The publication of this, the seventh volume of the Koobi Fora Research Project marks a milestone in the study of the Koobi Fora fossils. It is the final volume in the originally projected seven volumes that were planned by the late Glynn Isaac and myself to report on our work at Koobi Fora. The Carnivora is also the last of the major mammal groups present in the fauna to be the subject of monographic treatment.

The Koobi Fora Research Project itself continues to this day, but it operates now under the overall coordination of the newly established Turkana Basin Institute, a collaborative arrangement between the Stony Brook University and the National Museums of Kenya. Although the original publication commitment has been met, further volumes in this series are to be expected, indeed are already in preparation.

Previous volumes in this series have dealt with the hominids and their material culture (Volumes 1, 4, and 5), the ungulates (Volumes 2 and 3), the non-human primates (Volume 6), as well as investigations of the stratigraphy, palaeoecology, and palaeoenvironment of Koobi Fora. This, the seventh volume on the Carnivora, brings with it a new set of questions and a new set of challenges. Previous studies of mammal groups in this series have dealt with specific families or family groups while the present volume covers an entire order of mammals, and a species-rich one at that. This richness is counterbalanced by the relative scarcity of fossils of species high up in the trophic pyramid, which is mirrored by their scarcity in life. Thus, taxonomic difficulties in dealing with carnivores are very different from those encountered in dealing with ungulates. In the one case there are many species with few fossils of each, in the other, few species with often many fossils of each. In this way, carnivores more resemble primates, and especially hominids.

Our collecting policy at Koobi Fora reflects this similarity. From the beginning of field work in 1968 we followed a deliberate policy of collecting all material that could be identified as primate, whereas for common taxa such as suids and bovids, only selected elements were collected. The primate policy was also followed for carnivores; every bone that could be identified as carnivore, even potentially, was collected. The wisdom of this approach is seen in the present volume, which documents an extraordinary diversity of carnivores, especially of such previously poorly known groups as otters and civets. It is also an object lesson to see how many species of carnivore are documented by postcranial skeletal elements alone, with no skulls or teeth to match. While such identifications may be somewhat less secure than those based on teeth, since teeth form the basis for identification of most carnivore species elsewhere, they record a diversity of carnivores that would otherwise have remained hidden.

I believe that this comprehensive volume will form a benchmark for future studies of carnivores from other Pliocene and Pleistocene sites in Africa and elsewhere. I hope that it will lead to a better integration of carnivores into studies of the palaeofaunas of the African Plio-Pleistocene.

Richard E. F. Leakey
Nairobi
July 2013
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CHAPTER 1
INTRODUCTION

This monograph describes and discusses those Koobi Fora Formation fossils that can be confidently referred to the Order Carnivora. Within this order, there are currently 13 families recognized. Of these, eight are known from the African mainland and one, Eupleridae, from Madagascar only. Of these families, two, Herpestidae and Nandiniidae, are not known from Koobi Fora, while material of the six remaining families is described herein. Separate chapters on these six families form the bulk of the monograph. In addition, there are brief chapters on stratigraphic and biogeographic patterns, as well as an introductory chapter on the history of study of the Koobi Fora carnivorans. The Carnivora is well represented at Koobi Fora and is the last of the major mammal groups to form the basis for a monographic treatment.

This project has had a long gestation time. Dr. Meave Leakey invited us in the mid-1990s to carry out this study. The long time between this invitation and the appearance of the present publication can be attributed to several causes. First, of course, the extensive and often complicated Koobi Fora material, which had only been studied in one publication before we began our work (see Chapter 2). Second, the ongoing fieldwork at Koobi Fora, which has added significantly to the collections during the course of our work. To limit this problem, we have here not included Koobi Fora material collected after early 2005. Extensive material has been collected subsequent to this date and will be considered in a future publication. Third, the lack of well-studied comparative collections and our relative inexperience at the outset of this project. During the past decade, we have had the opportunity to study other Plio-Pleistocene fossil carnivorans from Kenya, as well as Ethiopia and Tanzania, but when we began most collections were unstudied and the majority of publications outdated, with the exception of the very important publication on the West Turkana fossils, including carnivorans (Harris et al. 1988). Unfortunately, the West Turkana collections do not include many post-2.0 Ma carnivorans, whereas the bulk of the Koobi Fora material is from that part of the record. Nevertheless, that publication was our most important starting point for this work, along with the earlier publications on Koobi Fora, Laetoli, and Olduvai carnivorans (Barry 1987; Leakey 1976; Petter 1973, 1987).

In this project we have worked within a specific geographic and stratigraphic context developed by previously published studies of other mammal groups at Koobi Fora. The recent publication on Cercopithecidae has been the most important source in this regard, as it incorporates recent revisions to stratigraphy and other essential information on Koobi Fora. Figure 1.1 shows the geographic position of Koobi Fora in eastern Africa, and the extent of the Koobi Fora Formation in relation to other sedimentary formations in the Turkana Basin.

A detailed map of Koobi Fora and adjacent regions east of Lake Turkana showing the distribution of collecting areas is presented in Figure 1.2. The numbering of the areas recurs in Appendix 1, from which it can be determined where specific specimens were collected at Koobi Fora. Preliminary analy-
Fig. 1.1: The Turkana Basin, showing the location of the geological formations surrounding Lake Turkana. The Koobi Fora Formation to the east of the lake has the largest areal extent of all the formations of the Omo Group. (Map by George Chaplin; from Jablonski and Leakey 2008, after Brown and Feibel 1991).
Fig. 1.2: Collecting areas of the Koobi Fora Formation and surrounding regions east of Lake Turkana. Area numbers match those in Appendix 1. (Map by George Chaplin; from Jablonski and Leakey 2008, after Brown and Feibel 1991).

...ses of the distribution of carnivoran fossils at Koobi Fora showed that, unlike, e.g., the Cercopithecidae (Jablonski and Leakey 2008) there is no discernible geographic pattern except that dictated by the availability of sediments of different members. We have therefore chosen not to pursue such an analysis in this volume.

The stratigraphic context, shown in Fig. 1.3, has changed greatly over the years (compare this figure with contributions in Coppens et al. 1976). The outline shown in
Fig. 1.3 (opposite): Diagram showing the stratigraphic context of the fossils discussed in this monograph. Dates for the Moiti Tuff, Tulu Bor Tuff, and Burgi Tuff from McDougall and Brown (2007), for the Lokochot Tuff from deMenocal and Brown (1999), and for the KBS, Okote, and Chari Tuffs from Brown et al. (2006). The Okote Tuff, which marks the base of the Okote Member, has not been dated but is estimated to be $1.56 \pm 0.05$ myr from its position between the Morutot Tuff ($1.607 \pm 0.019$ myr) and the Morte Tuff ($1.510 \pm 0.016$ myr). The Okote Tuff Complex, which includes the Lower Okote Tuff ($\leq 1.607$ myr), is in the KBS Member. Thus the Okote Tuff Complex, which is not indicated here, begins $\sim 1.6$ myr (McDougall and Brown 2006). Not to scale.
Fig. 1.3 is taken from Jablonski and Leakey (2008) and represents a recent, if not the most recent, summary of Koobi Fora stratigraphy. Hence, the stratigraphic context used herein is directly comparable to that of the previous volume in this series. We do not have stratigraphic information at the sub-member level for a sufficient number of carnivoran specimens to make more detailed stratigraphic discussions meaningful, and therefore the member is the smallest stratigraphic unit used herein.

Each of the six descriptive chapters, one for each family of carnivoran present, follows a similar pattern. Where applicable, taxa are grouped into subfamilial units, each of which is described in a separate section. Within these sections each genus and species has a section that includes general background, nomenclatural information, a diagnosis, holotype information (for fossil taxa only), type locality, and information on stratigraphic range in Africa and at Koobi Fora specifically. After this basic information there are descriptive sections for craniodental and postcranial material separately. The most informative specimens are illustrated with photographs (color photographs of these and all other Koobi Fora carnivoran specimens investigated for this volume are available in the DVD that accompanies the book). We end each descriptive section with remarks on the taxon generally.

Chapter 9 provides the complete faunal list and discusses changes through time on a member-by-member basis. Chapter 10 places the Koobi Fora carnivoran assemblage in a broader context of African carnivoran evolution. The text ends with two appendices: the first lists all specimens by taxon, while the second includes all tables of measurements of the specimens studied. The DVD includes a database of all specimens and their information in searchable form.

MATERIAL AND METHODS

The material described in this monograph is the carnivoran material from Koobi Fora collected prior to mid-2005. It is comprised of >1000 numbered fossils from >270 individual animals. All of this material is housed in the paleontology collections of the National Museums of Kenya (KNM). Comparative material has been studied at numerous collections in different parts of the world. These include (with collections acronym) the American Museum of Natural History, New York (AMNH), the Field Museum of Natural History (FMNH), Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), National Museum of Natural History, Smithsonian Institution, Washington DC (NMNH), University of California Museum of Paleontology (UCMP), The Natural History Museum, London (NHM), Powell-Cotton Museum, Birchington (no acronym), Swedish Museum of Natural History, Stockholm (NRM), Museum für Naturkunde, Berlin (MfN), Naturhistorisches Museum Wien, Vienna (NMW), Museum national d’Histoire naturelle, Paris (MNHN), Iziko South African Museum, Cape Town (SAM), Ditsong National Museum of Natural History, Pretoria (formerly the Transvaal Museum, TM), Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg (BPI), National Museum of Ethiopia, Addis Ababa (NME), National Museum of Tanzania (NMT).

The paleontological collections of the National Museums of Kenya use acronyms to identify collecting areas. The Koobi Fora collection has the acronym ER (East Rudolf
– the old name for Lake Turkana). Other acronyms from this collection used herein are: EG, Eshoa Kakurongori, LT, Lothagam, WT, West Turkana. Other locality or collection acronyms include TM, Toros Menalla, Chad (housed in CNAR, service des collections, N’Djamena, Chad), PQ-L, Langebaanweg, South Africa (housed in the Iziko South African Museum), KA, KB, Kromdraai A & B, South Africa (housed in the Ditsong National Museum of Natural History); OM, Osteological Collection, National Museums of Kenya, Nairobi. All materials in the Koobi Fora collection were prepared by National Museums of Kenya staff using standard mechanical preparation techniques.

Measurement abbreviations used herein are as follows: L, tooth length; W, tooth width; c, lower canine; p and P, lower and upper premolars, respectively; m and M, lower and upper molars, respectively. Special measurements are as follows: Lpp4, length of main cusp of p4; Ltm1, length of trigonid of m1; Wtri, width of trigonid of m1; Wtal1, width of talonid of m1; LeP4, buccal length of P4; LpP4, lingual length of P4 (including protocone); WaP4, anterior width of P4; WblP4, width of anterior part of metastyle of P4; LpP4, length of paracone of P4; LmP4, length of metastyle of P4; p2-m1, length of tooth row from mesial end of p2 to distal end of m1; p3-m1, as previous, but from mesial end of p3; Hbehm1, height of mandibular ramus beneath distal end of m1; Hdia, minimum height of mandibular ramus at diastema; HPC, height of the coronoid process of the mandible; Cond-ang, distance from superior surface of mandibular condyle to inferior surface of angular process; PL, length of palate; BL, basilar length of skull; C-C, width of snout between lateral sides of canines; P-P, width of palate between buccal sides of P4 metastyle; IOB, minimum interorbital width; POC, minimum postorbital constriction width; ZAW, maximum width of zygomatic arch; ML, mediolateral; AP, anteroposterior; DV, dorsoventral; PD, proximodistal; SI, superoinferior. The prefix log indicates that the variable was log10 transformed. Other abbreviations are: Fm., Formation; Mb., Member.

Statistical analyses were run using PAST (Hammer et al. 2001); graphing was done with Aabel v. 3 (Gigawiz Ltd.) with post-processing in Illustrator v. 16 (Adobe Systems Inc.). All photographic post-processing was done in Lightroom v. 4 and Photoshop v. 13 (Adobe Systems Inc.). Text editing was done in Word v. 14 (Microsoft Corp.), with layout and typesetting in InDesign v. 8 (Adobe Systems Inc.).

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Thanks go to Patrick Gathogo and Lawrence Nzube, who provided vital information on stratigraphy and specimens at various times during the work process. Many people have assisted us with advice, information and collaborative efforts related to fossil carnivorans and this project in particular. It is impossible to mention everyone by name here; however, we would like to specifically mention Kaye E. Reed, Stéphane Peigné, Michael R. Lague, Alan Shabel, Yohannes Haile-Selassie, and Scott W. Simpson. Stéphane Peigné also read and commented on a portion of the present text. Nina G. Jablonski assisted in many respects with fossil identification as well as with publication of this monograph and allowing us to use illustrations from the previous Koobi Fora volume, on monkeys. These illustrations were expertly prepared by George Chaplin. Special thanks to Luke Lomeiku Lonyaman for help with Dassenech words. Zeresenay Alemseged, Alan Leaviton and staff of the California Academy of Sciences were instrumental in making this monograph possible. MEL also thanks her children, Zachary and Jackson, for putting up with mom’s traveling. Permits to carry out research related to this project were obtained from The Office of the President (Kenya), the Tanzania Commission of Science and Technology (COSTECH), and the Authority for Research and Conservation of Cultural Heritage (ARCCH, Ethiopia). Our research has been funded by grants from The Swedish Research Council (to LW), the LSB Leakey Foundation (to MEL and KE Reed), the NSF (DBS-9222721 to MEL), Sigma Xi (to MEL), Stockton Distinguished Faculty Fellowships (to MEL) and a Stockton CDC Grant (to MEL). Finally, we would like to thank all of the many tireless field workers and people who collected the fossils that we describe here. Without their skill and dedication our research would not be possible. We dedicate this volume to them.

REFERENCES


Chapter 2
HISTORY OF STUDY

The history of exploration and collection in the Koobi Fora region of the Turkana Basin is well known and will not be reviewed here. We refer the interested reader to Harris et al. (2006) for this information. Our introduction will instead focus on the history of study of the Carnivora of Koobi Fora. This history is of necessity brief, as this group of animals in our opinion has been unfairly neglected in studies of the Koobi Fora fauna over the past 40 years.

Collecting began at Koobi Fora in 1968. In the material we have studied, specimens ER 330, ER 322, and ER 5345, although cataloged at different times, all have field numbers indicating that they were collected in that first year. However, there has been surprisingly little written about these carnivores. Those studies that do mention Koobi Fora carnivores have rarely been first-hand descriptive accounts, but have either emphasized other aspects, such as the paleoecological or paleoanthropological implications of the carnivore fauna, have been compilations based on earlier work, or have been incidental mentions in broader, mainly taxonomic, work. Thus, more than 40 years after the first Koobi Fora Carnivora were discovered, there exists no complete and fully referenced faunal list for the order. As will become clear from this volume, this is unfortunate, since due to its quantity and quality, the carnivore material from the Koobi Fora sequence is critical for understanding the evolution of the order in eastern Africa, and provides a benchmark for the eastern African Plio-Pleistocene. Not only is the material very extensive, matched in eastern Africa only by material from Laetoli (Werdelin and Dehghani 2011), it also offers an unparalleled view of carnivore diversity at a crucial time in human evolution, the time of the appearance of ‘erectus-group’ hominins, i.e., hominins with derived dietary strategies that led to increased human-carnivore conflict (Lewis and Werdelin 2007; Werdelin and Lewis 2013). Our understanding of ecosystem change at this time has therefore been greatly hampered by this relative lack of attention to the Koobi Fora carnivore record.

Published study of the Koobi Fora carnivores begins with the important paper of Leakey (1976). Remarkably, this work remains the only paper on the subject dedicated to providing a listing of the taxa present and their stratigraphic provenience. It was based on work presented at a workshop held in 1973, and thus incorporates only material found up to that point. This accounts for a little over half of the specimens (in terms of catalogue numbers) discussed in the present volume. The stratigraphic context in which the fossils were placed by Leakey (1976) is now obsolete, but it is of some interest to consider the taxonomic identifications and the extent to which they have been altered. Leakey (1976) provides a short summary of information on each species identified, including number of specimens, stratigraphic context, type of specimens, and brief information on each set of specimens. No illustrations were provided, however. Only a few specimens are specifically listed by catalogue number, though many more are alluded to. Table 1.1 shows the faunal list published by Leakey (1976, table 1), together with an indication
Table 2.1: The carnivoran fauna of Koobi Fora as identified by Leakey (1976), along with a listing of specimens of each taxon identified therein. For comparison with tables in Appendix 1.

In terms of the number of species, the faunal list of Leakey (1976) is dominated by felids, with at least six species and possibly as many as eight. The majority of the specimens identified as felid were assigned to *Homotherium* sp., with two cranial and ten postcranial specimens. Nearly all of these specimens are retained in *Homotherium* herein, though for reasons discussed in...
the text none have been assigned to a specific species. Two cranial specimens were referred to *Megantereon eurynodon* and both are here retained in that genus, though the species-level taxonomy of the genus has changed in subsequent years and *M. eurynodon* is now considered a synonym of *Megantereon whitei*. In addition, Leakey (1976) referred 10 postcranial specimens to *cf. Megantereon*. We have not found it possible to identify all of these specimens, but of the identified ones, several remain assigned to *Megantereon* while others are unidentified to genus within the Felidae. One specimen was identified by Leakey (1976) as *Dinofelis barlowi*. This specimen remains in *Dinofelis*, but was reassigned by Werdelin and Lewis (2001) to the new species *D. aronoki*, which thus far is only known from the Koobi Fora Fm. A single specimen was also assigned to *D. cf. piveteaui* by Leakey (1976), an identification confirmed by Werdelin and Lewis (2001). Additional cranial and postcranial material was referred to *cf. Dinofelis*, and although with the exception of ER 365, now assigned to *D. aronoki*, we cannot positively identify the exact specimens alluded to, all *Dinofelis* material from Koobi Fora was reviewed by Werdelin and Lewis (2001) and is further discussed herein. Two postcranial specimens were identified as *Panthera cf. leo* by Leakey (1976). These could not be positively identified by us, but there are a number of specimens found at the time of the writing of Leakey (1976) that we here refer to *Panthera leo*, and we feel confident that the two specimens mentioned by Leakey are among them. Finally, Leakey (1976) referred two postcranial specimens to *Panthera cf. crassidens*. This species was a problem taxon, with a variety of different materials from southern and eastern Africa assigned to, it until Turner (1984) showed definitively that the original description of the species by Broom (1948) was based on a mixture of material of leopard and cheetah. Thus, it is not surprising that Leakey (1976) pointed out several features characteristic of *Acinonyx* in this material. Indeed, we now believe that these specimens should, in fact, be referred to *Acinonyx*.

In terms of the number of specimens, *Crocuta crocuta* is the most common species in the review by Leakey (1976), with 29 cranial and postcranial specimens. All of the specimens we can positively identify are still referred to *Crocuta*, though our specific allocations have changed along with changing views of the evolution of the genus (Lewis and Werdelin 1997, 2000; Werdelin and Lewis 2008). Striped hyenas, genus *Hyaena*, are rare at Koobi Fora compared to their spotted confamilials, and in Leakey (1976) six cranial and postcranial specimens were identified to the extant species *H. hyaena*. As in the case of *Crocuta*, species-level allocations have changed somewhat, but all these specimens remain identified as *Hyaena*.

Leakey (1976) referred four mandibular specimens to the Canidae, subfamily Caninae. Of these, three were referred to *Canis mesomelas*, black-backed jackal. The taxonomy of jackals has changed since 1976, and we find these specimens to differ from the extant jackal species. This is reflected in our new species list. The fourth canid specimen is an edentulous mandibular fragment that Leakey (1976) correctly noted is larger than the other specimens. She suggested that it may belong in *Canis* or *Lycaon*, but we here refer this specimen to the Viverridae.

Nearly all mustelid specimens from Koobi Fora belong to the subfamily Lutrinae. This is reflected in Leakey (1976), in which mention is made of two cranial and
four postcranial specimens tentatively referred to cf. *Aonyx*. In our work all of these specimens have been reassigned to the tribe Lutrini, rather than Aonyxini.

Finally, Leakey (1976) referred a few specimens to the Viverridae. These included one specimen of *Genetta* *cf.* *genetta*. This specimen, a palate with teeth, is indistinguishable from the living species. Four specimens are referred to *Pseudocivetta ingens*. Two of these are teeth that match the type material of the species closely and are retained in this species herein. The third is a cranium, which we here refer to cf. *Civetictis* sp. The fourth specimen is postcranial and in view of the fact that we now know of several large-sized viverrids from Koobi Fora, it has been removed from *Pseudocivetta* and placed in an indeterminate viverrid species in this work.

