706	229.0	36.2	40.0	20.8	17.8	40.7	25.7	24.2	19.9
	LP3707	232.5	37.9	41.4	21.9	19.5	40.2	-	-	-
	LP3708	237.6	37.9	41.1	22.2	18.2	40.5	25.9	23.6	19.5
	MP56	222.5	35.9	36.8	19.2	17.2	40.7	24.6	22.5	18.5
Kareepan										
	BH1229	222.3	34.0	-	22.5	18.3	-	-	23.0	18.1
	BH1219	235.0	37.3	-	22.6	19.3	41.4	26.7	24.4	20.3
	BH1230	234.0	-	-	22.3	19.1	43.2	28.1	25.9	20.7
	BH1221	228.1	39.3	41.6	21.0	19.3	42.3	27.0	24.3	20.7
	BH1220	229.6	36.5	41.0	22.0	19.8	43.8	-	24.2	21.7
	BH1223	228.8	38.9	41.6	22.4	19.6	45.3	27.0	24.4	21.1
	BH1222	231.4	37.7	44.1	21.8	19.3	-	-	-	-
	BH1224	230.5	39.0	41.0	22.7	20.0	-	-	-	-
	BH1227	223.0	-	-	21.5	18.5	40.0	25.2	23.4	19.3
	BH1228	226.0	-	-	20.9	20.2	-	-	-	-
	BH1217	235.0	39.5	-	25.2	20.2	43.3	-	24.5	21.0
	BH1215	229.0	39.4	42.7	22.7	19.4	43.8	-	23.6	20.5
	BH1421	230.6	36.5	42.3	20.1	18.8	42.7	-	-	-
	BH1218	237.3	37.2	42.9	22.3	20.0	44.4	-	25.0	20.5
	BH1208	224.0	37.3	43.0	21.2	19.2	41.6	25.7	24.0	20.0
	BH1216	243.3	38.6	43.8	21.6	19.7	43.4	28.2	25.8	21.5
	BH1226	227.7	38.2	41.5	24.0	19.7	-	-	24.4	20.3
Swartklip										
	ZW6338	212.3	-	39.6	20.4	17.0	39.0	23.7	-	-
	ZW2120	204.0	-	38.6	22.9	19.0	40.3	24.8	-	-
	ZW5746	202.7	34.7	37.3	21.3	18.7	40.1	24.2	-	-
	ZW2113	215.0	36.4	38.6	20.5	20.1	39.5	24.5	-	-
	ZW4057	215.4	36.7	38.8	-	19.4	41.6	25.2	-	-
	ZW1621	208.1	36.2	37.9	19.4	18.7	40.0	24.6	-	-
	ZW4056	207.8	35.6	38.0	24.4	20.0	40.8	24.8	-	-
	ZW2112	215.6	-	37.0	-	-	38.3	24.4	-	-
	ZW3331	216.5	35.5	38.0	22.6	19.6	40.6	24.2	-	-
	ZW1727	207.8	36.6	39.8	-	19.0	38.4	23.0	-	-
	ZW1726	208.3	35.4	38.9	23.1	19.1	40.0	25.0	-	-
	ZW2441	-	36.3	37.3	-	-	-	-	-	-
	ZW6524	-	35.1	37.6	-	-	-	-	-	-
	ZW5678	-	35.3	37.6	-	-	-	-	-	-
	ZW4058	-	36.2	38.6	-	-	-	-	-	-
	ZW2437	-	36.1	38.8	20.2	-	-	-	-	-
	ZW2114	206.3	34.4	37.0	19.4	18.8	-	-	-	-
	ZW2111	-	34.2	38.7	-	-	-	-	-	-
	ZW5953	-	-	-	-	18.2	41.3	24.5	-	-
	ZW6132	-	-	-	-	-	36.0	23.7	-	-
	ZW2438	-	-	-	-	19.0	38.9	23.4	-	-