Thus, a comparison between Table 2.1 and the present faunal list (Table 9.1) shows that at a general level the present work does not drastically alter the information provided in Leakey (1976), but does add significantly to it, both in the form of more data on the species present, and in the form of a greatly expanded faunal list. Nevertheless, at the species level past and ongoing work on carnivoran taxonomy and evolution in Africa and elsewhere has significantly changed the identifications made by Leakey (1976). Most importantly, new developments have made it possible to better integrate African carnivoran taxonomy with that of Eurasia. This makes data on the relatively rich Koobi Fora carnivoran assemblage especially valuable in that they have the potential to provide insights into migrations within Africa and between Africa and Eurasia.

The next paper referring to Koobi Fora Carnivora, and the first to provide an illustration of a specimen, is Turner’s (1987) taxonomic review of the genus *Megantereon*. In this paper, Turner (1987, fig. 2.1) provides a drawing of a cast of the right mandibular ramus ER 793B. As noted above, Leakey (1976) assigned this specimen to *M. euryndodon*, a species described from Kromdraai in South Africa by Ewer (1955). Turner (1987) reassigns the Koobi Fora specimen and all other African *Megantereon* to the Eurasian species *M. cultridens*, suggesting that the degree of variation seen in *Megantereon* cannot justify separation at the species level of any set of specimens. The Koobi Fora specimen is important in this regard as it is the best preserved African specimen of *Megantereon*. Turner (1987) does not mention the associated skull, ER 793A, however.

Numerous papers on African *Megantereon*, with ER 793B as a key specimen, were published subsequently. The first of these are the publications of Martínez Navarro and Palmqvist (1995, 1996). The Koobi Fora specimen is illustrated in both of these papers (1995, fig. 6.12; 1996, fig. 1, in the latter incorrectly labeled Elandsfontein), though only redrawn after the illustration in Turner (1987). These authors disagree with Turner (1987) regarding the species allocation of African *Megantereon*, placing ER 793B together with all other African specimens in *M. whitei*, a species described by Broom (1937) from Schurveberg in South Africa. Palmqvist and colleagues (now including Turner) reiterate this position in Palmqvist et al. (2007). In this paper they provide photographs of the Koobi Fora specimens ER 793A and B (Palmqvist et al. 2007, fig. 1E, H). The former of these is shown in mirror image, although this is not stated in their text.

Most recently, specimen ER 793 has been discussed by Lewis and Werdelin
(2010), who, while reaffirming the allocation of the specimen to *M. whitei*, also bring up some unanswered questions that arise from detailed analysis of this and other specimens assigned to the species. This paper also includes photographs of ER 793A and B.

Lewis (1995, 1997) discussed the carnivoran paleoguilds of the African Pliopleistocene and their implications for palaeoanthropology. Among the guilds discussed are those from the Upper Burgi, KBS, and Okote Members of the Koobi Fora Formation. This work is chiefly concerned with morphotypes and for the most part only discusses taxa at the genus level (e.g., ‘eastern African *Canis*’, ‘Koobi Fora *Dinofelis*’). Nevertheless, in order to place specific specimens in these morphotypes, some taxonomic discussion was involved. For example, Lewis (1995) suggested on the basis of statistical analyses that specimens identified by Leakey (1976) as *Panthera cf. crassidens* and later catalogued as *Panthera sp. A*, may belong to *Acinonyx*. We here reaffirm these identifications.

In a paper on the hyenid genus *Pachycrocuta* in eastern Africa, Werdelin (1999) briefly mentioned one Koobi Fora specimen, ER 3748. This is a fragment of a right mandibular ramus with a damaged m1. Werdelin (1999) tentatively assigned this specimen to *Pachycrocuta*. However, on the basis of new specimens from West Turkana, we now believe it more likely that this specimen belongs in *Crocuta*, though in the new and aberrant species *C. eturono* (Werdelin and Lewis 2008). This is in accordance with the morphology of m1 as preserved in the specimen.

A decade ago, Werdelin and Lewis (2001) published a revision of the genus *Dinofelis*, incorporating a large amount of previously undescribed material from Koobi Fora. Two new species of *Dinofelis* were described in this paper, both with type specimens from Koobi Fora: *D. petteri* (type specimen ER 2612 from the Tulu Bor Mb.) and *D. aronoki* (type specimen ER 3880 from the Upper Burgi Mb.). Some of this information is reiterated herein, along with additional data and illustrations of the three species of *Dinofelis* known from the Koobi Fora Formation.

A few other publications utilize information on Koobi Fora Carnivora in their analyses, or mention them in passing (e.g., Werdelin and Lewis 2005), but papers the discussed above are the only ones that have discussed the Carnivora from Koobi Fora explicitly.

REFERENCES


cago.


While canids are not common in the African fossil record, they are not unknown. The earliest African canid is a fox, *Vulpes rufifrontae*, from Tores-Menalla in Chad (ca. 7 Ma; Bonis et al. 2007). Members of the tribe Canini first appear in Africa in the form *Eucyon intrepidus* from the Tugen Hills (Morales et al. 2005) and Lemudong’o (Howell and Garcia 2007), both in Kenya, and *Eucyon* sp. from Kuseralle, Ethiopia (Haile-Selassie and Howell 2009). *Eucyon* later appears in southern Africa at Langebaanweg (5.3–5.0 Ma; Hendey 1974; Rook 1993). A subsequent appearance of *Eucyon* at Aramis (Garcia 2008) has been removed from this genus and possibly even the tribe Canini by Sotnikova and Rook (2010). The oldest record of *Canis sensu stricto* is from South Turkwel, Kenya (3.58–3.2 Ma; Werdelin and Lewis 2000). Very few of the described canids are represented by more than teeth and jaws.

The current fossil record of eastern African canids (Werdelin and Lewis 2005; Werdelin and Peigné 2010) is surely not representative of the true diversity of canids during the last six million years. While this may be due to a true scarcity or to a preservational bias, it is also likely that the known eastern African Plio-Pleistocene fossil localities have not adequately sampled the preferred habitats of canids, despite sampling a variety of habitats (e.g., Olduvai Gorge vs. Koobi Fora localities). Nevertheless, it is surprising that jackals are not better represented, particularly as the carnivoran guild moved more towards its modern form after the last eastern African carnivoran extinction event (Werdelin and Lewis 2005). Today, in addition to wild dogs (*Lycaon pictus*), there are also three species of jackals (*Canis aureus*, *Lupulella adusta*, and *L. mesomelas*) and the Ethiopian wolf (*Canis simensis*) in eastern Africa. In no place are these all sympatric, however.

Members of the family Canidae are exceedingly rare at Koobi Fora compared to the majority of carnivoran families. All except one of the specimens belong to jackal-sized forms, with the remaining specimen referable to a small fox. Thus, to date, Koobi Fora has not yielded any material that could be assigned to “*Canis africanus*” (=*Canis* [or *Xenocyon*] *falconeri* [Martinez-Navarro and Rook 2003]), which is known from Bed II at Olduvai (i.e., broadly coeval with the KBS and Okote Mbs.). The absence of these taxa may, in the light of the presence of numerous specimens of other families within the relevant size range, indicate a general absence of canids from the particular habitats being sampled. This stands in stark contrast to older sites such as Hadar and, in particular, Laetoli (Werdelin and Dehghani 2011), where canids, though not abundant, are comparatively diverse.

**Tribe Canini Fischer de Waldheim, 1817**

The early history of Canini was recently reviewed by Tedford et al. (2009). The tribe clearly originated in North America in the late
Miocene, with the earliest recognized species of the derived “Canis-group” being *C. ferox* from late Hemphillian deposits in the southwest United States and Mexico (Miller and Carranza-Castañeda 1998).

In Eurasia, the earliest suggestion of the presence of *Canis* is “Canis” *cipio* from the late Miocene site of Concud in Spain (Cru–safont Pairó 1950). However, this generic attribution has been strongly questioned by Rook (1992) as well as Tedford et al. (2009) and must surely be discounted, at least until more diagnostic material has been recovered. Instead, the oldest *Canis* in Eurasia are taxa that followed the so-called “Canis-event” in the middle Pliocene, such as *C. cf. C. etrusc-us* in China (Flynn et al. 1991; Tedford et al. 1991) and *Canis* sp. from the Vialette fauna in France (Lacombat et al. 2008), both dated ca 3 Ma or slightly younger. Better known taxa such as *C. longdanensis* and *C. brevicephalus* from China and the *C. arnensis* group further west in Europe and western Eurasia followed shortly after (see the important discussion in Sotnikova and Rook 2010).

The discussion of Eurasian *Canis* has, however, not taken into account the find of undoubted *Canis* remains from South Turkwel (Werdelin and Lewis 2000), as well as more uncertainly attributed remains from the Upper Laetolil Beds (Werdelin and Dehghani 2011). The former site is dated ca. 3.5-3.2 Ma (and more likely towards the older end of this interval), while the Upper Laetolil Beds are now dated at 3.85 – 3.63 Ma (Deino 2011). This makes *Canis* in Africa older than *Canis* in Eurasia. This situation can surely only explained by the generally poor fossil record of carnivorans in the lower Pliocene of Eurasia. Their absence from China, e.g., may be explained by a migration route either north or south of central Asia. Regardless, the African dates push the immigration of *Canis* from North America further back into the early Pliocene, likely as far back as 4 Ma or further.

**Genus Lupulella Hilzheimer, 1906**

*Type species: Canis mesomelas* Schreber, 1776

*Generic diagnosis:* None possible at this time (see remarks below).

*Stratigraphic range in Africa:* Earliest Pleistocene – Recent based on FAD at Ahl al Oughlam, Morocco (ca. 2.5 Ma; Geraads 2011).

*Stratigraphic range at Koobi Fora:* Early Pleistocene based on FAD in the Upper Burgi Mb. (≤ca 2.0 Ma Ma) and LAD in the KBS Mb. (≥1.56 Ma).

Recent studies, mainly based on sequence data, (Lindblad-Toh et al. 2005; Zrzavý and Ricánková 2004) have shown that *Canis*, as traditionally conceived, is paraphyletic, with the black-backed and side-striped jackals as sister taxa to derived Canini. This has left two options (Hartstone-Rose et al. 2010; Zrzavý and Ricánková 2004): either place the wild dog (*Lycaon pictus*) and the dhole (*Cuon alpinus*) in *Canis*, or place the jackals in a genus, or genera, of their own. Given that the most comprehensive study to date (Lindblad-Toh et al. 2005) has shown the black-backed and side-striped jackals to be sister-taxa, a one genus solution is currently the most parsimonious. As noted by Geraads (2011) the generic name *Lupulella* Hilzheimer, 1906 is available for this genus, with the two extant species *Lupulella mesomelas* (black-backed jackal) and *Lupulella adusta* (side-striped jackal).
(The generic name *Thos* Oken, 1816, based on *Canis mesomelas*, has been ruled unavailable [ICZN 1956]). Since the phylogenetic topology presently accepted is based almost exclusively on sequence data, no morphological diagnosis of *Lupulella* as conceived here is possible at present.

**Lupulella sp.**  
Figs. 3.1-3.6

The material of *Lupulella* sp. from Koobi Fora is quite limited and includes only nine numbered specimens, of which one, ER 3741, includes both craniodental and postcranial remains. The remaining material consists of seven craniodental specimens and a single postcranial specimen.

**KO OBI FORA MATERIAL**

CRANIODENTAL

Specimen ER 3755 consists of the posterior part of a right mandibular corpus with roots of m2 and m3. The corpus is broken anterior to

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Fig. 3.1: *Lupulella* sp., ER 3767, cranium. a) right lateral view; b) ventral view; c) dorsal view.
m2 and at the middle of the masseteric fossa. It is tall and quite robust. The m2 is elongated while m3 is a small, round tooth. The masseteric fossa ends anteriorly between m2 and m3.

The skull ER 3767 (Fig. 3.1) lacks the premaxillae, the left side from distal to P2 to the orbit, the left side of the braincase and the nuchal region. The snout is low and long, with long, slender nasals. The entire skull is fragmented, making it difficult or impossible to identify sutures, except for the nasomaxillary suture, as the nasals are pushed ventrally into the snout. The skull is relatively broad across the orbits and the postorbital processes are wide and broad. The lyriform crests are substantial and join at the midline to form a well developed sagittal crest. The braincase is round. The palate is very flat and reaches the posterior end of M2. The anterior premolars, P1 to P3, are slender, increasing in length from anterior to posterior. The P4 is also slender, with a small protocone but no parastyle. The paracone is tall and triangular. The metastyle is low and short. The M1 is rhomboidal in shape. The paracone is the largest cusp on M1 and is situated at the mesiobuccal corner of the tooth. The protocone is low and broad, with a low crest leading to an incipient hypocone. The metacone is large and round, though somewhat smaller than the paracone. The mesial cingulum runs from the distobuccal side of the paracone to the mesial side of the protocone. The distal cingulum runs around the metacone. The M2 is similar to the M1 in morphology but is smaller.

Specimen ER 668 is a partial right mandibular corpus with c and p3 and alveoli for p1-p2, p4 and anterior alveolus for m1. The corpus is low and slender, with two mental foramina. The anterior lies below the distal end of p1/mesial end of p2, while the posterior mental foramen lies below the middle of p3. The canine is slender and strongly recurved. It is moderately laterally compressed. The p3 is long and slender, with a tall main cusp. There are no accessory cusps on this tooth. At the mesial and distal ends of p3 the basal cingulum is formed into very small cingulum cusps.

Specimen ER 332 (Fig. 3.2a-c) is a partial right mandibular corpus with broken c, alveolus for p1, broken p2-p4, complete m2 and root of m3. The mandible is long and slender, with a narrow cross-section. The canine is small. The alveolus for p1 is substantial. The p2 is slender and has no distal accessory cusp. The same is true of p3. The p4 is also slender, but has a substantial distal accessory cusp and a small cingulum cusp. The m2 is rectangular to ovoid in occlusal outline. The cusps are worn, the lingual ones more so than the buccal ones. The protoconid is the largest cusp, followed by metaconid, entoconid, and hypoconid.

Specimen ER 895 (Fig. 3.2d-f) is a partial right mandibular corpus with p4-m2 and part of the alveolus for m3. The corpus is low and slender, with a narrow cross-section. The masseteric fossa ends at the distal extremity of m2. The p4 is a tall tooth. There is no mesial accessory or mesial cingulum cusp. The main cusp has a slightly convex mesial margin and short, straight distal margin leading to a substantial but narrow distal accessory cusp. There is also a small cusp distal to the distal accessory cusp, as well as a minute distal cingulum cusp that continues lingually as a low crest to the distolingual corner of the tooth. The m1 is substantial, with two thirds of its length made up of the trigonid. The paraconid is low, with its apex set far anteriorly. The protoconid is a much taller cusp and has a convex cutting edge. The metaconid is set slightly distal to the protoconid. It is very
low and only about half the height of the paraconid. The talonid has a large entoconid and smaller hypoconid. There is no entoconulid. The m2 is rectangular. The paraconid is reduced but the protoconid and metaconid are large (subequal in size). The talonid of m2 has a large entoconid and smaller hypoconid and a possible hypoconulid.

Apart from the postcrania described below, ER 3741 includes two craniodental pieces. The more substantial of these is a right mandibular fragment with roots of m1-m2. The specimen is very broken and worn. Its m1 is robust and the m2 long and slender, judging from the position and shape of the roots. The masseteric fossa does not reach the distal end of m2. The second specimen is a right mandibular fragment with very damaged crown of p2, roots of p3, anterior root of p4, and an isolated p3 crown. All of these tooth fragments are very broken and worn, providing no morphological information for the identification.
of the specimen.

Specimen ER 44951 is a damaged cranium of a jackal-sized dog. The bone is in fragments, but the matrix is hard and preserves the shape of the snout, which is long and slender. The skull is broken at the anterior part of the brain case. The nasals, maxillae and premaxillae are preserved only as bone fragments. The frontals are better preserved and the fronto-maxillary suture ends posterior to the anterior end of the orbits. The postorbital processes are short and blunt. The frontal sinuses are clearly marked. Of the teeth only the left and right I2-3 and left P2 are preserved. The incisors are small and unremarkable; any distinguishing features are lost because of post-mortem damage. The P2 is a long, slender tooth lacking accessory cusps. Its buccal face is damaged.

Specimen ER 45538 is a mandibular fragment with the roots of p1-p3. The corpus is long and slender. The p1 is single-rooted and short, while p2 and p3 are two-rooted, slender and long.

**POSTCRANIA**

The morphology of the ER 3741 forelimb is typical for jackals, despite the presence of pathology discussed below. The ulna (ER 3741G; Fig. 1) is quite typical of the Canini in morphology despite the large amount of pathology around the articular surfaces. The olecranon process angles superomedially, as in all *Canis* and *Lupulella*, with some medial lipping from the tip of the olecranon. The process is very rectangular in medial or lateral view. The semilunar notch is tall and mediolaterally narrow. The medial coronoid process is partially missing. The radial notch is too pathological to assess. The shaft is elongated and gracile, as in *Lupulella*, although the distal end of the spec-

![Fig. 3.3: Lupulella sp., ER 3741G, left ulna lacking the distal end; a) lateral view; b) anterior view. Note the typical canid morphology and extreme pathology.](image-url)
grooves are clearly marked on the anterior surface of the distal radius. The carpal articulation has the relatively parallel anterior and posterior edges seen in most Canini.

The pisiform (ER 3741D; 3.5) is robust, but appears similar to those of modern
 CHAPTER 3: FAMILY CANIDAE

*Lupulella*. Unfortunately, it is the most pathological of all of the bones preserved.

The metacarpals (Fig. 3.6a-b) are both gracile and long. They do not seem distinguishable from modern *Lupulella*. The fourth metacarpal (Fig. 3.6a) is missing the ventral edge of the proximal articulation. The fifth metacarpal (Fig. 3.6b) is complete, but pathological.

The only other canid postcranial specimen is a non-pathological left fifth metacarpal, ER 45536 (Fig. 3.6c). This specimen is a little smaller than ER 3741C. The lack of pathology gives it a more typical canid appearance than that seen in the ER 3741 metacarpals.

**Pathology**

The ER 3741 partial skeleton is characterized by hyperostosis in varying degrees in each postcranial element. In the ulna (Fig. 3.3), for example, there is a large amount of periostosis. There are no obvious cloacae, although there is some pitting (see lateral side of olecranon process, Fig. 3.3). There are also no involucra or areas of sequestration. Also, in the ulna, a layer of subchondral plaque can be seen in the semilunar notch. The shaft is affected, but to a lesser degree than the proximal end. The shafts look relatively normal in cross-section. While it is difficult to tell, there do seem to be some age-related changes in the joints in addition to the larger pathology. The overall pathological nature of this specimen is consistent with some type of infectious disease. Given the preference of the disease for non-metaphyseal regions and the lack of sequestration, this individual may have suffered from a systemic infection.

**Discussion of postcrania**

The partial forelimb, ER 3741, is within the larger end of the range of modern jackals. The length of the radius is within the upper range of both black-backed and side-striped jackals. The robusticity of the proximal articular surface and shaft, however, is at the extreme upper range of jackals and is similar only to the largest male jackals. The distal articular surface is relatively small for the length of the radius, as in golden and side-striped jackals but not black-backed jackals. Although the length of the ulna is unknown, the robusticity of the ulnar shaft is outside the range of modern jackals. The metacarpals also have robust shafts relative to their overall length. When considering robusticity, however, it must be remembered that with the exception of ER 45536, all of the specimens are pathological. While the shafts are less affected than the proximal and distal ends, they are not pathology free.

**REMARKS**

All of the specimens described above, craniodental as well as postcranial, are in the same general size range, and in the size range of all three modern jackal species, *Canis aureus* (golden jackal), *Lupulella mesomelas* (black-backed jackal), and *L. adusta* (side-striped jackal). Of these three, *C. aureus* and *L. mesomelas* are today sympatric in the Koobi Fora region, though this is due to a relatively recent (within the last 0.5 Ma) range extension of *C. aureus* into northern and eastern Africa. The third species, *L. adusta*, is not currently found in this region, but is found in more vegetated areas to the extreme west of Kenya, not far from Koobi Fora.

Osteologically, the species are very similar, but show a characteristic pattern of morphological divergence, with the closely related *L. mesomelas* and *L. adusta* having diverged the most, while the recently sympatric
C. aureus is very similar in most respects to L. mesomelas, despite the fact that the genera Canis and Lupulella have been distinct for at least 3 Ma and probably more (Lindblad-Toh et al. 2005). This pattern of divergence among jackal species is discussed in detail by Van Valkenburgh and Wayne (1994).