ZW3333	-	-	-	-	19.2	40.6	24.1	-	-	
ZW2958	-	-	-	-	19.5	39.9	23.6	-	-	
ZW2436	-	-	-	-	-	41.0	25.9	-	-	
ZW6595	-	-	-	-	-	37.9	23.5	-	-	
ZW6107	-	-	-	-	-	36.0	21.8	-	-	
ZW3336	-	34.0	36.7	-	-	-	-	-	-	
ZW2731	203.2	32.7	36.7	17.9	17.4	36.0	-	-	-	
ZW6578	197.8	-	-	-	-	36.3	-	-	-	
ZW6234	200.0	-	-	-	20.1	38.9	24.1	-	-	
ZW2727	-	33.3	-	-	-	-	-	-	-	
ZW306	-	-	-	-	-	36.8	23.0	-	-	
Elandsfontein										
EFT20344	243.8	39.4	41.5	23.4	20.1	44.8	27.8	-	-	
EFT20878	200.5	35.1	38.3	18.7	19.2	39.6	24.2	-	-	
EFT20820	202.0	34.8	37.4	19.7	18.5	37.9	23.3	-	-	
EFT20819	212.5	36.0	39.3	21.5	20.0	40.9	25.5	-	-	
EFT12148	230.0	37.0	38.5	22.4	20.1	42.7	27.7	20.7	18.7	
EFT20344	243.8	39.2	41.9	23.6	20.0	44.8	27.8	20.0	19.9	
EFT11515	229.8	41.7	41.8	26.2	21.4	47.2	27.6	20.1	18.8	
EFT20269	230	39.0	39.0	22.7	22.0	-	-	-	19.6	
Elandsfontein b/c										
EFT15833	208.5	34.7	36.4	18.8	18.0	37.7	23.7	-	-	
EFT15833	200.0	33.9	35.0	19.0	17.2	35.3	23.0	-	-	
EFT15833	204.0	35.6	-	-	19.1	37.3	24.3	-	-	
EFT15833	-	36.0	40.0	-	-	-	-	-	-	
EFT15833	212.0	32.8	37.6	18.8	18.6	36.8	23.7	-	-	
N8/1	203.5	33.9	34.5	19.3	17.4	35.5	23.0	17.4	15.6	
N8/2	208.4	34.8	36.3	19.0	17.9	37.7	23.8	18.1	16.1	
E9/1	204.0	35.7	-	-	19.2	37.4	24.3	18.3	16.4	
Sea Harvest										
S1628	207.2	37.2	40.9	22.2	20.0	41.6	25.3	-	-	
S1794	215.4	38.3	42.9	23.7	19.8	41.6	25.3	-	-	
S195	205.5	35.3	36.6	19.4	18.8	38.0	-	-	-	
S2102	208.4	37.7	41.0	20.0	19.3	42.7	25.2	-	-	
S1340	-	36.1	39.4	-	-	-	-	-	-	
S1939	-	-	-	-	-	42.0	25.2	-	-	
S1339	-	-	-	-	-	38.4	-	-	-	
Aïn Boucherit										
1949-5	-	32.5	36.5	18.5	-	-	-	-	-	
1954-13	-	-	-	-	-	35.9	-	23.0	18.6	
1954-13	-	35.9	40.0	20.2	-	-	-	-	-	

**APPENDIX C. PRELIMINARY REPORT ON A CAPRINE FROM THE
CAPE MOUNTAINS, SOUTH AFRICA (PUBLISHED PAPER)**

APPENDIX D. SELECTED PUBLICATIONS RELEVANT TO THIS STUDY

The texts of a selection of published manuscripts are given here. These works appeared in the course of this study and have direct bearing on the study.