For various reasons, most eastern and southern African fossil jackal specimens have been referred to L. mesomelas (as “Canis mesomelas”). Presumably this is because L. adusta is quite distinct in dental morphology, while C. aureus is a late-comer to Africa. However, no in-depth analysis has been carried out to determine whether these specimens actually belong in the extant species or should be assigned to some extinct species. Although the divergence time of the two Lupulella species is not given in Lindblad-Toh et al. (2005), an earlier figure of 2 Ma for jackal divergence was given in Wayne et al. (1989), which is precisely in the time range of the Upper Burgi Mb. at Koobi Fora, from which the majority of the described specimens originate. Thus, an analysis to determine the specific status of the Koobi Fora jackals is essential.

The Koobi Fora sample includes more lower dentitions than upper, and even though the lower dentition generally is less informative about relationships than the upper, we will begin there. Fig. 3.7a shows the length/width relationship of p3 in two Koobi Fora specimens, compared with samples of all three species of extant jackal. The two Koobi Fora specimens differ considerably from each other. While ER 332 lies falls quite centrally in the sample of extant jackals (though it is on the slender side of all of these samples), ER 668 is longer and relatively more slender than any of the extant jackals in the samples. Based on this limited result, ER 332 could be-

Fig. 3.7: Metric analyses of jackal lower dentitions. a) length and width of p3; b) principal components analysis of characters relevant to ER 332; c) principal components analysis of characters relevant to ER 895.
long to any of the three extant species, while ER 668 is unlikely to belong to any of them.

Since ER 332 and ER 895 are more complete than ER 668, but show incomplete overlap, two separate principal components analyses were carried out, maximizing the available data for each specimen. The first two components of the ER 332 analysis are shown in the diagram in Fig. 3.7b (component loadings are presented in Table 3.1). This analysis shows ER 332 to fall very close to the center of the distribution of all jackal specimens combined, making it impossible to assign it to any of them.

The first two components of the ER 895 analysis are shown in Fig. 3.7c (component loadings are presented in Table 3.2). This diagram shows ER 895 to be distinct from *L. adusta*, but to lie within the scatter of both *L. mesomelas* and *C. aureus*.

Summarizing these analyses of the lower dentition, ER 668 is unlikely to represent any extant jackal species, while ER 332 and ER 895 may belong to some extant species. Excluding the relatively recently immigrated *C. aureus*, ER 332 could represent either of the species of *Lupulella*, while ER 895 might represent *L. mesomelas* (but not *L. adusta*). However, these analyses also show that the lower dentition as expected has poor discriminatory power among these taxa, and ER 332 and ER 895 might equally plausibly be assigned to some unknown taxon ancestral to either or both species of *Lupulella*.

Since ER 44951 retains only one tooth, P2, the first upper dentition analysis is of the length/width relationship of that tooth and also includes ER 3767 (Fig. 3.8A). The latter lies at the large end of the range of extant jackals (and is larger than any sampled *L. mesomelas*), while ER 44951 is longer and more slender than all but one extant specimen. It should be noted that due to breakage, the width of the ER 44951 P2 may have been underestimated and this result should not carry too much weight. However, the diagram shows that both specimens have a very long P2 relative to extant jackals.

Figure 3.8b shows the relationship between P4 length and M2 width in ER 3767 and extant jackals. The fossil specimen lies clearly outside the scatter of any extant species in this relationship, and has a considerably longer upper carnassial and bucco-

---

Table 3.1: Principal components analysis of characters relevant to ER 332.

<table>
<thead>
<tr>
<th></th>
<th>PC 1</th>
<th>PC 2</th>
</tr>
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<tbody>
<tr>
<td>Eigenvalues</td>
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<td>0.002</td>
</tr>
<tr>
<td>% Variance</td>
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<tr>
<td>Cumulative %</td>
<td>57.842</td>
<td>86.606</td>
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<th></th>
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<th>logWp3</th>
<th>logLp4</th>
<th>logWp4</th>
<th>logLm2</th>
<th>logWm2</th>
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<td></td>
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<td>0.449</td>
<td>0.381</td>
<td>0.483</td>
<td>0.353</td>
<td>0.363</td>
</tr>
</tbody>
</table>

Table 3.2: Principal components analysis of characters relevant to ER 895.

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<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
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<td>Eigenvalues</td>
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<td>0.003</td>
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<tr>
<td>% Variance</td>
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<tr>
<td>Cumulative %</td>
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<th>logWm1</th>
<th>logLm2</th>
<th>logWm2</th>
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<tbody>
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<td></td>
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<td>0.468</td>
<td>0.374</td>
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</table>

25
Fig. 3.8: Metric analyses of jackal upper dentitions. a) length and width of P2; b) length of P4 versus width of M2; c) principal components analysis of upper dentition.

Since ER 3767 is dentally relatively complete, a principal components analysis with this specimen and the extant jackals was carried out. The first two components from this analysis are shown in Fig. 3.8c (component loadings are presented in Table 3.3). The Koobi Fora specimen lies within the scatter of *C. aureus*, but outside the scatters of either species of *Lupulella* (and very distantly from *L. adusta*).

In summary, the upper dentition metrics strongly suggest that ER 3767 (and perhaps ER 44951 as well, though the latter is poorly preserved) does not fit comfortably into any of the extant jackal species.

Thus, the results of these metric analyses suggest that none of the jackal specimens from Koobi Fora can confidently be assigned to an extant species. On their own, the lower dentition specimens ER 332 and ER 895 might tentatively have been consid-

Table 3.3: Principal components analysis of jackal upper dentitions.

<table>
<thead>
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<th>PC 2</th>
</tr>
</thead>
<tbody>
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<tr>
<td>logWM1</td>
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<tr>
<td>logLM2</td>
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<tr>
<td>logWM2</td>
<td>0.109</td>
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</table>

lingually relatively narrower M2 than any extant specimen.
erred to belong to *L. mesomelas*, but taken in conjunction with the results of the upper dentition specimens, especially ER 3767, the results for ER 332 and ER 895 might more plausibly be ascribed to the poor discriminatory power of the lower dentition. Neither can the Koobi Fora specimens, given the limited material available, confidently be assigned to some extinct species of jackal. Geraads (2011) recently named a new species of *Lupulella*, *L. paralius*, on the basis of material from Ahl al Oughlam, Morocco. Evaluating this species relative to the Koobi Fora material is beyond the scope of this contribution, but we can note that the narrow M2 seen in ER 3767 is not a feature of the single relevant specimen of *L. paralius*. Excluding *C. aureus* from consideration due to its relatively recent appearance in Africa, we therefore place all Koobi Fora jackal specimens in *Lupulella* sp. This result is based on the analyses of the craniodental specimens, but there is nothing in the limited and mostly pathological postcranial material that precludes such an assignment.

Tribe *Vulpini* Hemprich and Ehrenberg, 1832

**Genus Vulpes** Frisch, 1775

*Type species:* *Canis vulpes* Linnaeus, 1758

*Generic diagnosis:* Modified after Munthe (1998). Skull with long, sharp muzzle; postorbital process thin and concave dorsally; frontal bones less convex than in *Canis*; simple incisors; canine teeth slender, relatively longer than in *Canis*; cheek teeth slender with sharp, well-defined cusps and crests.

*Stratigraphic range in Africa:* Late Miocene – Recent based on FAD at Toros Menalla, Chad (ca 7 Ma; Lebatard et al. 2008)

**Stratigraphic range at Koobi Fora:** Early Pleistocene based on FAD in the Upper Burgi Mb. (≤ca 2.0 Ma) and LAD in the KBS Mb. (≥1.56 Ma).

**Vulpes sp.**

The single specimen assigned to this taxon, ER 3121, is an anterior fragment of a right mandibular corpus with partial c alveolus, roots of p2, and complete p3. The corpus is slender yet relatively robust in the symphysis region. There is a single mental foramen beneath the postcanine diastema. The p2 had a small mesial and larger distal root. The p3 is a long, slender tooth. There is a low bump on the mesial face of the main cusp and a small distal accessory cusp on the distal face. Distoventral to this there is a small cingulum cusp.

**REMARKS**

The specimen described above clearly represents a very small member of the Canidae. On the basis of a very limited sample of Vulpini, the specimen is smaller than *Vulpes chama* and the South African fossil foxes *V. pulcher* and *V. pattisoni* (Broom 1939, 1948). It is likely to be of the size of *V. zerda*, for which we have no adult comparative specimens. However, even if we had, the specimen does not have any diagnostic characters beyond size to identify it, and for this reason we have assigned it to *Vulpes* sp.

*cf. Canidae indet.*

Specimen ER 44131 is a poorly preserved piece of mandibular corpus with roots of p3-
m1. It can tentatively be identified as canid on the basis of the size relationship between p4 and m1, though the p4 seems large for a canid.

REFERENCES


Sotnikova, M., Rook, L. (2010). Dispersal of the Canini (Mammalia, Canidae: Caninae) across Eurasia during the Late Miocene to Early Pleistocene. *Quaternary*


**Chapter 4**

**FAMILY MUSTELIDAE**

Mustelidae is the most speciose carnivoran family today, with more than 40 species in several clades at the subfamily or tribe level. This count does not include the skunks, which were previously placed in the Mustelidae, but are now generally considered to constitute a distinct family, Mephitidae (e.g., Dragoo and Honeycutt 1997). Although the phylogeny of Mustelidae is in the process of being resolved (Agnarsson et al. 2010; Koepfli et al. 2008; Sato et al. 2003), there is as yet no consensus regarding its suprageneric taxonomy, and we will here minimize reference to subfamilial clades.

Mustelidae is generally poorly represented in Africa, perhaps because in Africa, Herpestidae and Viverridae occupy many of the niches for small carnivorans that are filled by Mustelidae in northern continents, particularly in temperate regions. Hence, a speciose genus such as *Martes* is only known from a single Miocene record in Africa (Ginsburg 1977; Werdelin and Peigné 2010), while the likewise common and speciose *Mustela* is only known from a single Late Pleistocene record (Aouraghe 2000).

**Subfamily Lutrinae Bonaparte, 1838**

The African fossil record of Mustelidae is dominated by otters from several different groups including both completely extinct lineages and lineages leading to the extant African genera *Aonyx*, clawless otters, and *Hydrichtis*, spotted-necked otters. This subfamily is the most common mustelid group at Koobi Fora.

**Genus Enhydriodon Falconer, 1868**

*Type species:* *Enhydriodon sivalensis* Falconer, 1868

*Generic diagnosis:* Not diagnosable at present.

*Stratigraphic range in Africa:* Late Miocene – ?Early Pleistocene based on FAD at Toros Menalla, Chad (≤7 Ma) and LAD in the Koobi Fora Fm., Upper Burgi Mb. (>1.87 Ma).

*Stratigraphic range at Koobi Fora:* Early – ?Early Pleistocene based on FAD in the Lonyumun Mb. (≤4.35 Ma) and LAD in the Upper Burgi Mb. (>1.87 Ma).

**REMARKS**

*Enhydriodon* (and/or *Sivaonyx*, see below) is a genus of large to very large otters known from the late Miocene to early Pleistocene in Africa and the Indian subcontinent. They have traditionally been thought to be related to the sea otter, *Enhydra lutris*, but it is clear that the fossil genera belong to an entirely different lineage and Morales and Pickford (2005b) placed them in a new tribe, Enhydriodontini.

There is a great deal of confusion about the content of *Enhydriodon* and the re-
lated genus *Sivaonyx*. Most African species have generally been referred to *Enhydriodon*, but Morales and Pickford (2005b) referred them to *Sivaonyx*. Pickford (2007) attempted to provide diagnoses of the two genera, although neither these diagnoses nor the accompanying discussion in that paper or in Morales and Pickford (2005b) provide a differential diagnosis of the two genera. It is clear that the P4 of *Enhydriodon falconeri* is very different from that of, e.g., *Sivaonyx bathynathus* (Pickford 2007, fig. 9), but it is less clear that this observation translates to the poorly preserved P4 of *E. sivalensis* (Pickford 2007, fig. 12). These problems, in combination with the absence of overlapping characters in the diagnoses, makes it difficult to assess the Pickford and Morales conception of the two genera, and to assign species-level taxa to them. Werdelin and Peigné (2010) accepted the view that *Sivaonyx* is the only genus present in Africa, but Geraads et al. (2011) disagreed. Pending revision of both genera, especially the African material, we have here decided to use the genus *Enhydriodon* to label the Koobi Fora material. *Enhydriodon* is the senior of the two genera, being named by Falconer (1868), while *Sivaonyx* was named by Pilgrim (1931). Other taxa in this group will here be labeled with their original generic attribution.

Regardless of this taxonomic confusion, *Enhydriodon* is one of the most interesting carnivoran lineages of the African Neogene. It must have had a fairly wide distribution and been relatively abundant, as it is found at some Miocene and most Pliocene sites in central and eastern Africa. Thus far, seven species have been described (those listed in Werdelin and Peigné 2010) under *Sivaonyx*, with the addition of the recently described *E. dikikae* (Geraads et al. 2011).

**Enhydriodon afman sp. nov.**

*Fig. 4.1*

**Specific diagnosis:** Lower carnassial with unicuspid paraconid set transversely at the mesial end of the tooth; protoconid very large, occupying most of the central basin of the trigonid; postprotocristid prominent, leading to a large hypoconid that occupies nearly the entire length of the buccal side of the talonid; entoconulid and entoconid very prominent, set close to each other and subequal in size; distal end of tooth not bordered by small cusplets; talonid relatively short; m2 very large.

**Holotype:** KNM-ER 3110, partial left horizontal ramus with m1, roots of p4, alveoli for p3, m2, and partial alveolus for c (Fig. 4.1).

**Horizon and locality:** Lokochot Member of the Koobi Fora Formation, Area 117 of the Il Naibar Lowlands. Age between 3.58 Ma (Lokochot Tuff) and 3.44 Ma (Tulu Bor Tuff) (McDougall and Brown 2008).

**Hypodigm:** Holotype only.

**Etymology:** From the Dassenech *af man*, meaning blunt, in reference to the low, rounded m1 cusps.

**KOOBI FORA MATERIAL**

The ramus is very large and robust, with a short pre-carnassial part and long carnassial to condyle part. The alveolus for the lower canine is set nearly vertically. Neither p1 nor p2 was present. There are three distinct mental foramina, all set in the dorsal half of the ramus. The anteriormost and largest, which is set beneath the distal part of p3, is elongated. The other two mental foramina are
smaller. One is set directly posterior to the first and beneath the mesial root of p4, while the other is set beneath and slightly anterior to the one just mentioned. The ramus deepens slightly from its anteriormost preserved point to a point beneath the distal root of p4, after which the depth decreases slightly. The buccal side of the ramus angles buccoventrally until just before the midpoint of the depth of the ramus, where there is a low ridge. Ventral to this ridge the angle changes to linguoventral. The slant of the lingual wall follows that of the buccal, but is more gradual. The masseteric fossa ends beneath the distalmost point of m2. It is deep and there is a broad masseteric shelf that runs from the anteriormost point of the masseteric fossa all the way to the condyle. It also continues to the angular process, which is broken. The condyle is broken medially, but appears to have been quite small for the size of the ramus. The coronoid process is missing.

The lower carnassial is massive, with low, blunt cusps. In occlusal view the trigonid cusps range in size from the protoconid (largest) to paraconid to metaconid (smallest). The paraconid has its main axis at near right angles to the mesiodistal axis of the tooth. It is thus transversely elongated, with an apex that has been worn flat. The protoconid is diamond-shaped in occlusal view due to the extent of the cristids connecting
it to the metaconid and hypoconid. The apex of the protoconid is worn flat, but obliquely, with the wear facet angling from mesiolingual to distobuccal. The paraconid and protoconid are separated from each other by a shallow valley and the protoconid and metaconid from each other by a much deeper valley. The postparacristid and preprotocristid are indistinct. The metaconid is the smallest trigonid cusp in occlusal view, but is also the tallest in the specimen as preserved, as it is almost unworn. Because of the considerable wear on the paraconid and protoconid, the relative heights of the unworn cusps cannot be determined. There is a small, shallow basin in the space between the trigonid cusps. The talonid is low and wide, though its central basin is not flat but concave. The hypoconid is large and low. On the lingual side there are two distinct cusps representing the entoconid and entoconulid. The basal cingulum begins on the mesiolingual side of the paraconid and continues around the mesial and buccal sides of the tooth to the mesial part of the hypoconid.

The p4 was two-rooted, with the distal root much the larger. The p3, on the other hand, was single-rooted, as was the m2, though the alveolus for the latter is of about the size of the two alveoli of p4 combined.

REMARKS

Out of the seven named species of *Enhydriodon/Sivaonyx* in Africa, only two, *S. kamuhangirei* Morales and Pickford, 2005 and *E. dikikae* Geraads et al., 2011 are relevant to the taxonomy of ER 3110. The remaining species, *E. africanus* (Stromer, 1931), *S. beyi* Peigné et al., 2008, *E. ekecaman* Werdelin, 2003, *S. hendeyi* Morales and Pickford, 2005, and *S. soriae* Morales and Pickford, 2005 (like Peigné et al. 2008 we consider *S. senutae* Morales and Pickford, 2005 a junior synonym of *E. soriae*) are much smaller than the Koobi Fora specimen. Despite difficulties in assessing intraspecific variation in species of *Enhydriodon* due to the limited material from any given site, in the few instances where there is more than one specimen at a site, size variation is small. Of the above smaller species, the m1 of *S. hendeyi* and *E. ekecaman* are closest in size to that of ER 3110, yet are 20% shorter and 15% narrower, while those of *S. kamuhangirei* and *E. dikikae* are similar in size to, or larger than, ER 3110.

The Koobi Fora specimen is quite different from *E. dikikae* in its much more distinct hypoconid, entoconid, and entoconulid. *E. dikikae* also had a broad, shallow talonid basin bounded distally by low cusplets. The talonid basin in ER 3110 is smaller and deeper, and there are no distal cusplets. Similarities with *S. kamuhangirei* are greater. The type specimen of the latter (Morales and Pickford 2005b, fig. 2M) shares with ER 3110 the stronger development of the hypoconid, while the entoconid and entoconulid are less developed than in the Koobi Fora specimen. Neither specimen appears to have the distal enamel cusplets, but the distal margin of the m1 of *S. kamuhangirei* is more curved than in ER 3110, where it is squared-off. In addition, the trigonid cusps of *S. kamuhangirei* are set closer together and the basin between them is of minimal extent. Nevertheless, the Koobi Fora specimen appears more closely related to *S. kamuhangirei* (holotype only: we agree with Geraads et al. 2011 that the *S. kamuhangirei* paratype, an m1 talonid from Warwire [Morales and Pickford 2005b, fig. 2N], is likely to belong to a different taxon) than it is to *E. dikikae.*
KNM-ER 3108 is a left m2. The tooth is very flat, with a few crest-like cusps. It comes from the left side and is wider than long, as is typical of Enhydridodontini and Aonyxini. It has a transverse, ridge-like paraconid that is connected to the protoconid by a pair of low crests separated by a shallow valley. The protoconid is large and has a distal accessory cusp as in the m1 of other Enhydriodon. The metaconid is more cusp-like and well isolated from the other trigonid cusps, though connected to the protoconid by a low ridge. In the talonid there is a single cusp that by analogy with m1 presumably is the hypoconid. It is set at the distal end of the tooth. The talonid basin is short, little more than a shallow valley. There is a short but well developed buccal cingulum between the paraconid and protoconid. This tooth appears to be a little smaller than the missing m2 of ER 3110.

KNM-ER 3871 is a probably represents a third upper incisor. The crown of this tooth is slightly longer than wide and the medial side is slightly flattened where it contacts the second incisor. The crown of the tooth angles slightly from medial to lateral as seen from root to apex. The enamel-dentine juncture is lower on the lateral side than on the medial. There is a strong basal cingulum that surrounds the crown, except at the medialmost point, where the tooth was in contact with the second incisor. The root is short, straight, and robust.

Specimen ER 3107 (Fig. 4.2) is a right astragalus. It is very similar to a specimen from Eshoa Kakurongori, Kenya (?3.0 Ma; EG 27420F), but is much less well-preserved. The head is broken superomedially and both edges of the trochlea are broken off. Thus, the facet for the lateral malleolus on the lateral side of the trochlea is missing. Only the ventralmost portion of the region for the medial malleolus is preserved. The ventral surface is well-preserved.

The specimen is also generally similar to a published astragalus from Toros Menalla in Chad, TM 171-01-033, part of the holotype of S. beyi (Peigné et al. 2008). The Toros Menalla specimen is smaller (max length 34.9 mm vs. 45.8 mm in the Koobi Fora
Although these two specimens are broken or eroded in different regions, their overall similarity can be seen. Major differences include a much shorter neck in the Koobi Fora specimen than in *S. beyi*. The Koobi Fora specimen also appears to have a wider lateral facet for articulation with the calcaneum.

The Koobi Fora specimen is clearly not a felid, as can be demonstrated by numerous non-felid characteristics. For example, there is a large, square shelf at the posterior end of the trochlea that is more characteristics of otters, colobine monkeys, and pandas than felids. This astragalar shelf or tubercle can also be seen in the *S. beyi* astragalus (Peigné et al., 2008), although it appears to be more distinct and shelf-like in the Koobi Fora astragalus. A groove for the triceps surae tendon occurs on the shelf. This groove is much deeper in extant lutrines. The shelf curves dorsally and the two calcaneal facets extend onto it. In medial view, the shelf adds to the very deeply curved surface for the calcaneum (Fig. 4.2b) and limits the rotation of the astragalus on the tibia.

The angle of the head/neck and the trochlea are also quite different from those of felids, and their long axes run almost at right angles to one another (or at least they are less in line than in felids). The head is rotated so that the long axis forms a more acute angle with the ground than in felids. As in *S. beyi* (Peigné et al. 2008), the articular surface for the navicular is strongly convex and there is a small facet for the cuboid on the ventrolateral region of the neck.

The lateral edge of the trochlea extends much further anteriorly than the medial edge. The lateral edge of the neck also extends further laterally to the midpoint of the anterior edge of the trochlea than in felids. The anterior edge of the trochlea is grooved.

In inferior view, the lateral facet flares anterolaterally and the medial facet flares anteromedially. In fact, the medial facet flares so far onto the ventral surface of the neck that it is almost touching the ventral edge of the head. As in *S. beyi*, the medial facet does not extend as far posteriorly as the lateral facet. The anterior extension of the lateral facet is eroded. The interfacet groove extends to the previously mentioned shelf on the posterior end of the trochlea, but is not carried onto it. The facets abut one another on the shelf; this gives the ventral surface a triangular shape. The lateral facet is wider than the medial facet; both are widest anteriorly. The medial facet is almost a right triangle, with the 90° angle in the anterolateral corner and with the posterolateral point squared off and running up onto the shelf. The lateral facet is more rectangular than in felids, although the edges are not parallel. It is not straight-edged anteriorly.

In dorsal view, the lateral extension of the calcaneal facet has resulted in an extremely pointed projection under the fibula. This is partially preserved in ER 3107, but can clearly be seen in EG 27420F.

**REMARKS**

The specimens described above can all be placed in *Enhydriodon* as here conceived, based on morphology and size. It is probable that they belong to *E. afman* sp. nov., but this cannot be demonstrated at present on morphological grounds. Also, the presence of two species of *Enhydriodon* at Kanapoi (Werdelin and Manthi 2012) suggests that the same might be true at other sites. Therefore, we here retain them as *E. cf. E. afman*.

The two craniodental specimens are
of limited interest. On the other hand, postcranial material of the giant bunodont otters is rare in Africa. Although quite a few species have been named, most are represented by dental material only (Bonis et al. 2008; Haile-Selassie 2008; Haile-Selassie and Howell 2009; Morales and Pickford 2005b; Werdelin 2003a; Werdelin and Manthi 2012).

Various postcrania from Langebaanweg, South Africa, including an astragalus, were assigned by Hendey (1978) to *E. africanus*. This material was later removed from this taxon and placed in the new species *S. hendeyi* (Morales and Pickford 2005b; Morales et al. 2005) Several researchers (Peigné et al. 2008; Pickford 2005) have noted that the astragalus is actually that of an aardvark. The *S. hendeyi* femur is distinct morphologically from eastern (Lewis 2008) and central (Peigné et al. 2008) African bunodont lutrines. It is much smaller than material from Omo and Dikika (Geraads et al. 2011; Lewis 2008). The Koobi Fora material is unlikely to belong to either *E. africanus* or *S. hendeyi*.

Numerous postcranial elements, including an astragalus, have been found at the Late Miocene site of Toros-Menalla in Chad and placed in the species *S. beyi* (Peigné et al. 2008). As mentioned above, the Koobi Fora specimen (and similar Eshoa Kakurongori specimen) are larger and distinct morphologically from *S. beyi*.

Femoral and humeral material of an extremely large species, *E. dikikae*, has been reported from the Pliocene Dikika site in the Lower Awash of Ethiopia (Geraads et al. 2011) If this species has the same relative proportions of astragalar length to femoral length as seen in the *S. beyi* holotype, then *E. dikikae* would have had an astragalus roughly within the size range of the Koobi Fora astragalus.

Femora belonging to bunodont otters have been reported from West Turkana, Kenya and Hadar and Omo, Ethiopia (Lewis 2008). None of these sites have astragali attributable to giant bunodont otters (Lewis, personal observations). While the Omo material is larger than *E. dikikae*, the Hadar femur is slightly smaller and may also be within the size range of the Koobi Fora *Enhydridodon*. Consequently, Geraads et al. (2011) have noted that the Hadar femur is similar to that of *E. dikikae*. The West Turkana material is smaller than the Hadar material and morphologically distinct from other *Sivaonyx/Enhydridodon* material. If it does belong to a bunodont otter, it may have been too small for the Koobi Fora astragalus.

**Genus Torolutra Petter, Pickford and Howell, 1991**

*Type species:* *Torolutra ougandensis* Petter, Pickford and Howell, 1991

*Generic diagnosis:* Masseteric fossa relatively deep, distinctly separated from ventral border, with anterior end distal to m2 alveolus; p4 robust, oval in occlusal outline, surrounded by a thick and continuous basal cingulum; m1 with sharp trigonid cusps, protoconid taller than paraconid and metaconid, narrow, with flattened and obliquely oriented surface formed by the lingual face of the hypoconid (Translated and modified from Petter et al. 1991).

*Stratigraphic range in Africa:* Late Miocene – Early Pleistocene based on FAD in the Nkondo Fm., (≤6 Ma?) and LAD in the KBS Mb., Koobi Fora Fm. (≥1.56 Ma).

*Stratigraphic range at Koobi Fora:* Early
Pleistocene based on FAD in the Upper Burgi Mb. (≤ca 2.0 Ma) and LAD in the KBS Mb. (≥1.56 Ma).

**REMARKS**

*Torolutra* was described on the basis of some mandibular specimens from the lower Pliocene of Uganda (Petter et al. 1991). The same authors also tentatively assigned material from the Brown Sands of the Usno Fm., Ethiopia (Howell and Petter 1976) and from Wadi Natrun, Egypt (Stromer 1911) to *Torolutra*. However, no subsequent revision or analysis of the taxon has been carried out, and the relationship between the genus *Torolutra* and the extant genera *Lutra* and *Hydrictis* has not been examined.

*Torolutra cf. T.ougandensis*

Figs. 4.3 – 4.5

Stratigraphic range at Koobi Fora: Early Pleistocene based on FAD in the Upper Burgi Mb (≤ca 2.0 Ma) and LAD in the KBS Mb (≥1.56 Ma).

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Fig. 4.3: *Torolutra cf. T.ougandensis*, ER 5895. a-b) severely damaged cranium in a) left lateral and b) ventral view; c-e) left and fragment of right ramus in c) occlusal, d) buccal, and e) lingual view.
KOObI FORA MATERIAL

CRANIODENTAL

ER 5895 includes numerous associated craniodental and postcranial fragments. ER 5895A is a crushed anterior skull fragment with P4, roots of left I3, C, M1 and alveoli for I1-I2, and roots of right C, P2-P3 and alveoli for I1-I3 and P1 (Fig. 4.3a-b). The P4 is heavily worn. The parastyle is broken, but was clearly small. There is a ridge running from its anterior end to the apex of the paracone. A second ridge runs from the apex of the protocone to the mesiobuccal part of the protocone shelf. The protocone shelf is long and low, with the protocone seen only as a low ridge on the lingualmost edge. The shelf ends level with the lowest point of the metastyle. The paracone is tall and slender. There is no carnassial notch and the metacone is prominent but low. The extent of the cingula is uncertain due to damage to the tooth. The remains of M1 indicate that it was short and broad.

ER 5895B is a left mandibular ramus (and small fraction of the anterior right ramus) with alveoli for incisors (homology uncertain), damaged p2-p4, and complete m1 (Fig. 4.3c-e). The ramus is relatively tall and broad. It has several mental foramina of which the largest is situated beneath the juncture of p2 and p3. The masseteric fossa nearly reaches the distal end of p4. The symphysis is fused. The p2 is short and its distal end is much broader than its mesial one. The crown is damaged, but both mesial and distal accessory cusps appear to have been small if present. The p3 is similar in occlusal outline to p2. There is no mesial accessory cusp, but a low ridge leads from the mesial end of the tooth to the apex of the main cusp. The distal accessory cusp was large and appressed to the distobuccal side of the main cusp. The distal shelf is broken but must have been well developed. The lingual side of p4 is broken, making it difficult to determine its occlusal proportions. The mesial end of the tooth is similar to that of p3, while at the distal end the accessory cusp is situated close to the buccal margin of the tooth. There was a prominent basal cingulum but its exact extent cannot be determined. The m1 has three well developed trigonid cusps, of which the paraconid is the largest and the protoconid the tallest. The pre- and post-cuspid cristae are not well developed. The protolophid is well developed and situated transversely almost exactly in the mesiobuccal part of the tooth. The talonid is long and trenchant, with a prominent hypoconid. The lingual margin lacks cusps and is composed of a single, low cingulum ridge. The m1 is terminated distally by a substantial cusp that is confluent with the lingual cingulum. On the buccal side there is a lower cingulum that extends all around the trigonid from the mesial part of the protoconid to the mesial end of the (poorly developed) premetacristid.

ER 5895C includes a dorsal portion of the left coronoid process and other mandibular fragments.

ER 5895D includes skull fragments with P4 and M1 in matrix.

ER 5895E is a part of the right mandibular ramus with distal root of p4 and roots of m1.

ER 4568 is a partial right mandible broken anterior to p3 and in the anterior third of the masseteric fossa, with broken p3, complete p4-m1, and alveolus for m2 (Fig. 4.4a-c). The ramus is robust but not deep. The p3 consists of fragments only. It has a very short distal shelf. The p4 is tall, with a minute mesial cingulum cusp. The main cusp is tall, with straight mesial and distal faces. It has a slight lingual bulge at the center of its base. The dis-
tal shelf is short and somewhat overhung by the anterior end of m1. There appears to be a small distal cingulum cusp but it is partly obscured by sediment. The m1 is long and low. The trigonid cusps are worn, but the protoconid appears to have been the tallest, followed by the paraconid and metaconid. The shearing blade is only slightly angled relative to the anteroposterior axis of the ramus. Both paraconid and protoconid are elongated, the former more so than the latter. The protoconid, on the other hand, is the more pyramidal. The metaconid is triangular in occlusal view and is set level with the distal half of the protoconid. The talonid has a long, well developed hypoconid, separated from the protoconid by a shallow valley. Posterior to the hypoconid there is an additional small cusp. From the metaconid a deep valley leads to the talonid, but there is no entoconid. The talonid is narrower than the trigonid and tapers strongly towards its distal end. The alveolus for m2 indicates that this tooth was substantial.

ER 44462 is a right mandibular ramus with complete p3-m1 (Fig. 4.4d-f). The ramus is broken anterior to p3 and at the anterior end of the coronoid process. The ramus is robust and tall. There are two mental foramina located at the mesial and distal ends of p3. The anterior mental foramen is the larger of the two. The masseteric fossa does not reach the distal end of m1. The distal half of a robust canine alveolus is present. There are small alveoli for p1 and p2, set bunched up between the canine and p3: p1 buccally and p2 linguually. The p3 is short and broad. There is no mesial accessory cusp, only a small mesial cingulum. The main cusp is set mesial to the midline of the tooth. The distal shelf is large with a lingual extension almost to the level of the main cusp. There is no distal accessory cusp. The p4 is tall and relatively slender. There is no mesial accessory cusp, but a well developed mesial cingulum is present. The main cusp is tall and straight. The distal shelf is relatively narrow in this tooth. There is no distal accessory cusp, but there is a crest running down the distal face of the main cusp. This crest has a distinct wear facet. The paraconid and protoconid of m1 are low and robust. The protoconid is set level with the metaconid. The former is the largest trigonid cusp the latter the smallest. The talonid has a distinct and crest-like hypoconid and a smaller distal cusp; it is not basined. There
is no entoconid. The alveolus for m2 is oval in occlusal view.

POSTCRANIAL

In addition to the skull, ER 5895 has both axial and appendicular elements of the postcranial skeleton. Most of the axial material is fragmentary, including numerous cervical vertebral fragments (ER 5895F, G, H, I, Q) and rib fragments (ER 5895AE through AS). Several vertebrae are reasonably complete, including several thoracic vertebrae (ER 5895J, K, L, N, O) and a lumbar vertebra (ER 5895M). The axis (ER 5895P; Fig. 4.5a-b) is well-preserved. Other vertebral fragments are present (ER 5895U, W, Y). There are numerous bone fragments (ER 5895S, X). The manubrium (ER 5895AU) is missing the caudal portion. The alae are fairly short and do not project much. The cranial end is also broken off.

Only a small portion of the appendicular skeleton is present. The left scapula (ER 5895R; Fig. 4.5c-d) includes the glenoid and part of the spine. Although the glenoid displays the characteristic upside-down keyhole shape, it is very rounded. The supraglenoid tubercle is not particularly large. The origin of the spine is relatively posterior on the neck, such that the infraspinous fossa is not as wide as the supraspinous fossa, at least in the portion preserved. The spine is broken, but is tall.

Fig. 4.5: Selected portions of the partial postcranial skeleton of Torolutra cf. T. ougandensis, ER 5895. a-b) axis ER 5895P in a) dorsal and b) right lateral view. Note that the dens is missing; c-d) left scapula, ER 5895R, in c) lateral and d) anterior view; e-f) distal right humerus ER 5895T in e) anterior and f) posterior view; g, i, k) left third metatarsal ER 5895AB in g) dorsal, i) lateral, and k) proximal view; h, j, l) left fourth metatarsal ER 5895AC in h) dorsal, j) lateral, and l) proximal view.
There is also a distal right humerus (ER 5895T; Fig. 4.5e-f). In posterior view, the lateral and medial walls of the trochlea are subparallel and the trochlea is deep. The olecranon fossa is skewed so that the proximalmost end is skewed laterally. The olecranon fossa is not very tall proximodistally. The lateral epicondyle is much smaller than the medial epicondyle. A large supinator crest rises straight proximally from the edge of the lateral epicondyle before curving medially back to the shaft. The entepicondylar foramen and bar over it are not visible in posterior view. In distal view, the whole specimen is not wide anteroposteriorly. This is the expected condition in lutrines. The capitulum is not particularly rounded and projects very little anteriorly. In anterior view, there is a slight excavation representing the anconea fossa. The lateral side is swept posterolaterally for the supinator crest.

This humerus is similar in size to the humerus referred to *Torolutra ougandensis* from the Middle Awash (Haile-Selassie 2008). However, ER 5895 has a much larger medial epicondyle indicating greater leverage for the carpal and digital flexors.

The hindlimb is represented by the only complete mustelid metatarsals known from Koobi Fora, metatarsal 3 (ER 5895AB; Fig. 4.5g, i, k) and metatarsal 4 (ER 5895AC; Fig. 4.5h, j, l). These specimens articulate. Although ER 5895AC is the longer specimen, when they are articulated, they are roughly equal in length. In both specimens, the articular surfaces between metatarsals are deep. When articulated, the metatarsals are slightly splayed.

The third metatarsal head (Fig. 4.5k) is symmetrically proportioned. The shaft is mediolaterally wider distally than it is proximally, although not by much. In lateral view (Fig. 4.5i), the shaft is not particularly curved.

The proximal end of ER 5895AB (Fig. 4.5k) is the “T-shape” expected in all carnivores. The ventral portion of the “T” is rather blocky and square. The dorsal portion is wider than the ventral, but not by much. The shaft is somewhat short in comparison to cursorial carnivore third metatarsals. It is also relatively wide, although not overly so.

The left metatarsal 4 (ER 5895AC; Fig. 4.5h, j, k) changes more along the shaft than the third metatarsal in that the distal end is much more noticeably wider than the proximal end. In addition, the shaft is more curved when viewed laterally. The proximal end is much wider mediolaterally on the dorsal edge than the ventral, and much more so than in the MT3. The lateral side of the head slopes more than the medial, as would be expected in MT4.

**REMARKS**

The three mandibular specimens described above are very similar to one another and on the basis of morphology alone clearly belong to a single species. This can be confirmed by metric analysis, which shows them to be very similar in the size and proportions of the teeth (Fig. 4.6). However, these metric analyses also show that they differ from the previously described material of *Torolutra ougandensis*. Primarily, the p4 is relatively much more slender in the Koobi Fora specimens (Fig. 4.6c). This graph shows the three Koobi Fora specimens to be close to one another and the two Ugandan specimens to be close, while the two groups are well separated. The proportions of the m1 are much more similar in the two groups, however. This distinct difference in the p4 makes us hesitant to ascribe the Koobi Fora specimens to the species *T. ougandensis*. The difference may simply reflect anagenetic change within the lineage, as the Koobi Fora
Fig. 4.6: Metric analysis of Lutrinae from Koobi Fora and some other African sites, compared with a modern sample of *L. lutra* from Finland. a) length and width of m1, showing the greater size of the Koobi Fora *Torolutra* specimens compared to modern *L. lutra*, but their similarity to each other and to the holotype of *T. ougandensis* from Uganda; b) length of m1 versus trigonid length of the same tooth. This also shows the size of the Koobi Fora *Torolutra* specimens and their similarity of the holotype, but also the much shorter trigonid of ER 1486, here identified as a new species of *Hydrictis*; c) length and width of p4, showing a notable difference between the Koobi Fora *Torolutra* specimens and those from Uganda, including the holotype, leading us to tentatively suggest a specific difference between these two groups; d) length and width of p3, showing much greater width of this tooth in *Torolutra* than in extant *Lutra*. Note in a) and c) that *L. fatimazohrae* from Ahl al Oughlam (Geraads 1997) is more similar to extant *Lutra* than are any of the Koobi Fora or Uganda specimens.
specimens are much younger than the Ugandan ones, but may also reflect a species difference. We have therefore placed the Koobi Fora specimens in *Torolutra*, but in open nomenclature. The difference also raises the question of whether the Usno Fm specimens tentatively referred by Petter et al. (1991) to *T. ougandensis* really belong in that species. If the Koobi Fora material could be shown to belong to a distinct species of *Torolutra*, then the Usno Fm specimens, which are closer in age to the Koobi Fora material than to the Ugandan specimens, might also belong to this species.

The diagrams in Fig. 4.6 also show that *Torolutra* is considerably larger than extant *Lutra lutra*, but also differs from that taxon in the proportions of the dentition. However, extant *Hydrictis maculicollis* is similar to *L. lutra* in dental proportions, so this does not ally *Torolutra* more closely with *Hydrictis* than with *Lutra*.

The relationships of *Torolutra* have not been extensively discussed. Metrically, it is similar to *Lutra* and *Hydrictis*, as noted above, although differences exist. However, as pointed out by Grohé (2011) in a discussion of the mandible of *Vishnuonyx*, that genus and *Torolutra* are among the very few lutrines to lack a basined m1 talonid. Also, the P4 of *Vishnuonyx* and that of *Torolutra* are quite similar, so similar that Morales et al. (2005) imply (but do not explicitly state) that *Vishnuonyx angololensis*, identified by Werdelin (2003b) on the basis of an isolated P4, may be conspecific with *T. ougandensis*. These similarities, although not conclusive, suggest that *Torolutra* may be closely related to *Vishnuonyx* and hence a member of the Enhydriodontini *sensu* Pickford (2007).

The ER 5895 postcranial specimens are consistent in morphology with other semi-aquatic lutrines and consistent in size with *Torolutra*. They are larger than the homologous elements of the largest living Lutrini.

cf. *Torolutra* sp.
Figs. 4.7 – 4.12

Stratigraphic range at Koobi Fora: Early Pleistocene based on FAD in the Upper Burgi Mb (≤ca 2.0 Ma) and LAD in the Okote Mb (≥1.38 Ma).

KOBO FORA MATERIAL

POSTCRANIAL

A considerable number of postcranial remains including a partial skeleton (ER 6076) are tentatively referred to this taxon (see Appendix 1). The individual represented by the partial skeleton may be within the larger end of the possible size range of *Torolutra*. Much of this material is fragmentary. The appendicular skeleton is in better condition than the axial material.