1. Brink, J.S. 1993. Postcranial evidence for the evolution of the black wildebeest, *Connochaetes gnou*: an exploratory study. *Palaeontologia Africana* 30: 61-69.
2. Brink, J.S. 1994. An ass, *Equus (Asinus)* sp., from late Quaternary mammalian assemblages of Florisbad and Vlakkraal, central Southern Africa. *South African Journal of Science* 90: 497-500.
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AUTHOR INDEX

Acocks 1975.....	34
Arambourg 1970.....	79, 80
Arambourg 1979.....	79, 80, 146, 152, 165, 201, 202
Arambourg and Hofstetter 1963.....	80
Attwell 1977.....	36, 99, 147
Avery, D.M. 1982, 1987, 2002.....	12
Avery, G. 1988.....	12, 69, 71, 76, 77
Avery, G. <i>et al.</i> 1984.....	12, 71
Avery, G. <i>et al.</i> 1998.....	12, 71
Axelrod & Raven 1978.....	31, 32, 33
Balinsky 1962.....	13
Ball 1976.....	16
Bell 1969.....	99
Bell 1971.....	88, 100, 119
Bender & Brink 1992.....	69, 100
Benecke 1994.....	21
Berry & Louw 1982.....	147
Bigalke 1972.....	118
Bigalke 1978.....	xxxi, 30
Boessneck 1958.....	3, 20, 26
Boessneck 1985.....	20, 21, 107
Boessneck & Von den Driesch 1978.....	20, 26
Boessneck <i>et al.</i> 1964.....	7, 20, 24, 25, 92, 93, 124
Bosold 1966.....	23
Bousman <i>et al.</i> 1988.....	34
Brain 1958.....	9
Brain 1967, 1974, 1976, 1980.....	9
Brain 1981.....	9, 69, 166
Brain 1985.....	30, 32
Brain 1993.....	9, 69
Bräuer 1984.....	6, 84
Bräuer 2001.....	84
Brink 1984.....	4, 44
Brink 1987.....	3, 8, 45, 55, 56, 59, 60, 61, 62, 63, 66, 67, 68, 73, 85, 86, 88, 89, 101
Brink 1988.....	8, 45, 55, 59, 60, 63
Brink 1993.....	2, 3, 20, 38, 39, 59, 73, 76, 86, 94, 99, 113, 117, 127, 185, 192
Brink 1994.....	4, 20, 59, 61, 85
Brink 1999.....	44, 85
Brink 2002.....	69
Brink in press.....	45, 70, 72
Brink & Deacon 1982.....	75
Brink & Henderson 2001.....	59, 60, 66
Brink & Lee-Thorp 1992.....	59, 61, 87, 88, 89, 90, 100, 110, 204
Brink & Rossouw 2000.....	69, 70, 169
Brink <i>et al.</i> 1995.....	8, 34, 103, 105, 117
Brink <i>et al.</i> 1999.....	8, 20, 25, 26, 38, 58, 94, 173, 181, 192

Bronner <i>et al.</i> 2003.....	xxxii
Broom 1909a.....	5
Broom 1909b.....	5
Broom 1913.....	3, 5
Broom 1925.....	10
Brundin 1981.....	16
Butzer 1973.....	76
Butzer 1974.....	8, 69, 70, 71, 83
Butzer 1984.....	11, 45
Butzer 1988.....	58, 60
Churcher 1956, 1978, 1982, 1986, 1993.....	10
Churcher 2000.....	10
Churcher & Richardson 1978.....	1, 8, 10
Churcher <i>et al.</i> 1999.....	10
Churchill <i>et al.</i> 2000.....	53, 100
Clark 1957.....	12
Clark 1974.....	8, 69
Clarke 1985.....	8, 59
Clarke 1998.....	9
Clutton-Brock 1987.....	21
Coetzee & Brink 2003.....	59, 61, 64
Cooke 1939.....	11
Cooke 1949.....	11
Cooke 1950.....	4, 8
Cooke 1952.....	12, 101
Cooke 1957.....	13
Cooke 1964.....	59, 101
Cooke 1967.....	12
Cooke 1974.....	3, 8, 56, 69, 73, 84, 118
Cooke & Wells 1946.....	11
Cooke & Wilkinson 1978.....	7, 8
Corbet & Robinson 1991.....	197
Corbet <i>et al.</i> (1994).....	197
Cox 2001.....	15
Cox & Moore 1980.....	15, 40
Croizat 1981.....	15, 16
Cruz-Uribe 1991.....	69
Cullinan 1992.....	34, 38
Dart 1925.....	6, 8
Dart 1928.....	10
Dart 1949, 1957.....	9
Dart & Craig 1959.....	8
Deacon, H.J. 1976.....	11
Deacon, H.J. 1983.....	31, 193, 196
Deacon, H.J. 1992.....	77
Deacon, H.J. 1995.....	77
Deacon, H.J. 1998.....	11, 76, 77
Deacon, H.J. & J. Deacon 1999.....	53, 77, 187
Deacon, H.J. & Wurz 1996.....	77

Deacon, H.J. <i>et al.</i> 1984	44
Deacon, J. & Lancaster 1988	32
Dietrich 1992.....	16, 18, 19
Drennan 1935, 1937	6
Dreyer 1935.....	6, 59
Dreyer 1938.....	59, 63, 64
Dreyer 1947.....	6
Dreyer & Lyle 1931	6, 59, 101
Dupont & Leroy 1995	32
Du Toit 1954	32
Duvernoy 1851.....	5
Eisenmann 1979.....	27
Eisenmann 1985, 1992.....	1
Eisenmann 1997	19
Eisenmann 2000.....	4, 85
Eisenmann 2004.....	4, 85
Eisenmann & Brink 2000.....	4, 7, 26
Eisenmann & De Giuli 1974	7
Eisenmann <i>et al.</i> 1988.....	4
Eldredge & Gould 1972	18, 186
Estes 1969	36
Estes 1991	36
Ewer 1955a, 1955b, 1956a, 1956b, 1956c, 1956d.....	10
Ewer 1957	8
Ewer 1958	10
Ewer 1962	8, 10
Ewer & Cooke 1964.....	8, 12, 68
Fabricius <i>et al.</i> 1988.....	39
Foley & Lahr 1997	68
Ford 1955	17, 19, 194
Fosse <i>et al.</i> 1998.....	69
Gautier & Muzzolini 1991	5, 28
Geist 1971	39, 96, 97, 140, 142, 195
Gentry 1970a.....	44
Gentry 1970b.....	93, 96, 114
Gentry 1978.....	1, 10, 79, 94, 100, 114, 144, 145, 146, 147, 185, 201
Gentry 1980.....	10, 79, 93, 111, 157
Gentry 1985.....	147
Gentry 1990.....	10, 145, 147
Gentry 1992.....	xxx, 27, 28, 94, 97, 111, 119, 137, 138
Gentry 1995.....	10
Gentry 1996.....	44
Gentry 2000.....	119, 137, 138, 139, 140, 142, 190, 199
Gentry & Gentry 1978 ..	1, 5, 10, 19, 38, 39, 44, 56, 73, 74, 76, 80, 81, 83, 84, 94, 97, 99, 100, 101, 102, 109, 113, 114, 117, 127, 128, 134, 138, 146, 147, 151, 167, 169, 170, 185, 198
Gentry <i>et al.</i> 1995.....	100, 101, 151
Geraads 1981.....	38, 81, 117, 146, 147, 185
Geraads 1992.....	28
Geraads <i>et al.</i> 1986.....	79, 80, 81