Axial skeleton

Only two cervical vertebrae are known, ER 6076M and Q. ER 6076M includes only the centrum, which has the characteristic angled articular surfaces of cervical vertebrae. ER 6076Q is just a fragment.

Thoracic vertebrae are represented by a vertebral centrum (ER 6076I). This specimen may be T4 or close to it. While the sides of the centrum flare somewhat like those of a cervical vertebra, the overall centrum shape and presence of the superior costal facet indicates that this is a thoracic vertebra.

Thoracic limb

The right proximal humerus (ER 6076B) be-
longing to the partial skeleton is poorly preserved and may be somewhat deformed (see shape of head, Fig. 4.7a). This specimen has a low, rounded greater tuberosity. The head is relatively rounded anteroposteriorly. The bicipital groove is large and flat as the greater tuberosity angles laterally away from it. The lesser tuberosity is large. On the inferior surface of the neck, the arc from the head to the shaft is wider and flatter, resulting in less lipping than in *Mellivora*. The remnant of the shaft appears to angle anteriorly more than in *Mellivora*. Although the deltoid tuberosity is not preserved, what remains indicates that it was relatively large. This specimen is similar to a possible *Torolutra* humerus from Lothagam, LT 25130, but is smaller and has a straighter shaft.

Fig. 4.7: Humeral specimens belonging to cf. *Torolutra* sp. a) lateral view of the right proximal humerus, ER 6076B. Note the poor condition and possible deformation; b-d) right humerus ER 389 in b) posterior, c) lateral, and d) superior view; e-g) proximal right humerus ER 4406A in e) posterior, f), medial, and g) superior view; h-j) distal right humerus ER 4406C in h) anterior, i) posterior, and j) lateral view.
Among the specimens that are not part of the partial skeleton, one of the best preserved is the right humerus, ER 389 (Fig. 4.7b-d). The superior portion of the head is very rounded in comparison to the flatter heads of terrestrial carnivorans. The head is curved to such a degree that it arches above the low greater tuberosity. The inferior portion of the head projects distinctly from the shaft. The deltoid crest extends posteroinferiorly almost to the midshaft, while the tuberosity is wide and nicely triangular. In terms of robusticity, the tuberosity is similar to that of *Aonyx*.

The shaft of ER 389 is curved, as in all mustelids. The posteriormost point of the shaft occurs where the deltoid tuberosity ends, slightly above midshaft. The S-shaped appearance of the shaft is accentuated by the large, curved supinator crest. The crest begins two-thirds of the way down the shaft and curves anteriorly before moving posteriorly to the lateral epicondyle. The shaft is slightly laterally offset from the olecranon fossa and trochlea. The medial epicondyle is large and supports a large entepicondylar foramen. As with the ER 5895T humerus, the medial epicondyle appears larger than in the Middle Awash *T. ougandensis* humerus as described by Haile-Sellassie (2008). The trochlea is relatively wide and flat, while the capitulum is rounded and wide. The olecranon fossa has a rounded triangular shape, as in many otter species. There is an unusual groove in the capitulum that is not seen in any modern otter and that may be pathological.

The humerus, ER 389, differs from *Aonyx* in several ways. The head projects less posteriorly and the shaft is angled to a greater degree than in *Aonyx*. The greater tuberosity has less of a median extension. The bicipital groove is therefore angled slightly more anteriorly with less of a shelf from the greater tuberosity bordering it. In addition, there is more of a distinction between the head and both tuberosities. The lesser tuberosity is more compact and extends more anteromedially, such that it does not extend as far medially as that of *Aonyx*. The deltoid tuberosity is angled more laterally and has less lateral lipping. The angle and curvature of the shaft is greater such that the distal end is much more medial. Increases in curvature suggest increased aquatic ability (Willemsen 1992). The supinator crest extends more posteriorly and begins slightly lower relative to the length of the shaft than in *Aonyx*. The epicondyle is more robust.

When compared to *Lutra*, ER 389 is similar in the angle of the greater and lesser tuberosities. The more pointed shape of the head and the increased shaft curvature seen in *Lutra* are more similar to this specimen than either *Lutra* or this specimen is to *Aonyx*.

Another possible *Torolutra* humerus (ER 4406; Fig. 4.7e-g) is in three pieces. The head (ER 4406B) does not conjoin with the other specimens, although the shaft (ER 4406A) and distal end (ER 4406C) do. The shaft and distal end are also pathological. This specimen is among the larger *Torolutra*-like material, but is not as large as ER 6076.

Other, more fragmentary humeral material tentatively referred to *Torolutra* include a proximal humerus (ER 3751) that is similar in size to ER 4406. There are also two left humeral shafts (ER 167, ER 5674) and a left distal shaft fragment (ER 5673). ER 5673 and ER 5674 do not conjoin, although they may be from the same individual, as discussed later in this section.

The right ulnar fragment (ER 6076A; Fig. 4.8a-c) includes the proximal portion of the right ulna from the olecranon process.
down to the proximal shaft. This proximal ulna is clearly lutrine. The olecranon process bends far to the medial side while the top of the trochlear notch is skewed slightly laterally so that the anconal process is directly above the radial notch. The medial portion of the olecranon process is broken. The medial coronoid process and anconal process protrude equally from the shaft. In medial view, the olecranon is relatively rectangular. The flat radial notch is anteriorly directed such that the radius is relatively anterior to the ulnar shaft. The shaft is narrow mediolaterally.

The left ulna of this individual (ER 6076C) is extremely weathered and only includes the proximal end. From what can be seen, it appears to have the same features as the right side. The distal ulna (ER 6076Q; Fig. 4.8d) is very short. From the side, it is very mitten-shaped, although the “thumb” portion does not project greatly. The distal end is very rounded in lateral view and the articulation is very narrow.

Several radii are known, although none are complete. Left proximal radius and shaft ER 6076D and left proximal end ER 48 share the same morphology (Fig. 4.9), although ER 6076D is relatively eroded. The head in both specimens is relatively flat and lima bean-shaped, but is not as elongated as in Mellivora. The anterior tubercle is large and causes the medial side of the head to be more superior than the lateral side. The bicipital tuberosity is large. The shaft is relatively round in circumference, with numerous muscle markings. The distal end of ER 6076D is missing, but the shaft flares just before it is broken, suggesting that not much is missing.

Two metacarpals (ER 44574, Fig. 4.10) are reasonably well-preserved. Metacarpal

Fig. 4.8: Ulnae belonging to partial skeleton ER 6076, cf. Torolutra sp. a-c) right proximal ulna ER 6076A in a) anterior, b) lateral, and c) medial view; d) lateral view of left distal ulna ER 6076Q.
2 (ER 44574A) includes the entire proximal half, with only the palmar portion of the articular surface missing. Metacarpal 5 (ER 44574B) is complete, although the palmar surface of the head is broken off. This specimen has the enlarged, but narrow and rounded head characteristic of lutrines. The shaft is relatively gracile. The medial lip of articulation with metacarpal 4 does not project very far medially. A similar condition is seen in the second metacarpal. However, given the partial preservation of the articular surface, little can be said about this specimen. These specimens are smaller and less robust than the lutrine metacarpals from South Turkwel (WT 37433; Werdelin and Lewis, 2000).

No definite metacarpals are known from partial skeleton ER 6076. One distal metapodial may be a fifth metacarpal due to the lateral slope of the head (ER 6076U). Another distal end (ER 6076W) is so fragmentary that it is impossible to tell whether it is a metacarpal or metatarsal.

**Pelvic limb**

Several femoral specimens from Koobi Fora have been referred tentatively to *Torolutra*. A proximal left femur, ER 75 (Fig. 4.11a-d), is identical in size but different in morphology from the presumed Aonyxini ER 5040. The
ARTICLE 4: FAMILY MUSTELIDAE

Fig. 4.10: Associated metacarpals of cf. Torolutra sp. a-b) left metacarpal ER 44574A in a), dorsal and b) proximal view; c-e) left metacarpal 5 ER 44574B in c) dorsal, d) medial, and e) proximal view.

Articular surface of the head is not as anteriorly rotated as that of ER 5040. Another difference from ER 5040 is the slightly greater lateral projection of the greater trochanter in ER 75. Other than these differences, the two femora are relatively similar. The specimen is broken just below the lesser trochanter.

In comparison to Lutra, ER 75 is relatively more gracile and has a longer neck. The greater trochanter is not as anteromedially oriented, while the lesser trochanter is oriented similarly to that of Lutra. The lesser trochanter extends further than in Aonyx and the greater trochanter is more curved medially at the superior end. The intertrochanteric fossa is deep and does not extend as far distally. As in Lutra, the head is not angled as far anteriorly from the shaft as is the head of Aonyx. The anterior surface of the head, however, is more rounded than in either extant taxon. The fovea capitis is also quite large.

A second femoral specimen, a left distal femur, ER 76 (Fig. 4.11e-f), is well preserved, with only the medial lip of the patellar groove missing. The shaft leading to the distal end is wide and the epicondylar regions are robust and rounded. The posterior surface of the shaft is flat leading to the condyles. The patellar groove is relatively deep, but the width cannot be assessed. The condyles are short and do not project far posteriorly or inferiorly. The femur is quite valgus. The intercondylar fossa is relatively wide. The tubercle for the lateral gastrocnemius is pronounced. No tubercle for the medial gastrocnemius is visible.

In general, ER 76 is quite similar to femora of Lutra, but is almost twice as large. The shape of the intercondylar groove differs from Lutra in that the anteriormost point is lateral. The lateral condyle is also more robust and there is more lateral angulation of the femoral shaft.

As might be expected, ER 76 differs from Aonyx in some features. For example, it is flatter anteroposteriorly. There is also much greater posterior projection of the medial condyle, a condition more similar to Lutra than Aonyx. The patellar groove, however, is more narrow and appears deeper than in either Lutra or Aonyx.

Like ER 75, ER 76 is of unknown provenience. It is certainly possible that they are from the same individual. Both were recovered in 1969.

Two well-preserved femoral shaft fragments (ER 5671, ER 5672) are also tentatively assigned to Torolutra. They are very similar to ER 75, although slightly smaller. The right
specimen (ER 5671) includes all of the proximal end except the head and neck and extends slightly below midshaft. The left specimen (ER 5672) includes the lesser trochanter and gluteal tuberosity. The lesser trochanter is large and projects laterally to a great degree. The shape of the shaft suggests a relatively short bone. The greater trochanter is similar in shape to that of ER 75.

Two patellae (ER 6076G and H) are known. Of these specimens, ER 6076G (Fig. 4.12a) is better preserved. In lateral view, the ventral surface of the superior end projects posteriorly to a great degree, rather than being flat, as in many carnivorans. The articular surface appears to continue onto this projection. This probably limited the range of movement. The apex is fairly pointed and the dorsal surface is flattened below the main insertion of the patellar tendon.

A right tibial shaft fragment (ER 5675), is tentatively assigned to *Torolutra*. This specimen is too fragmented to discern much.

A fragment of what may be a distal fibula is included in the ER 6076 skeleton. Only the portion of the lateral malleolus with
CHAPTER 4: FAMILY MUSTELIDAE

the groove for the fibularis longus and brevis tendons is preserved (ER 6076S). The processes around the groove are extremely rounded.

The left astragalus fragment (ER 6076F; Fig. 4.12b) includes the head and neck and the anterior portion of the trochlea. The medial astragalar facet projects medially from under the medial edge of the trochlea such that it forms a shelf jutting out from the neck. The head is very narrow and almost T-shaped. Relative to the axis of the trochlea, the head is offset to a great degree and the lateral edge of the head is just lateral to the medial edge of the trochlea.

The left navicular (ER 6076J; Fig. 4.12c) is more narrow mediolaterally than dorsoventrally. In distal view, the navicular looks like a rectangle with a pointed ventral apex. In proximal view, the facet for the astragalar head is very deep, reflecting the very curved head of the astragalus. This specimen articulates with the astragalus (ER 6076F).

The robust right cuboid (ER 6076N; Fig. 4.12d) is complete and does not seem distorted. The ventral groove is almost a canal, as an anterior lip of bone curls down to almost meet the larger posterior curled lip. The posterior lip projects further laterally. The calcaneal facet is an oval that is slightly arched dorsally. The metatarsal facet is very round with only a slight inferomedial indentation. The left cuboid (ER 6076P) is missing the ventral surface and projections.

Of the three cuneiforms, only the entocuneiform is known (ER 6076X; Fig. 4.12e). This specimen is relatively rectangular, with the proximoventral surface sloping distally. The distal surface is concave. The proximal articular surface is roughly kite-shaped, for articulation with the second metatarsal.

The proximal end of a possible first metatarsal is known (ER 6076V). This specimen is very slender, but flares at the base. It is very small in comparison to the other metatarsals.

The third metatarsal is incomplete and includes only the proximal half (ER 6076O). The classic T-shaped articulation of the third metatarsal is visible. The upper bar of the T is not particularly wide, suggesting that the metatarsals might be somewhat compressed (less so than in a hyenid, but more than in a felid).

The left fourth metatarsal (ER 6076K; Fig. 4.12f-g) includes the proximal end and a portion of the shaft. The articular surface

Fig. 4.12: Additional pelvic limb material attributable to cf. Torolutra sp. a) anterior view of patella ER 6076G; b) dorsal view of fragmentary left astragalus ER 6076F; c) proximal view of left navicular ER 6076J; d) ventral view of right cuboid ER 6076N; e) lateral view of entocuneiform ER 6076X; f-g) left fourth metatarsal ER 6076K in f) dorsal and g) proximal view; h) dorsal view of the distal end of the fifth metatarsal ER 6076T.
is unusual for carnivorans. While the specimen is recognizable, the articular surface is extremely wide mediolaterally. The facet for the cuneiforms is normal, but is angled such that the dorsal end lies far lateral to the ventral end. This leaves a wide area of articulation for the third metatarsal. This suggests a highly splayed set of metatarsals.

The poorly preserved proximal (ER 6076R) and distal (ER 6076T) portions of the fifth metatarsal are known. The proximal end expands greatly as in a fifth metacarpal, but the ventral surface is excavated such that the lateral expansion is just a concave shelf in ventral view. Another curved ridge of bone projects proximally just lateral to a groove.

The distal end (ER 6076T; Fig. 4.12h) has the sloping head of a metatarsal 5. The head is very narrow mediolaterally and a little pointed. In contrast, the shaft seems wide mediolaterally. This specimen does not conjoin with the proximal fifth metatarsal, but may only be lacking a small bit of bone.

Phalanges
Five phalanges from the partial skeleton have been found (ER 6076L). These specimens vary in size and are very fragmentary. There is one small complete specimen and a slightly larger specimen that is missing the head. The largest phalanx is one of two proximal specimens. There is also a very curved flat proximal phalanx that is missing the base and some of the shaft.

REMARKS

As is the case with the material described as T. cf. T. ougandensis, the above listed postcranial material is most compatible with assignment to Torolutra. However, in the absence of associated craniodental material and in view of the poor preservation of the partial skeleton ER 6076 in particular, we prefer to leave the taxonomic assignment of the material open.

That said, it is worth noting that specimens ER 5671, 5672, 5673, 5674, and 5675 are all shaft fragments from Area 105, the same area where the maxilla ER 1499, here assigned to Mustelidae indet. was found. This fragmentary postcranial material all shares the same field number, with ER 1499 having the consecutive field number. This material may represent one individual and is smaller than the other material.

Genus Hydrictis Pocock, 1921

Type species: Lutra maculicollis Lichtenstein, 1835

Generic diagnosis: Differentiated from sympatric clawless otters (Aonyx capensis and A. congicus) by smaller size (3–5 kg versus 12–18 kg for Aonyx), slimmer body, white markings on neck, fully webbed forefeet, and presence of claws on all 4 feet. (Modified from species diagnosis of Larivière 2002b – see further below.)

Stratigraphic range in Africa: Early Pleistocene – Recent based on FAD in the Upper Burgi Mb, Koobi Fora Fm (≤ca 2.0 Ma).

Stratigraphic range at Koobi Fora: Early Pleistocene based on FAD and LAD in the Upper Burgi Mb (ca 2.0 Ma – 1.87 Ma).

REMARKS

The spotted-necked otter, Hydrictis maculicollis has most commonly been considered a species of Lutra, although some have accorded it generic status (Davis 1978; Pocock...
1921). More recently, molecular phylogenetic studies have found the genus *Lutra* to be paraphyletic and have split the included species among the genera *Lutra*, *Lontra*, and *Hydrictis*, with the latter as sister taxon to *Enhydra*, the sea otter, albeit with a deep split separating them (Koepfli and Wayne 2003; Koepfli et al. 2008). This makes diagnosing the genus on the basis of morphology difficult. We have therefore retained the diagnosis given above despite its limited value for diagnosing fossils. There is little risk of generic confusion, as *Lutra* is not known from sub-Saharan Africa. The assignment of the material described below is thus based on its similarity to the extant *H. maculicollis*, but also on the much greater probability that it belongs in *Hydrictis* than in *Lutra*.

*Hydrictis gudho* sp. nov.

*Fig. 4.13*

Specific diagnosis: Lutrine larger than *Hydrictis maculicollis* and smaller than *Torolutraougandensis*; Mandibular ramus tall but narrow; m1 short and wide; proportions similar to those of *H. maculicollis*, but widest point mesial to metaconid; talonid basined; lingual cingulum prominent.

*Holotype:* KNM-ER 1486, neurocranium with attached posterior part of a left mandible with m1, and distal half of p4, anterior part of snout with roots of I3, C, P1, complete P2, and posterior part of right mandible with m1 and alveolus of m2.

*Horizon and locality:* Upper Burgi Member of the Koobi Fora Formation, Area 130 of the Karari Ridge. Age between ca 2.0 Ma Ma and 1.87 Ma (KBS Tuff; Brown 1994).

*Hypodigm:* Holotype only.

*Etymology:* From the Dassenech *gudho* meaning big, in reference to the greater size of this species compared to extant *Hydrictis*.

**KOOBI FORA MATERIAL**

ER 1486 is a neurocranium with attached posterior part of a left mandible with m1, and distal half of p4, anterior part of snout with roots of I3, C, P1, complete P2, and posterior part of right mandible with m1 and alveolus of m2 (4.13a-e). The neurocranium is broad, expanding posteriorly from the postorbital constriction to the nuchal crests to give it a triangular outline in dorsal view. The sagittal crest is broken, but was clearly low. The specimen is damaged and shows no sign of the lyroform crests. The nuchal crests are low. The nuchal region is badly damaged, but was low and wide. The foramen magnum is small. The basicranium is damaged, preserving only some of the left auditory bulla, which has a long and robust bony external auditory meatus. The bulla itself is small and uninflated.

The mandible has a small, vertically ascending coronoid process. The masseteric fossa is relatively deep and reaches nearly to the distal end of m2. There is too little of the p4 remaining for morphological description, aside from noting that there was only a very short shelf distal to the main cusp. The m1 is very worn on all cusps. The paraconid is angled at 30 degrees to the sagittal plane and has a subtriangular base. The protoconid is more in line with the sagittal plane and is a truncated ellipse, as the distal end of the main cusp is worn nearly vertical. The metaconid is level with the distal half of the protoconid and its distal end is also worn nearly vertical. The tooth is broadest at the metaconid. The talonid is worn nearly flat, but it is evident that it was narrower than the widest point of the trigonid, and tapering to-
wards the rear. It is clear that, unlike in *Torolutra*, the talonid was basined. There was a ridge-like hypoconid, while the other talonid cusps are worn away. The m2 is small and slightly wider than long. It is oriented with its occlusal surface nearly vertical, at 90° to m1. The right p4 was apparently lost in life and the alveolus is closed. The upper premolars are squeezed-in lingual to the canine (especially P1, which lies entirely lingual to the canine).

**REMARKS**

The holotype of *Hydrichtis gudho* differs morphologically from the material described as *Torolutra* herein mainly in its smaller size and differently proportioned m1, with its basined talonid. This clearly distinguishes ER 1486 from the trenchant talonid group comprised of *Vishnuonyx* and *Torolutra* and places it with the extant genera *Lutra*, *Lontra*, and *Hydrichtis*. Of these, *Hydrichtis* is the only genus present in Africa today.

In the fossil record, the only species that may possibly be referable to *Lutra* is *L. fatimazohrae* from Ahl al Oughlam in Morocco (Geraads 1997). That a North African species may belong to the Eurasian genus *Lutra* is not implausible, but the likelihood that the same would apply to an eastern African species is slim. In addition, Fig. 4.6a shows that ER 1486 differs greatly from *L. fatimazohrae* in size as well as in morphology. Therefore, we here refer ER 1486 to a new species of *Hydrichtis* that is markedly larger than the living species.
KOOBI FORA MATERIAL

Specimen ER 3778 is a nearly complete skull with damaged nuchal region, zygomatics, and snout (Fig. 4.14). The ventral side of the skull is strongly abraded and part of the braincase on the right side is missing. There are alveoli for C, P1, and P4 and broken left P2 and P3 and right P3 and P4. Due to the damage to the specimen there are few features that can usefully be described.