Geraads <i>et al.</i> 2004.....	32, 79, 81, 147
Goldschmidt 1940.....	17, 18, 19, 186
Goldschmidt 1952.....	18, 19, 20, 85
Gould 1977.....	19, 189
Gould 1992.....	18, 19, 189
Grobler & Looock 1988.....	58, 60
Grün 1997.....	65
Grün <i>et al.</i> 1996.....	2, 59, 68, 73, 84, 87
Harley 1988.....	197
Harris 1991.....	1, 38, 44, 81, 127, 146, 147, 202
Harris & White 1979.....	7, 73, 84
Harris <i>et al.</i> 1988.....	38, 81, 146
Haughton 1922.....	10
Haughton 1932a, 1932b.....	8
Henderson 2001.....	60, 66
Hendey 1968.....	11
Hendey 1974a.....	11, 12, 13, 76, 87
Hendey 1974b.....	12, 13, 68, 82, 85
Hendey & H.J Deacon 1977.....	11, 76
Hendey & Hendey 1968.....	11, 78, 79, 86, 87
Hendey & Singer 1980.....	11
Hennig 1966.....	16
Hill 1995.....	31
Hoffman 1953.....	8, 56, 101, 107, 122, 142, 144
Hoffman 1955.....	8, 59
Hofmann & Stewart 1972.....	35, 100, 110, 119
Humphreys & Parenti 1986.....	16
Jarman 1974.....	35
King 1978.....	32, 33
Kingdon 1982.....	74, 110, 119, 134, 138, 139, 151, 158
Kingdon 1997.....	19, 108
Kitching 1951, 1953, 1965.....	9
Klein 1970.....	2
Klein 1972.....	11, 75, 87, 194
Klein 1975.....	38, 78, 79, 87
Klein 1976.....	11, 86
Klein 1978.....	4
Klein 1980.....	11, 82
Klein 1983.....	38, 78, 79, 86, 87, 193
Klein 1984.....	11, 58, 73, 82, 85, 87, 109
Klein 1986.....	11, 192, 196
Klein 1994.....	20, 28, 56, 144
Klein 1999.....	2, 78
Klein & Cruz-Urbe 1991.....	11, 76, 172, 173
Klein & Cruz-Urbe 1996.....	196
Klein <i>et al.</i> 1999.....	75, 83, 84, 172
Kok & Vrahimis 1995.....	37
Kruuk 1972.....	71
Kuman 1989.....	59, 60, 63, 66

Kuman & Clarke 1986	8, 59
Lacruz <i>et al.</i> 2002.....	44, 84, 85, 87, 90, 110
Lauder 1995	21
Leuthold 1977	15, 21, 35, 36
Lewontin 1992	21
Liversidge 1972.....	118
Looock & Grobler 1988.....	33, 58, 88, 90
Low & Rebelo 1996.....	xxx, 1, 33, 34, 51
Mabbutt 1956	76
MacArthur & Wilson 1967	19
Maglio 1978	1
Maglio & Cooke 1978.....	30
Marean and Gifford-Gonzalez 1991	114
Mayr 1942	17
Mayr 2001	16, 17, 21, 23, 26, 120, 165, 190, 201
McBrearty & Brooks 2000.....	6, 68, 87
McCarthy <i>et al.</i> 2000	88
McDonald <i>et al.</i> 1973.....	35
McKee 1993	12
Meiring 1956.....	8
Mennell 1929	6
Mills, 1990	71
Moen 1973	21, 35, 196
Nelson & Platnick 1981	15, 17
Nickel <i>et al.</i> 1992	3, 20, 122, 130, 131, 177
Odum 1971.....	16
Oppenheimer 2004.....	19, 167
Padian 1995.....	21
Partridge & Maud 2000.....	32, 33
Partridge <i>et al.</i> 1995	31
Paterson 1985	16
Patterson 1981	20
Peters 1986.....	25, 92, 93, 144
Peters & Brink 1992.....	20, 92, 93, 132, 137, 144, 160
Peters <i>et al.</i> 1994	20, 28
Peters <i>et al.</i> 1997.....	20, 24, 42, 92, 125, 126, 130
Pickford 2001	31
Pickford & Senut 1999, 2003.....	31
Pickford & Thomas 1984	101
Plug 1989, 1990, 1992, 1993a, 1996a, 1996b.....	10
Plug & Badenhorst 2001	10, 20, 34, 38
Plug & Engela 1992	10, 38, 54, 58
Plug & Peters 1991	20, 92, 93
Plug & Roodt 1990	10
Plug & Skelton 1991	10
Plug <i>et al.</i> 1997	10
Plug <i>et al.</i> 2003	10
Pomel 1894	146, 147
Rau 1974	1, 19