ER 395 is a damaged snout with alveoli for I1-I3, C, right and left P1, roots of left P2-P3. The specimen is worn and abraded but shows features very similar to those of ER 1486 and ER 3778.

REMARKS

Neither ER 3778 nor ER 395 presents characters useful for taxonomic identification, though both are clearly lutrine. However, they match in size specimen ER 1486 and we suggest that they may belong to *Hydrictis*, though we leave them in open nomenclature. ER 3778 also in-

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Fig. 4.14: cf. *Hydrictis* sp., damaged partial cranium ER 3778. a) dorsal view; b) ventral view; c) left lateral view.
cludes an ulna fragment that is larger than the homologous element in modern *Lutra lutra*, which is also the case with *Hydrictis gudho* sp. nov., as described above.

**Genus Aonyx Lesson, 1827**

*Type species:* *Lutra capensis* Schinz, 1821

*Generic diagnosis:* Dentition more robust than *Lutra*; teeth broad; P4 with large talon, protocone elongated, extending distally nearly to the metacone, no hypocone; m1 with talonid broader than trigonid, hypoconid present, smaller than hypoconid, buccal cingulum of talonid strong. (After Willemsen 1992).

*Stratigraphic range in Africa:* Early Pleistocene – Recent based on FAD in Olduvai Bed I (≤1.92 Ma).

*Stratigraphic range at Koobi Fora:* Early Pleistocene based on FAD and LAD in the KBS Mb (1.87 – 1.56 Ma).

**REMARKS**

As is the case with *Hydrictis, Aonyx* is very poorly known in the fossil record. The stratigraphic records above are based on those few specimens that have been specifically referred to the genus (Petter 1973). Other Aonyxini have been described, but their generic attribution is not clear (Peigné et al. 2008; Werdelin and Dehghani 2011).

**cf. Aonyx sp.**

Fig. 4.15

**KOOBI FORA MATERIAL**

The morphology of the right femur, ER 5040 (Fig. 4.15), is more similar to that of modern *Aonyx* than to any other otter. This specimen is much longer than that of most extant otters, including the giant otter *Pteronura*, and is within the upper limits of sea otter (*Enhydra*) femoral length. Despite its length, it is relatively gracile in comparison to both the slightly larger lutrine femur, ER 3881 (see below), and extant *Enhydra*. ER 5040 is similar in size to femora tentatively assigned to *Torolutra*, although the two differ in their proportions.

The articular surface of the head does not extend inferiorly, meaning that this surface is oriented superiorly. Unlike in the much larger bunodont otter *Enhydriodon* (Lewis 2008), the neck does not angle any more superiorly than in extant *Aonyx*. As in ER 3881, the flattened edge of the head occurs more posteroinferiorly than in material attributed to *Torolutra* (ER 75). The neck originates slightly more anteriorly on the shaft than in ER 3881.

The greater trochanter is more pointed and straighter than in ER 3881 and projects further superiorly than in *Aonyx*. The intertrochanteric fossa is deep and narrow and extends superiorly onto the posterior surface of the greater trochanter. The lesser trochanter is smaller and there is less of a connection between the intertrochanteric crest and the lesser trochanter. The lesser trochanter projects more posteriorly than medially. It does not extend beyond the medial edge of the shaft.

The shaft is relatively gracile. There is only a slight increase in width proximally and distally. Thus, the distal end flares outward abruptly from the shaft in contrast to a *Melivora*- or *Enhydriodon*-like distal femur. The ridge for the adductors is sharp and runs from the greater trochanter down the posterolateral edge to about midshaft. The insertion of the lateral head of the gastrocnemius is indicated only by the slightest of bumps that is percep-
Fig. 4.15: Complete right femur ER 5040 tentatively assigned to *Aonyx*, although it is larger than extant members of this genus. a) anterior view; b) posterior view; c) medial view; d) proximal view; e) distal view.

tible more by touch than vision. The patellar groove is relatively more narrow than in *Aonyx*. The groove also extends more anteriorly, making the specimen wider anteroposteriorly than *Aonyx*.

The condyles project far posteriorly, similar to those of *Aonyx*. The medial condyle projects more posteriorly and only slightly more inferiorly than the lateral. As a result, the femur is only slightly valgus.

A complete femur from Toros Menalla, TM 219-05-001 was also assigned to cf. *Aonyx* (Peigné et al., 2008). ER 5040 is nearly identical in size to this specimen and the morphology is quite similar. ER 5040 differs from TM 219-05-001 in being more gracile, particularly in the neck and the shaft. The distal end of ER 5040 is slightly more narrow mediolaterally, yet slightly wider anteroposteriorly.

**REMARKS**

Extant *Aonyx capensis* is distributed across portions of western, eastern and southern Africa (Nowak, 2005). The Congo clawless otter is often placed in a separate species, *A. con-
Aonyx is relatively rare in the African fossil record, even though it has been recorded in both eastern and southern Africa localities (albeit the southern African material is exclusively Middle and Late Pleistocene, cf. Werdelin and Peigné 2010), suggesting a distribution not unlike extant forms. The Koobi Fora Aonyx is larger than extant Aonyx, although it was by no means “giant” in the sense of Enhydriodon. This specimen represents the only occurrence of Aonyx-like species at Koobi Fora. Although rare, the presence of this taxon at Koobi Fora is not surprising given the paleohabitat reconstructions of the Koobi Fora region (Brown and Feibel 1991; Feibel et al. 1991).

Molecular studies have suggested that Aonyx may have originated in Eurasia during a burst of mustelid diversification in the Pliocene (Marmi et al., 2004; Koepfli et al., 2008). However, given the possible affinities of the Late Miocene Toros Menalla femur to Aonyx, the origination point of Aonyx in time and space may need to be reconsidered. As noted above, ER 5040 is quite similar in size and morphology to the Toros Menalla cf. Aonyx femur, but is more gracile. It is quite possible that the Toros Menalla femur represents either an early Aonyx or immediate ancestor, while the 4-5 million years younger Koobi Fora femur represents a slightly more derived, gracile form.

**Lutrinae gen. et sp. nov.**

*Fig. 4.16*

**Stratigraphic range at Koobi Fora:** Early Pleistocene based on FAD and LAD in the Upper Burgi Mb (ca 2.0 Ma – 1.87Ma).

**KOOBI FORA MATERIAL**

Specimen ER 3881 is a robust left femur (Fig. 4.16) that is quite distinct from the other mustelid material from Koobi Fora. Despite being only slightly larger than the Koobi Fora Aonyx and Torolutra material, it is quite different in morphology and much more robust.

The head is round and large relative to the overall size and the neck is short and thick. The fovea capitis is very large and pear shaped. The articular surface of the head extends onto the femoral neck, as in carnivorans that walk with abducted limbs (e.g., Heinrich and Houde 2006). This feature is common in otters and particularly pronounced in Lontra. The head is large, round and robust and the neck is quite short. On the posterior surface, there is an extremely large tubercle for the capsular ligament just inferolateral to the lateral extension of the articular surface.

The greater trochanter does not extend above the level of the head. The intertrochanteric fossa extends superiorly as a groove medial to the greater trochanter. It does not extend all the way to the lesser trochanter.

The lesser trochanter is unusually regular in shape for a carnivoran and is circular in cross-section. It projects primarily medially and slightly posteriorly. This is what one tends to find in climbing carnivorans (Heinrich and Houde 2006) or in some swimming carnivorans (e.g., Lontra).

The tubercle for the insertion of the lateral head of the gastrocnemius is pronounced and excavated inferiorly. There is no mark in the region of the medial head. The fabellar pits are not particularly large, although the medial one is more pronounced. The medial epicondyle is larger than the lateral. The shaft broadens distally to meet the epicon-
Fig. 4.16: Complete left femur ER 3881 of Lutrinae gen et sp. nov. in a) anterior, b) posterior, c) medial, d) proximal, and e) distal view. Note the robusticity of the specimen.

dyles.

When stood on its condyles, this specimen is very valgus. However, when oriented this way, the patellar groove is oriented straight supero-inferiorly. Not surprisingly, the patellar groove is relatively deep and wide with a lateral lip that is more pronounced than the medial lip.

The distal end is robust, short and squat with short, thick condyles. The shaft is robust. The length of the entire specimen is relatively short in comparison to the size of the distal end.

This specimen does share some general similarities with *Aonyx*. The morphology of the shaft and medial condyle and placement of the lesser trochanter are more like *Aonyx*. However, this specimen also differs in numerous ways from the *Aonyx*-like ER 5040 (Fig. 4.14). ER 3881 is slightly longer, but is much more robust than ER 5040. The head, shaft and distal end are all much larger relative to the overall size of the specimen. In medial view, the origin of the neck is more in the midline than that of ER 5040. The neck is short and thick and supports a less superiorly rotated head. The distinction between the inferior surface of the head and the neck is slight in comparison to that of ER 5040. The greater trochanter is wider
and appears to project more anteriorly, although this region is broken in ER 5040. It is clear, however, that the greater trochanter does project slightly less proximally than in ER 5040. The lesser trochanter is larger and more laterally projecting than in ER 5040. As one moves distally, the shaft widens to a greater degree than in ER 5040. While the robust epicondyles are more rounded, they are similar in the amount of projection. The condyles, however, do not project as far posteriorly. The overall effect is of a much less valgus knee than in ER 5040.

Specimen ER 3881 is also somewhat similar to the older cf. Aonyx specimen from Toros Menalla (TM 219-05-001; Peigné et al. 2008), although much of the similarity is due to the robust nature of both specimens. As discussed above, while superficially similar to Aonyx, ER 3881 is unlikely to belong to this genus. ER 3881 differs from the Toros Menalla femur in the possession of a relatively larger head and even thicker neck. The distal end is quite similar, but appears to be even larger relative to the shaft than in TM 219-05-001.

REMARKS

Everything about the ER 3881 femur is robust; even the muscle scars are rugose. While this specimen is similar to Lontra (e.g., the northern river otter, L. canadensis, and the marine otter, L. felina), it is roughly twice the size of the larger of the two (L. canadensis). There are some similarities to Pteronura and a few to Aonyx, but none to Enhydra.

This specimen is similar to the larger Enhydriodon material. The head is round and large relative to the overall size. The neck is short and the greater trochanter protrudes anteriorly as a large triangular wedge, as with large Enhydriodon material. The overall proportions are similar to those of larger Enhydriodon. ER 3881 is smaller and quite morphologically distinct from the Langebaanweg Enhydriodon, the smallest representative of this genus in Africa. The Langebaanweg femur, however, is also distinct from eastern African Enhydriodon femora (Lewis 2008).

The general similarity to the Toros-Menalla femur TM 219-05-001 cannot be ignored. Peigné et al. (2008) note the difference in size and morphology between their specimen and S. beyi, which itself differs in morphology from other eastern African Enhydriodontini, as discussed above. It is possible that the Toros-Menalla femur belongs to a primitive otter that persists into the Upper Burgi, becoming a little larger (from 129 mm to 135.8 mm in total length) and more robust. Proportions of the articular surfaces, in particular, would increase relative to overall size. Given the lack of material other than femora, it is not possible to say whether this lineage has relationships to other extant or extinct African otters. As did Peigné and colleagues, we prefer to wait for future discoveries before erecting a new species and possibly genus for this material.

Lutrinae gen. et sp. indet.

Fig. 4.17

KOOBI FORA MATERIAL

Specimen ER 2036 includes both craniodental and postcranial elements. However, while the craniodental material is extremely fragmentary and difficult to identify, the ER 2036 postcranial elements are clearly those of an elderly lutrine. The postcranial material includes both thoracic and pelvic limbs and axial elements. All show signs of age-related degeneration.

The left humerus is fragmentary and includes only the proximal half (ER 2036A;
Fig. 4.17a-c) and the distal shaft (ER 2036E). Only the shaft is known from the right humerus (ER 2036D). The humeral head is very rounded. The greater tuberosity is short and the head projects proximally to a great degree. The lesser tuberosity projects medially, but not to a great degree. There is some slight lippling of the edge of the greater tuberosity over the groove, although this may be age-related growth.

The deltoid tuberosity forms a triangle (with the apex distal) leading to the greater tuberosity, as in all carnivores. The shaft bends at about a 30° angle at the point of the deltoid tuberosity, such that the midpoint of the shaft is far anterior to the head, as expected in lutrae.

The fragment of the left os coxae (ER 2036J; Fig. 4.17d) includes two-thirds of the acetabulum and a part of the ilium. A portion of the sacroiliac articular surface is present. The distal right femur (ER 2036B; Fig. 4.17e-f) includes the distal shaft and part of the distal end. The medial condyle is broken off and the entire specimen is eroded. It looks very much like ER 76, but is somewhat smaller. The patellar groove is relatively wide and the lateral and medial lips appear relatively similar in height with the deepest portion being in the middle of the groove.

A proximal right tibia (ER 2036C; Fig. 4.17g-h) is also preserved. The tibial tuberosity does not extend very far anteriorly. Although there is some excavation under the lateral side of the tuberosity, it is not as extensive as in canids or felids. The area of insertion of the patellar tendon is placed relatively high. The lateral condyle is much wider mediolaterally and sits at a more proximal level than the medial condyle. The lateral condyle laps onto the intercondylar eminence, so there is not a distinct eminence separate from the condyle.

The intercondylar region is very narrow as the condyles are very close together.

A distal right calcaneum with sustentaculum tali (ER 2036U; Fig. 4.17i) is known from this individual. The carpal articulation is also preserved.

A fragmentary distal half of a left metapodial (ER 2036K) may be a metacarpal 4, based on the symmetry of the head and shape of the shaft. It is smaller and less robust than the ER 6076 proximal fourth metatarsal. As one proceeds distally, the shaft flattens out to a slight degree.

Several vertebral centra are present (ER 2036M, N, O, Q), although not all are complete. Two caudal vertebrae (ER 2036R, S) and a spinous process fragment (ER 2036T) are also present. One sternebra is preserved (ER 2036P), while an additional fragment may be a rib (ER 2036L).

The sacrum (ER 2036I; Fig. 4.17j) is quite large and consists of three vertebral elements. The right transverse process of the first vertebra and part of the second is broken off. The spinous processes are broken off and the third neural arch is missing. The left side is reasonably well-preserved. The right side of the proximal portion of the centra is broken off. The specimen is large and robust in comparison to the femur. The auricular surface is very rounded although overall it is oval in shape. The ventral surfaces of the centra are relatively concave. The fusion of the centra is still visible due to a raised lip marking the fusion, although they have certainly been fused for some time. The caudal articular surface of the last centrum is quite large, suggesting a large tail. The three centra are long and wide. The medial processes present on the cranial end, however, indicate that much of the mediolateral width is due to the centra and not the transverse processes.
REMARKS

The partial skeleton ER 2036 is a relatively old individual. There is some osteophytic lipping on most of the articular surfaces. There is also some evidence of osteoporosis, but the preservation of the surface of the bones makes this hard to assess. It looks as if many of the joint surfaces have collapsed in on themselves. Thus, it looks rather different from other lutrines in all weight-bearing areas.

While the morphology of this specimen is clearly lutrine, it is smaller than the other Koobi Fora lutrine postcrania. As such, it falls within the size range of the second largest extant otters, the giant otter (*Pteronura*), and is smaller than the extant sea otter, *Enhydra*. It is slightly larger than extant *Aonyx capensis* and much larger than *H. maculicollis*, the two extant African otter species. However, as noted above, the morphology is most like material tentatively assigned to *Torolutra*. It is possible that this could be a small *Torolutra*, although the material is quite small even given age-related degeneration. While this material is the same age as the Koobi Fora *Hydricits* specimens, it seems quite large to belong to that species. Thus, given the smaller size and poor condition, it is at present best to leave this as an indeterminate lutrine.
Subfamily **Mellivorinae** Gray, 1865

**Genus Mellivora** Storr, 1780

*Type species:* *Viverra ratel* Sparrman, 1777 (=*Viverra capensis* Schreber, 1776)

*Generic diagnosis:* Large-sized Mustelidae; molar dentition reduced, dental formula I 3/3, C 1/1, P 3/3, M 1/1; premolars slender, m1 with short, trenchant talonid, metaconid low; M1 anteroposteriorly shortened, paracone and metacone small.

*Stratigraphic range in Africa:* Late Miocene – Recent based on FAD in the Adu Asa Fm., Ethiopia (≤ca 5.8 Ma).

*Stratigraphic range at Koobi Fora:* Early Pleistocene based on FAD in the Upper Burgi Mb (≤2.0 Ma) and LAD in the Okote Mb (≥1.38 Ma).

**REMARKS**

The extant honey badger or ratel, *Mellivora capensis*, is distributed across Africa and the Indian subcontinent. African mellivorines can be traced back to the Late Miocene with genera such as *Erokomellivora* from Kenya (Werdelin 2003b) and *Howellictis* from Chad (Bonis et al., 2009). *Erokomellivora* and *Howellictis* are both smaller than extant *Mellivora* and their postcranial morphology is unknown. Craniodentally, they are both more primitive than the extant genus.

Three species of *Mellivora* have been described from the fossil record of Africa. The oldest of these is *M. benfieldi* from Langebaanweg, which may be the starting point of the modern *M. capensis* lineage (or even conspecific with it (Hendey 1974, 1978; Petter 1987). Further material attributed to *M. aff. benfieldi* has also been reported from the Middle Awash (Haile-Selassie and Howell 2009), while material of the modern species has been described from a number of later Pleistocene sites in South Africa (Hendey 1974). The third described species species, *M. carolae* from Morocco, is only known from dental specimens, none of which have been figured, but from available information appear very similar to extant *M. capensis* (Michel 1988).

*Mellivora* sp.

Figs. 4.18 – 4.19

**KOObI FORA MATERIAL**

**CRANIODENTAL**

ER 3760 is a right posterior part of mandible lacking ascending ramus, but with a complete m1 (Fig. 4.18). The ramus is slender, with a narrow and tall cross-section. The masseteric fossa reaches anteriorly to just behind the distal end of m1. This tooth is long and slender, with relatively low cusps. The paraconid is lower than the protoconid. There is no metaconid. The talonid is single-cusped, retaining what appears to be the entoconid. This cusp is set in line with the paraconid and protoconid.

**POSTCRANIAL**

ER 44387 includes os coxae, right and left femora, and some additional postcranial fragments. This material belongs to a subadult individual. The os coxae fragments (ER 44387C, D, E) are almost too fragmentary to describe. While the acetabulum is present in ER 44387C, only in ER 44387D can it be seen to be quite wide. The final fragment, E, is a portion of the left ilium with a piece of the ac-
etabulum.

The right femur is missing all epiphyses (ER 44387A; Fig. 4.19a). Although this specimen is also damaged, the shape of the shaft is well-preserved and typical of mellivorines. This specimen is within the size range of modern *Mellivora*.

The left femur (ER 44387B; Fig. 4.19b) is better preserved, but only includes the proximal half of the specimen. The epiphysis of the head was clearly not fused, indicating that this was a subadult. The shaft is wide mediolaterally and flattened anteroposteriorly. While the intertrochanteric fossa is not well-preserved, it appears to have continued under the lateral wall formed by the greater trochanter. This individual was already within the size-range of extant *Mellivora capensis*, despite not being fully grown.

**REMARKS**

Given the subadult nature of ER 44387, it is likely that this individual would have been larger than extant *M. capensis* and *M. benfieldi*. The mandible, ER 3760, on the other hand, is close in size to the extant species. We conclude that these poorly preserved specimens are inadequate to allow any specific attribution for the Koobi Fora *Mellivora*.

Subfamily indet.

**Mustelidae indet. aff. Plesiogulo sp.**

Fig. 4.20

**KOOBI FORA MATERIAL**

Although similar to extant *Gulo* and *Mellivora*, the left distal femur ER 5476 is much larger than either of these taxa (Fig. 4.20). Unfortunately, the specimen is cracked and eroded.

![Fig. 4.18: Mellivora sp., ER 3760, right ramus. a) buc- ceral view; b) lingual view; c) occlusal view.](image)

The lateral condyle is eroded, as are the edges of the patellar groove. Despite this erosion, the patellar groove seems relatively deep with a steep medial lip. The medial condyle is large, but does not project far posteriorly. The lateral condyle is so eroded that it cannot be assessed. The shaft is wide and flat as it approaches the condyles. There does not appear to be an obvious tubercle for the lateral gastrocnemius.