Rau 1978	1
Reineck & Singh 1975	71
Rightmire & H.J. Deacon 1991	77
Rogers 1980	76
Rubidge & Brink 1985	8, 58, 60, 61
Ruse 1992.....	3, 21, 186
Sampson 1974.....	64
Savage & Russel 1983	12, 82
Schwartz 1999.....	16, 18, 20, 22, 186
Scott & Brink 1992	8, 45, 46, 59, 60, 64
Scott & Klein 1981	45, 46
Scott & Nyakale 2002	59, 63, 187
Shackleton 1995.....	32
Short 1981	16
Simpson 1941.....	27
Sinclair 1983	35
Singer 1958	11
Singer 1961	11
Singer & Boné 1960.....	8, 11
Singer & Fuller 1963.....	11, 78
Singer & Hooijer 1958.....	11
Singer & Wymer 1968	11, 76
Singer & Wymer 1982	11, 77
Skead 1980.....	34, 37, 38, 94
Skinner & Smithers 1990.....	1, 38, 40, 119, 134
Stringer 1992.....	6
Stynder <i>et al.</i> 2001	86, 87
Tamrat <i>et al.</i> 1995	73
Taylor 1978.....	1
Thackeray 1995.....	10
Thackeray <i>et al.</i> 1996.....	10, 73, 83
Thomas & Shaw 1993.....	90
Thomas 1884.....	79, 80, 146, 148, 149, 150, 155, 165, 202
Tobias 1997, 2001	8
Turnbull 2002.....	22, 165
Turner 1984, 1985, 1986, 1987.....	9
Udvardy 1969.....	15
Udvardy 1981.....	15
Uerpmann 1987.....	19, 32, 119
Van Andel 1989	33, 194
Van der Bank 1998	8
Van Hoepen 1930, 1932a.....	7, 69
Van Hoepen 1932b.....	7, 69, 101, 169
Van Hoepen 1947.....	7, 56, 69, 106
Van Kolfshoten & Gibbard 1998	xxxi
Van Zinderen Bakker 1957, 1989	59
Van Zyl 1965	35, 100
Visscher <i>et al.</i> 2001.....	197
Visser & Joubert 1991.....	58, 60, 63, 64, 88

Voigt 1979, 1986.....	10
Voigt & Plug 1984	10
Volman 1978.....	78
Von den Driesch 1976.....	3, 25
Von den Driesch 1983.....	3, 20
Von Richter 1972	36
Von Richter 1974	35, 36, 37
Vrahimis in press	35, 100
Vrba 1974.....	9
Vrba 1975.....	9, 193
Vrba 1976.....	3, 9, 19, 38, 81, 94, 147, 166
Vrba 1979.....	10, 25, 94, 99, 100, 101, 145, 147
Vrba 1985.....	1, 10, 17
Vrba 1988, 1995.....	10
Vrba 1997.. 1, 3, 10, 19, 38, 73, 74, 80, 81, 86, 94, 97, 100, 101, 102, 108, 109, 111, 127, 145, 146, 147, 148, 154, 155, 165, 193, 198, 200, 202	
Vrba 2000.....	10
Vrba <i>et al.</i> 1989.....	10
Wallis & Trewick 2001	16
Watson & Plug 1995	20
Watson <i>et al.</i> 1991	112, 113
Wells 1957	13
Wells 1959a.....	8, 10, 11
Wells 1959b	8, 144
Wells 1962	12, 13
Wells 1964a.....	11, 101, 144
Wells 1964b	8, 11
Wells 1967	12
Wells 1969	6, 12, 68
Wells 1970	88
Wells <i>et al.</i> 1942	6
West-Eberhard 1992	21, 22
Wiley <i>et al.</i> 1991	22, 23, 190
Wurz 2002.....	77
Zawada 2000.....	49