**REMARKS**

The morphology of the ER 5476 femur is clearly not that of a felid or ursid, but is most consistent with a non-lutrine mustelid. For example, in comparison to the giant otter *Enhydriodon*, the patellar groove is not angled relative to the long axis of the femur and is more compact mediolaterally. The entire distal femur indicates a less abducted femur than in *Enhydriodon*.

Large, non-lutrine mustelids can be found in eastern Africa beginning in the Miocene. The giant, cursorial mustelid *Ekorus* occurs in Late Miocene levels at Lothagam...
Fig. 4.19: Femora of subadult *Mellivora* specimen ER 44387. a) anterior view of right femur ER 44387A; b) anterior view of left femur ER 44387B. Note the missing epiphyses and overall fragmentary nature.

(Werdelin 2003b) and may be related to the Miocene Eurasian genus *Ischyrichtis*, which includes large, hypercarnivorous forms (Werdelin and Peigné 2010). *Ekorus* includes a nearly complete skeleton, but has a unique distal femoral morphology quite unlike that of ER 5476.

The musteline *Eomellivora tugenensis* has been named based on craniodental material found in the Ngorora Fm., Kenya (Morales and Pickford 2005a). This species is about the size of the extant honey badger, *Mellivora capensis*, and thus would be much smaller than the ER 5476 femur. Eurasian *Eomellivora* are larger, but their postcranial morphology is largely unknown.

*Plesiogulo* has a widespread distribution, with fossils found at localities in North America and Eurasia (e.g., Harrison 1981; Koufos 1982; Kurtén 1970; Teilhard de Chardin and Leroy 1945). Within Africa, it is known from Langebaanweg, South Africa (Hendey 1978), Middle Awash, Ethiopia (Haile-Selassie et al. 2004), and Lemudong’o, Kenya (Howell and García 2007).

*Plesiogulo monspessulanus* from Langebaanweg includes numerous postcranials, including femora belonging to the partial skeleton L40042 (Hendey 1978). This postcranial material is quite similar to extant *Gulo*, although much larger and more robust. Some of the differences between *Plesiogulo* and *Gulo* may be attributable to the large differences in size, although Hendey (1978) notes that *Plesiogulo* may have had a more plantigrade pes. While Hendey (1978) reports an estimated femoral length for this individual (L40042; c215 mm), the right femur is missing the distal end and the left has only a portion of the medial condyle preserved (Lewis, personal observations). Thus, the greater part of the distal morphology is not preserved for comparison with ER 5476. If the femoral proportions were the same in *P. monspessulanus* as they are in extant *Gulo*, then one would predict a much larger distal end given the size of the L40042 proximal end than is seen in ER 5476. The bicondylar width of ER 5476 is roughly 40.2 mm, while the predicted bicondylar width of L40042 would be more than 50 mm.

As there is not really any comparable material from Africa, the affinity to *Plesiogulo* is based on the affinities of ER 5476 to *Gulo* and the extreme size of this specimen. However, the possibility that this is a large melli- vorine cannot be ruled out based on the fragmentary nature of the specimen. Despite its
Fig. 4.20: Fragmentary left distal femur ER 5476 Mustela indet. aff. Plesiogulo sp. a) anterior view; b) medial view.

size, ER 5476 does have similarities to extant Mellivora and could belong to a large member of this genus. However, ER 5476 would have been from a much larger individual than has been found within any known African species of Mellivora (see above).

Mustela indet. aff. Ictonyx sp.

Fig. 4.21

KOObI FORA MATERIAL

The right calcaneum ER 3097 (Fig. 4.21) is similar to that of modern Ictonyx in appearance, but is much larger. The shape of the ventral side of the calcaneum, the flattened nature of the sustentaculum tali, and the lateral projection of the articular surface for the cuboid are typical of Ictonyx.

In dorsal view, the proximal half of the bone slopes gently medially, but turns almost immediately laterally before proceeding proximally. This results in the dorsal surface of the proximal half having a somewhat squared off tuber calcanei in dorsal view. The lateral turn is actually a lateral ledge, such that the ventral side of the proximal end is narrower mediolaterally than the dorsal side. In medial view, the ventrum is somewhat arched, not flat.

REMARKS

Ictonyx is known from across sub-Saharan Africa (I. striatus; Larivière 2002a) and around the northern, western and southern fringes of the Sahara (I. lybica; Hoffman et al. 2008). Their fossil record stretches from 2.5 Ma to the Recent of southern and northern Africa (Geraads 2008; Klein et al. 2007; Werdelin and Peigné 2010). This record includes only the extant taxa, as the extinct species “I.” bolti from Bolt’s Farm, South Africa (Cooke 1985) was transferred to the genus Prepoecilogale (Petter and Howell 1985). Both Ictonyx and Prepoecilogale (and the extant Poecilogale) are much smaller than this specimen. As a point of reference, the total length of the ER 3097 calcaneum (41.7 mm) is closer to the total length of the femur of extant I. striatus (52 mm average) than to its calcaneum (14 mm average). Given all of the above factors, it is unlikely that the specimen belonged to, or was closely related to, the genus Ictonyx. It is possible, however, that it represents a hitherto undocumented African branch of the subfamily Galictinae, to which Ictonyx belongs (Koepfl et al. 2008).

Mustela indet.

Fig. 4.22

KOObI FORA MATERIAL

ER 1499 is a maxilla fragment with partial right P4 and posterior root of P3. The tooth is of mustelid morphology, lacking a carnassial
notch and with only a very minute parastyle. The protocone is missing but the attachment between the protocone and paracone/para-
style was long, indicating that the specimen may belong in the Lutrinae. In size, the P4 matches the alveoli for P4 in ER 3778. The parastyle is minute, with a trace of a mesial cingulum cusp. There is a marked ridge from the mesial end of the tooth to the apex of the paracone and another from the mesiolateral side of the protocone shelf to the paracone apex. The metastyle was short and low, while the metacone is much worn, obscuring its true height. The carnassial shear from paracone to metacone is straight, unlike that in most Lutri-
nae in which it is gently curved. Also, there is no clear buccal cingulum bordering the meta-
style, unlike in the majority of Lutrinae. The specimen is heavily worn, which makes de-
termination difficult. However, it likely repres-
ts a lutrine, but does not match any of the other lutrines described above in morphology.

ER 4437 is a possible canine fragment with the tip of the crown broken off. There is a horizontal wear facet on the posterior face near the base of the crown. The crown is nearly round. The root is much more robust than the crown of the tooth. The roundness of the crown and the robust root, along with the wear facet, suggest that this may be a canine and if so it is of a mustelid of moderate size.

ER 3752 is a fragmentary proximal right ulna (Fig. 4.22) that is missing the olecranon process. Although the radial notch is broken, it appears to have been relatively short and anteriorly placed. The medial coronoid process is canid-like in being short and narrow. The preserved portion of the posterior edge of the specimen is rounded.

In comparison to living mustelids, this ulna is similar in morphology and size to the extant Eurasian badger, *Meles meles*. The posterior edge of the shaft is curved behind the semilunar notch. The medial coronoid process is relatively narrow and does not flare far medially. This condition is in contrast to that seen in extant *Mellivora*, where the medial coronoid process is much wider and flares more medially. *Mellivora* also has a straighter posterior edge of the shaft behind the semilunar notch. The narrowness of the medial coro-
noid process is viverrid-like, but none of the other morphology is.

In comparison to ER 6076A, the ER 3752 ulna is much smaller and less robust. The semilunar notch and medial coronoid process are more mediolaterally compressed than in ER 6076A. Other than that, there are some similarities, such as the shape and configura-
tion of the ulnar shaft posterior and inferior to the level of the medial coronoid process. In comparison to ER 3762, Carnivora indet., the medial coronoid process is not as tilted, but is flat (i.e., the surface is roughly perpendicular to the main axis of the bone).
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Ursids are currently not present in Africa. It has often been assumed that they became extinct in the sub-Saharan portion of the continent in the earliest Pliocene, with Langebaanweg (ca 5 Ma) as the last record (Hendey 1980). However, a minimum of three specimens from Koobi Fora testify to the presence of at least one, and possibly two species of bears in eastern Africa up until about 2.5 million years ago.

The fossil record of ursids in Africa is limited to two named species of *Agriotherium* (*A. aequatorialis* and *A. africanum*) from Kenya and South Africa, respectively (as well as several records of *Agriotherium* unassigned to species), two named species of *Ursus* (*U. arctos* and *U. etruscus*) from northern Africa, *Indarctos arctoides* from Algeria, and *Hemicyon* sp. from Kenya.

The record of *Hemicyon* (subfamily Hemicyoninae) is restricted to a single tooth from the early Miocene site of Rusinga, although this specimen may actually belong to the related genus, *Phoberocyon* (Schmidt-Kittler 1987; Werdelin and Peigné 2010). *Indarctos* is also known from a single record at the late Miocene site of Menacer, Algeria (Thomas and Petter 1986). These genera are quite different morphologically from members of the genus *Ursus*.

Members of the extant genus *Ursus* have been recorded in the northern African fossil record in the form of *Ursus etruscus* and *U. arctos*. *U. etruscus* appears in Africa by the mid-Pliocene (Werdelin and Peigné 2010). Although this species in some scenarios is ancestral to modern brown bears, *Ursus arctos*, it is clear that the two species migrated to Africa from Europe independently (Werdelin and Peigné 2010). Brown bears became extinct in northern Africa and other southerly regions during historic times (Calvignac et al. 2008; Hamdine et al. 1998; Nowak 2005) and today have a Holarctic distribution.

**Subfamily Ursinae Fischer, 1817**

This subfamily includes all living bears except the giant panda, *Ailuropoda melanoleuca*, which had split from the other living bears by at least the middle Miocene and is placed in its own subfamily, Ailuropodinae. Relationships within the Ursinae are not well established, but *Indarctos* and *Agriotherium* are clearly closely related and split from *Ursus* not long after the split from the giant panda.

**Genus Agriotherium Wagner, 1837**

*Type species: Ursus sivalensis* Falconer and Cautley, 1836

*Generic diagnosis:* Large-sized ursine with dental formula I 3/3, C 1/1, P 3–4/2–4, M 2/3; sexually dimorphic; short-snouted robust skull, somewhat brachycephalic; palate wide; premolar toothrow much shortened with anterior premolars reduced in size, single rooted, and low crowned; P4 robust, with strong parastylar cusp and protocone shelf; M2 with only...
rudimentary talon; m1–2 cusp pattern variable; premasseteric fossa present; symphyseal region of lower jaw ventrally produced as a “chin”; long-footed, plantigrade limbs. (Modified from Hunt [1998])

**Stratigraphic range in Africa:** Late Miocene – early Pliocene based on FAD at Sahabi, Libya (ca 6 Ma) and LAD in the Tulu Bor Member, Koobi Fora (≥2.62 Ma).

**Stratigraphic range at Koobi Fora:** Early Pleistocene based on FAD in the Lonyumun Member (≤4.35 Ma) and LAD in the Tulu Bor Member (≥2.62 Ma).

*Agriotherium* is represented in Africa by two named species, *A. aequatorialis* from Kenya and *A. africanum* from South Africa, as well as some material that has not been assigned to species (e.g. *A.* sp. from the Adu Asa and Saggontole Fms, Middle Awash, Ethiopia; Haile-Selassie et al. 2004). The best known of these is *A. africanum* from Langebaanweg, South Africa, which has yielded remains of several individuals, representing most of the skeleton (Hendey 1980).

**cf. Agriotherium sp.**

Fig. 5.1-5.3

KOOBI FORA MATERIAL

The Koobi Fora material here referred to cf. *Agriotherium* sp. consists of only two specimens, ER 2012, right proximal and distal femur and ER 3106, right proximal femur.

POSTCRANIAL

Two femoral fragments are attributable to *Ursidae*. The first, ER 2012 includes two parts: the femoral head and neck (ER 2012B; Fig. 5.1a, b) and the distal half of the femur (ER 2012A; Fig. 5.2a, b).

Although ER 2012B is roughly in the size range of *Homotherium*, a variety of features of the head differ from that of felids. The head is large and very round (Fig. 5.1b). The fovea capitis is very large and extends slightly more inferiorly than in felids. It is also very deep and not circular. Instead, it is a very rounded tall triangle filled anteriorly with an elongate oval pit and posteriorly with a small round pit. The inferior edge of the head does not lip over the neck, but instead the edge of the head and the neck meet at an obtuse angle. The superior surface of the head ends and then the neck immediately angles superolaterally giving a v-shape impression. All connections between the head and neck...
are less abrupt than in felids. In inferior view, the neck extends further proximally onto the head, whereas in felids, the articular surface continues further distally down onto the neck. In all, the articular surface is rotated more anteriorly on the head with more neck being seen posteriorly.

The distal half of the femur (ER 2012A) is quite different from most felids. The only felid from Koobi Fora that it shares any similarities with is *Homotherium*. Both *Homotherium* and this specimen have relatively flat shafts. However, this specimen is even wider mediolaterally relative to the anteroposterior width than in *Homotherium*. *Homotherium* still maintains a roughly circular shaft in cross-section while this specimen is oval. The cortical bone is extremely thick with a small oval marrow cavity. The distal end of the shaft is very wide and flat and merges smoothly with the distal epiphysis. The edges of the patellar groove do not extend very far although there is still a slight curvature to the groove itself. The medial and lateral epicondyles also do not project far medially or laterally respectively. The distal end, however, is not particularly compact mediolaterally, but the width of the shaft makes it appear so.

The patellar groove in ER 2012A not only lacks strongly projecting edges, but is also fairly wide. The sides are roughly parallel. In lateral or medial view, it can be seen that the patellar surface is not offset particularly anteriorly from the distal end in contrast to the felid condition.

In distal view, the medial condyle of ER 2012A does not project as far posteriorly as the lateral condyle, as in felids (though neither condyle projects particularly far posteriorly). Among the felids found at Koobi Fora, only *Homotherium* has a similar condition. However, the entire distal end of the *Homotherium* femur is more compact mediolaterally than is seen in this specimen. In ER 2012A, the intercondylar groove has relatively parallel sides in posterior view. In distal view, the medial edge continues along a line parallel to the long axis of the shaft, while the lateral edge runs anterolaterally. The anterior portion runs back medially, as in most large carnivores.
ment for the medial and lateral heads of gastrocnemius in ER 2012A are equally large and placed immediately above the outer edges of the condyles. This is not a felid condition. The condyles are slightly less tall (proximodistally) in posterior view, suggesting a slightly different knee posture (less crouching) than in Homotherium.

ER 2012 does exhibit some pathology. There is evidence of infection around the distal end. In fact, some of the lack of distinction between the head and neck is due to some remodeling from bone infection. Although there does not appear to be a significant amount of remodeling, some swelling around the patellar groove may account for its lack of distinction from the rest of the bone.

The second femoral specimen, ER 3106 (Fig. 5.3), is nearly identical to ER 2012B, but is much smaller. The head is a little more distinct from the neck than in ER 2012B, due to the pathology in that specimen. The fovea capitis is identical in shape and placement. This specimen also has some of the pitting seen in ER 2012 but does not appear to have the infection-caused remodeling.

Many features can be seen in ER 3106 that are not clear in ER 2012B due to the preservation of the entire proximal end in ER 3106. In anterior view, the greater trochanter does not project above the level of the head. It is short and less massive than in large felids. A V-shaped connection of the head to the rest of the femur is present. In this specimen, it is clear that the head is angled more superiorly than in felids, such that the superior portion of the neck is negligible and the sweep to the greater trochanter begins almost immediately.

In posterior view, there is in ER 3106 an inferolateral projection of the head onto the neck. Other than this, the neck is relatively flat and smooth. The lesser trochanter is elongated, flattened and rugose and much less projecting than in large mustelids, such as Enhydridodon (Lewis 2008, fig. 1). In fact,
the orientation of the head and neck relative to the shaft in combination with the differences in the size and placement of the greater and lesser trochanters make ER 3106 quite distinct in morphology from *Enhydriodon*. The intertrochanteric fossa is small and does not extend almost the length of the intertrochanteric crest, as it does in felids. The fossa is oval and extends anterolaterally into the greater trochanter. The region between the fossa and the lesser trochanter is flat, as in ursids. This is quite unlike any felid. The flatness of this region is carried down onto the posterior surface of the shaft. This is reminiscent of the distal shaft in ER 2012A.

In medial view, it can be seen that the head of ER 3106 is also set anteriorly on the neck. From the angle of the shaft below the lesser trochanter, it appears that the entire proximal end angles obliquely from the shaft towards the anterior direction. This is quite different from felids, where the neck and shaft are in alignment.

In superior view, ER 3106 seems rather compressed mediolaterally in comparison to similarly sized felids. However, this is due to the more superior orientation of the head rather than a compression of the head or greater trochanter.

**REMARKS**

The majority of ursids known from Africa are quite large, with the largest being the species of *Agriotherium* from the Late Miocene of the Middle Awash (Haile-Selassie et al. 2004). Smaller bears, such as black bears, are unknown from Africa, with the exception of *U. etruscus* in northern Africa (Geraads 1997, 2008).

The Koobi Fora ursid material is roughly the size of a large extant black bear or a small brown bear. While it is similar in size to the machairodont felid *Homotherium* and the giant otters such as *Enhydriodon*, the morphology is clearly unlike either of these taxa, as described above. Thus, this femoral material is much smaller than the extremely large *Agriotherium* femur from the Late Miocene of the Middle Awash, Ethiopia (KUS-VP-1/17; Haile-Selassie and Howell 2009). While conceivably it could belong to an amphicyonid, it appears to be morphologically distinct from amphicyonids and would also be a very late representative of this family.

Small representatives of *Agriotherium* exist. *Agriotherium* from North America is smaller than the Middle Awash form, but still larger than the Koobi Fora specimens (e.g., Harrison 1983). The Langebaanweg *A. africanaum*, which is much smaller than the Middle Awash *Agriotherium*, is also larger than the Koobi Fora material. Thus, if the Koobi Fora material belongs to *Agriotherium*, it would be the smallest known African *Agriotherium*; one that is within the overlap in size range of black and brown bears.

The Koobi Fora material shows features of both *Agriotherium* and *Ursus*, making taxonomic identification difficult. This is not surprising, as bear femora, even within a single taxon or population, can show considerable variation (Lewis, personal observations). Despite the presence of multiple femora at Langebaanweg (Hendey 1980), variation in *Agriotherium* is still poorly understood. The pathological nature of some of the Koobi Fora material only adds to the difficulty. Without a complete femur it is impossible to assess what the proportions of the proximal and distal ends relative to overall bone length would have been. Much has been made of the shaft morphology of *Agriotherium*, a region that is only partially
preserved in the pathological ER 2012A.

The Koobi Fora bear (primarily the non-pathological ER 3106) is distinguished from *U. arctos* in that the neck is shorter and not angled as superiorly and the greater trochanter extends further laterally. In other words, the head is not as high above the greater trochanter as in *Ursus*. This has been used as a key feature in assigning femora to *Agriotherium* rather to *Ursus* (e.g., Harrison 1983). The morphology of the greater trochanter is also more similar to *Agriotherium* than *Ursus*.

However, the Koobi Fora bear shares features with *U. arctos* that distinguish them from African *Agriotherium*, including a much rounder, relatively larger head, narrower superior-inferior neck diameter, and more inferior placement of the capsular ligament on the neck. However, it should be noted that North American *Agriotherium* does seem to have a larger, rounder head than *A. africanum* or the Middle Awash *Agriotherium* (see Harrison 1983, fig. 11). Aspects of head shape may have more to do with size and function, rather than phylogenetic relationships. The distal end is also much narrower relative to shaft width than one would expect for *Agriotherium*, but this may be due to pathological remodeling.

Thus, while the Koobi Fora material is not a perfect match for either *Ursus* or *Agriotherium*, ER 3106 does seem to share the characteristic relationship between the placement of the greater trochanter and femoral head seen in *Agriotherium* and not in *Ursus*. For this reason, we have tentatively assigned this material to *Agriotherium* until more material from this time period is recovered. If correctly assigned to *Agriotherium*, this material would be the youngest known of the genus in Africa.

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The family Viverridae has a fairly extensive, but poorly understood, fossil record in Africa. Some recent publications have attempted to systematize parts of this record (e.g., Morales and Pickford 2011; Peigne et al. 2008), but much work is still required to understand the radiation of Viverridae. This is especially true since many viverrids are arboreal and are rarely found in the fossil record. Thus, we are constrained for the most part to studying terrestrial African viverrids. One aspect of the fossil record is the occurrence of several genera and species of viverrid of much larger size than found in the modern fauna. This parallels the pattern in Mustelidae (especially enhydriodontine lutrines) discussed in Chapter 4 and suggests major differences between the larger carnivoran guild of the Pliocene and early Pleistocene and that of today (cf. Werdelin and Lewis 2013).

**Genus Civettictis** Pocock, 1915

*Type species:* *Viverra civetta* Schreber, 1776

*Generic diagnosis:* Large-sized Viverridae; dental formula I 3/3, C 1/1, P 4/4, M 2/2; P4 protocone enlarged, metastyle short; m1 with short trigonid and broad, three-cusped talonid; premolars robust but slender; m1 and M1–2 broad and with crushing adaptations.

*Stratigraphic range in Africa:* Early Pliocene – Recent based on FAD at South Turkwel (<ca 3.5 Ma). It should be noted that all early specimens of the genus (South Turkwel as well as Omo) are only tentatively referred to the genus.

**Stratigraphic range at Koobi Fora:** Early Pleistocene – Middle Pleistocene based on FAD in the Upper Burgi Mb (≤ca 2.0 Ma) and LAD in the Chari Mb (≥0.74 Ma).

**REMARKS**

The African civet is surprisingly rare in the fossil record, especially given its relatively large size and widespread modern distribution. However, it is at least plausible to suggest that for a large part of the Plio-Pleistocene, it had a smaller distribution, perhaps in the more forested areas of its current distribution, and was replaced in more open areas by representatives of the genus *Pseudocivetta*. The latter was apparently more frugivorous and/or herbivorous than the omnivorous *Civettictis* (Petter 1973) and the replacement of *Pseudocivetta* by *Civettictis* would be a part of the general transition in the Pleistocene from an ecosystem with many specialist taxa to one dominated by generalists (Werdelin and Lewis 2005, 2013; Lewis and Werdelin 2007).

**cf. Civettictis sp.**

*Stratigraphic range at Koobi Fora:* As for genus.

**KOOBI FORA MATERIAL**

The neurocranium ER 1663 is very long and
slender. There is a substantial occipital crest that appears to reach a maximum height at the anterior end of the preserved part. The nuchal crests are also very large, providing attachment for a massive masseter relative to the size of the animal. The nuchal region is large and rugose, forming a broad U-shape. The auditory bulla is strongly laterally compressed, with a sharp vertical keel. The paroccipital process is slender but very long, reaching ventrally twice as deep as the bulla. The occipital condyle is relatively strong.

ER 5342 is a posterior part of a neurocranium. The specimen is very similar to ER 1663 in its preserved parts. The nuchal crest is very large, whereas the occipital crest is relatively short and low. The right occipital condyle is present and set relatively far laterally.

Specimen ER 3749 is a snout with alveoli for C, P1, roots of P2-M1 and a partial alveolus for M2. The specimen is very broken and abraded and no sutures can be identified. The alveolus for the upper canine is large and that for P1 indicates that the tooth was single-rooted. The P2 and P3 were large but not extremely so. The P4 was relatively wide for its length, while as far as can be determined, M1-M2 were wide and short. The protocone of M1 is preserved but shows little discernible relief. The frontals are very flat and there is a large infraorbital foramen. Interorbital width seems to have been relatively great.

REMARKS

None of this material is diagnostic, and we merely note that, pace Leakey (1976), ER 1663 is similar to extant Civettictis in size, and not so dissimilar in morphology. Further, it is highly likely that ER 1663 and ER 5342 are conspecific, as they are similar in general shape and size. Unfortunately, ER 5342 is very poorly preserved and the comparison is not definitive. ER 3749 might also belong to the same taxon.

Genus Pseudocivetta Petter, 1967

Generic diagnosis: Civet of large size with bunodont dentition; M1 and M2 rectangular, with low, rounded cusps; p4 with large, rounded main cusp followed by a talonid with bunodont cusps. (From Petter 1973, modified and translated.)

Stratigraphic range in Africa: Early Pleistocene based on FAD in the Shungura Fm., Mb. E+F (<2.37 Ma) and LAD at Melka Kunturé (>0.8 Ma).

Stratigraphic range at Koobi Fora: Early Pleistocene based on FAD in the Upper Burgi Mb (≤ca 2.0 Ma) and LAD in the KBS Mb (≥1.56 Ma).

REMARKS

Pseudocivetta is a large-sized viverrid with very bunodont dentition. The molars all have very low relief and a number of low, bunodont cusps. The premolars are poorly characterized, though a single specimen from Olduvai (Petter 1973) shows a p4 with a low, rounded main cusp and a distal region supporting several smaller, bunodont cusps.

Unfortunately, apart from the material from Olduvai, Bed I reported by Petter (1967, 1973) the majority of material referred to Pseudocivetta consists of isolated teeth. Most of these have no counterpart in the Olduvai material (which lacks the carnassials), and are referred to the genus by default, being large-sized bunodont teeth that do not comfortably fit into any other taxon. This has led to some
apparently mutually contradictory assignments of specimens to *Pseudocivetta*. Thus, for example, it is hard to envisage both the m1 from Melka Kunturé, originally assigned to *Enhydriodon* by Geraads et al. (2004) but since referred by several authors to *Pseudocivetta* (Morales and Pickford 2011; Werdelin and Peigné 2010) and the m1 from Omo, O33-354 (Morales and Pickford 2011; Petter and Howell 1977) as belonging to the same genus- (or at least species-) level taxon.

The Melka Kunturé tooth has a trigonid that is longer than the talonid. The trigonid cusps are closely bunched together with only a narrow notch between paraconid and metaconid. The paraconid and protoconid are subequal in size and the metaconid only slightly smaller. The metaconid is set only slightly distal to the protoconid. There is only a very slight constriction between trigonid and talonid. The talonid has only two distinct cusps, presumably entoconid and hypoconid, with the former pronounced into a crest that stretches from the cusp apex to the distal margin. The overall outline of the tooth is very rectangular, with trigonid and talonid of about equal width.

Omo O33-354 has a trigonid that is shorter than the talonid. The trigonid cusps are set well apart with a paraconid that is distinctly larger than the protoconid. The metaconid is set well distal to the protoconid. There is a very distinct ‘waist’ between trigonid and talonid. The talonid is completely different in structure to the Melka Kunturé specimen. It has a well developed entoconulid mesial to the entoconid, the latter of which is set at the distolingual corner of the tooth. The entoconid has a short, crescent-shaped apex and there is a distinct distal cusp. The hypoconid is set well mesial to the entoconid and there is a well-developed hypoconulid. The talonid is distinctly broader than the trigonid.

We have not seen specimen O33-354, but there is another specimen in the Omo collections, L39-13 (Fig. 6.8), which is nearly identical to O33-354. This specimen has a very characteristic concave occlusal surface and lacks roots. It is, of course, nor clear which of the above specimens really belongs to *Pseudocivetta*, but the Melka Kunturé tooth seems the more likely candidate (there is a very similar tooth from Koobi Fora, as well as an unpublished specimen from Olduvai that matches these two in morphology). As regards the Omo teeth, we suggest, given the characteristics of the particular tooth we have studied, that these might be the deciduous carnassials (dp4) of *Enhydriodon* sp. This genus is known from other material in the Omo collections.

As we shall see, similar problems beset the identification of the upper carnassial of *Pseudocivetta*. Petter and Howell (1977) and Morales and Pickford (2011) suggest that another Omo tooth, L338 Y15, represents this tooth. However, we believe that this tooth is too short to match the lower carnassial of *Pseudocivetta*, regardless of which of the specimens discussed above may belong to the taxon. We here propose a different solution (see below), one that does not affect the identification of *Pseudocivetta howelli* as belonging to this genus (Morales and Pickford 2011).

**Pseudocivetta ingens** Petter, 1967

Fig. 6.1 – 6.3

**Synonyms:** *Enhydriodon aethiopicus* Geraads et al., 2004

**Holotype:** Olduvai 5360, left M1. Housed in the National Museum of Tanzania, Dar es Salaam.

**Type locality:** Olduvai, Bed I; dated ca 1.92 –
1.80 Ma (Deino 2012).

Specific diagnosis: As for genus (monotypic).

Stratigraphic range in Africa: As for genus.

Stratigraphic range at Koobi Fora: As for genus.

KOOBI FORA MATERIAL

CRANIODENTAL

ER 3757 is a right M1. The tooth is broad and robust and considerably abraded on the occlusal surface, reducing the relief, which was already quite low. The paracone is low and bulbous. It is rounded, with the diagonal from mesiobuccal to distolingual being its largest dimension, and is placed at the mesiobuccal corner. The apex of the protocone is situated somewhat distal to the midline on the lingual margin of the tooth. However, this cusp extends mesiobuccally to the middle of the mesial margin and is thus confluent with a very indistinct protoconule. The latter is connected to the paracone by a low ridge. On the lingual margin, mesial to the protocone, there is a strong cingulum and short shelf. The cingulum distal to the protocone is much less developed. The protocone continues along the distal margin of the tooth as a low ridge, but there is no distinct hypocone developed. The metacone is situated at the distobuccal corner of the tooth. It is round and smaller than the paracone.

ER 2134 (Fig. 6.1) is a right m1. This is a low-crowned tooth with bulbous cusps. The paraconid is set on the mesiolingual margin and is nearly round in occlusal view. The protoconid is larger and separated from the paraconid by a low, indistinct carnassial notch. It is set distobuccally to the paraconid. The mesial face of the protoconid is nearly flat and slopes down to the mesiobuccal margin of the tooth. The metaconid is smaller than the paraconid and protoconid and set on the lingual margin in the space between these two cusps. It is separated from them by distinct but shallow notches. The distalmost part of the talonid is worn off. What is left shows a low, bulbous hypoconid and entoconid. The former is separated from the protoconid by a notch, the latter from the metaconid by a shallow valley. This tooth is almost identical to an undescribed m1 from Olduvai assigned to *Pseudocivetta ingens*. It also matches the m1 from Melka Kunturé (see above) in morphology except that the ‘waist’ between trigonid and talonid is more pronounced in the specimen here described. It is quite different from the Omo specimen illustrated by Morales and Pickford (2011).

Specimen ER 2011 includes a right I3, a premolar fragment, broken M1, and complete M2. The I3 is large and robust, being superficially similar to the I3 of a hyenid, but with a stronger medial cingulum and more curved root. The premolar fragment lacks a mesial accessory cusp and is not identifiable to position. The M1 is very similar in structure and morphology to ER 3757, as well as to the holotype of *P. ingens*, though the distobuccal and mesiolingual corners are broken off. The tooth is longer relative to its width than the ER 3757 tooth and in this respect more closely matches the M1 of *Pseudocivetta ingens* from Olduvai. The trigon of M2 has a large paracone and smaller metacone located on the lingual margin. The buccal margin of the tooth has a series of low bumps that are difficult to homologize with any specific cusps. This tooth is similar in size and morphology to the M2 of *P. ingens* from Olduvai.
Fig. 6.1: *Pseudocivetta ingens*, ER 2134, right m1. a) lingual view; b) buccal view; c) occlusal view.

ER 44505 includes a damaged m1 (Fig. 6.2), as well as numerous postcranial fragments including vertebral centra, ribs, and os coxae, femur, and metapodial fragments (see below). The m1 is broken at the middle of the paraconid. All cusps are bulbous and low. The protoconid and metaconid are situated level with each other and are about equal in size. The talonid has a large hypoconid and smaller entoconid and hypoconulid. The tooth is very similar to the Melka Kunturé specimen and differs from ER 2134 only in the less pronounced ‘waist’ between trigonid and talonid.

Specimen ER 44291 includes right M1, M2, p4, and ?p3. The M1 is flat, with very low, bulbous cusps. The paracone is prominent. The metacone is low. There is a small paraconule distolingual to the paracone. The protocone is the largest cusp and has two indistinctly separated apexes. The hypocone is double. There is a cingulum that runs from the anterior end of the protocone to the hypocone. The M2 is very similar in morphology to the M1 but the metacone shelf is reduced and the hypocone single. Only the distal end of the p4 is preserved. There is a prominent distal accessory cusp and a strong lingual shelf in the form of a narrow groove. In general outline the preserved part strongly resembles the p4 of *P. ingens* described by Petter (1967, 1973; Petter and Howell, 1977), but lacks the cusplets fringing the distolingual part of the tooth.

**POSTCRANIAL**

The partial skeleton includes both axial and appendicular elements. The axial skeleton is not particularly well-preserved. An axis (ER 44505B) includes the cranial half of the body. The dens is broken off. Only the left superior
articulate surface is well-preserved. Four vertebral centra are preserved including a mid-cervical (C), two mid-thoracic (D and E), and a lumbar (F). The lumbar centrum is lacking the cranial surface, although the entire caudal articular surface is present. An extremely large ventral keel runs along the entire ventral surface. This keel is much larger than in other carnivorans of this size. It is deeply excavated on either side. The caudal articular surface seems very narrow dorsoventrally relative to mediolateral width. However, the robust, long caudal vertebra (G) indicates the presence of a long tail, as in smaller viverrids. Several rib fragments have also been found (I, J).

Two robust portions of the ossa coxae (K, L) include the same portions but on opposite sides of the body. Both include part of the auricular surface down to the top of the acetabular fossa. As such, little can be said about the overall morphology of the pelvis. However, some information about the ilium can be gleaned from these specimens. The ilium begins as a narrow flat branch from the acetabulum that then expands somewhat at the level of the sacral articulation. There is no evidence of the large, bowl-shaped expansion seen in hyenid os coxae. However, the ilium is clearly not the simple, parallel-sided blade seen in felids. The actual shape of the ilium may fall somewhere between the broad blades of hyenids and narrow blades of viverrids and felids. While it is hard to orient such abbreviated specimens, it appears that the acetabulum may have been relatively deeply excavated. The superior rim around the acetabulum is robust. It is long anteroposteriorly and relatively narrow mediolaterally.

Portions of the left femur have been preserved (ER 44505M, O). The smaller specimen is a fragment of the greater trochanter (O). The larger portion (M) includes much of the patellar groove and the shaft proximal to the groove. The lateral attachment for the gastrocnemius is preserved along with the anterior portion of the lateral epicondyle and condyle. However, all of the right condyle is broken off. As such, the true mediolateral width of the specimen and the posterior and mediolateral projection of the condyles and epicondyles are unclear. The shaft appears more gracile than in mustelids, but more robust than in hyenids. The patellar groove is relatively deeply grooved, although the edges of the patellar groove are not preserved. As the shaft approaches the midpoint, it becomes very round in cross-section.

A long bone shaft fragment (ER 44505P) may be a tibia, as it is triangular in cross-section. One side is exceedingly flat, much more so than in, e.g., hyenids.

Finally, the partial skeleton includes a well-preserved proximal left third metatarsal (ER 44505Q; Fig. 6.3). This specimen shows the characteristic T-shaped morphol-
ogy. There is nothing particularly distinctive about this specimen, other than its excellent preservation.

REMARKS

The dental specimens described above all conform to the morphology of the hypodigm of *P. ingens* from Olduvai. They add nothing specific to our understanding of this aberrant taxon, but confirm its presence in the Turkana Basin in the Early Pleistocene.

**cf. Pseudocivetta sp.**

Fig. 6.4 – 6.6

**Stratigraphic range at Koobi Fora:** Early Pleistocene based on FAD in the KBS Mb (≤1.87 Ma) and LAD in the Okote Mb (≥1.38 Ma).

**KOOBI FORA MATERIAL**

**CRANIODENTAL**

The skull ER 5339 (Fig. 6.4) is long and low with a narrow snout and somewhat wider braincase. The zygomatic arches are narrow, slender and long. The skull is short posterior to the zygomatic arch. The specimen is somewhat crushed and sutures are difficult to identify. The anterior end of the orbit reaches the notch between parastyle and paracone on P4. The palatine/zygomatic suture lies inside the orbit but not as far in as in the majority of viverrids. The zygomatic process of the frontal is short, while the postorbital constriction is broad and not very distinctly marked. The lyriform crests originate on the zygomatic processes and join at the midline just anterior to the fronto-parietal suture. The occipital crest is low and long, while the nuchal crests are large, with the nuchal area forming a blunt V. The occipital condyles are short and very small. The paroccipital processes are very long and the auditory bullae small.

The incisors form a gently curving row. They increase in size from medial to lateral, with I2 being slightly larger than I1 but only half the size of I3. All incisors have buccal cingula. The I1 and I2 are peg-like, with the tips worn flat. The I3 is less worn and somewhat caniniform. The incisor-canine diastema is long. The canine is small, short and very gently mesiodistally curved. The P1 is small and peg-like and slightly longer than wide. It has no accessory cusps, nor does it have a basal cingulum. The P2 is larger and relatively slender, with a triangular lateral outline. There are no accessory cusps, but a poorly developed basal cingulum is present on the lingual side. The P3 is larger and broader. There is a very small, bulbous mesiolingual accessory cusp. The main cusp is pyramidal. There is also a very small distal accessory cusp. The basal cingulum is prominent on the lingual side of the tooth, where it is formed into a low cusp. The P4 is the most characteristic tooth of this specimen. It is short and very broad, with a massive protocone. The parastyle is large, round, and blunt. It is separated from the paracone by a shallow notch and from the protocone by a deeper and wider one. The paracone is the tallest cusp and is about twice the size of the parastyle in occlusal view. It is connected to the parastyle and protocone by low pre- and postparacristae, punctuated by shallow notches. The metastyle is very short and broad. The protocone is by far the largest cusp in occlusal view. Its mesial end reaches well mesial to the mesialmost point of the parastyle. The cusp is characterized by five cristae extending from base to apex: anterior, mesiolingual, mesiobuccal, distobuccal...
Fig. 6.4: cf. *Pseudocivetta* sp., ER 5339, cranium. a) dorsal view; b) ventral view; c) left lateral view.
(towards the paracone), and distal, rendering the protocone almost pentagonal in occlusal view. There is a basal cingulum that extends around the entire tooth except the anterior part of the parastyle and distobuccal side of the metastyle. The cingulum is particularly broad and massive distal to the protocone, where it almost forms a small shelf. Wear is slight and only noticeable on the tips of the paracone and protocone.

Two teeth, right m2 and M2, make up ER 5340. These teeth were found close to the skull ER 5339 but it cannot be proven that they belong to the same specimen. The m2 has a short, wide trigonid and a slightly longer and even wider talonid. The three trigonid cusps are situated on the margin of the tooth; the paraconid mesially, the protoconid buccally and the metaconid lingually. The protoconid is the largest of the three, the metaconid the smallest. The talonid has a large lingual entoconid and an equally large, buccal hypoconid situated at the posterior corner. The talonid basin is wide and flat.

The M2 is a small, square tooth with heavily worn and possibly etched occlusal surface including paracone and metacone on the buccal rim and a lingual protocone. There are also small mesial and distal cusps (of uncertain homology) located between the main cusps, giving the occlusal surface the shape of a cross.

POSTCRANIAL

The right tibia, ER 3763, is missing the lateral condyle and the anterior portion of the proximal end (Fig. 6.5). The distal half is also missing. Viverrid features include the roundness of the medial condyle and the depression in the center of the condyle with a groove postero-laterally. The shape and curvature of the shaft are also viverrid-like. The shaft is relatively narrow mediolaterally with an overall oval shape at the level of the break (somewhere above midshaft). In terms of curvature, both anterior and posterior edges of the shaft are curved, giving the shaft a bowed appearance. Although the tibial tuberosity is missing, it does not appear that it would have projected very far anteriorly relative to the shaft. On the contrary, the curve of the shaft suggests that the condyles, or at least the medial condyle, projected relatively far posteriorly. The posterior curve is not completely smooth, however, as the shaft slopes smoothly until it nearly reaches the medial condyle where it plateaus posteriorly. While only a portion of the proximal surface is present, it does not appear to have had a particularly wide proximal end. This specimen fits the shape and size of the distal femur of *Pseudocivetta* ER 44505.

The three phalanges, ER 2014, include a complete proximal phalanx, ER 2014A and the proximal half (ER 2014B) and distal third (ER 2014C) of proximal phalanges (Fig. 6.6). They are the right morphology for a large viverrid. There is the possibility that these specimens may be associated with ER 2011, the teeth of *P. ingens*, which, if true, reinforces attribution to that taxon. They are very similar to extant *Civettictis* phalanges, but are much larger. The complete phalanx has a straight shaft. There do not seem to be any features that distinguish this phalanx from that of extant viverrids with the exception of size.

REMARKS

The assignment of the skull ER 5339 to *Pseudocivetta* is, of course, speculative. This specimen includes no teeth that have homologs among the previously described material.
of *Pseudocivetta*, making direct comparison impossible. The possibly associated M2 ER 5340 has homologs at Olduvai, but it is heavily worn and etched, compromising direct comparison. Hence, the taxonomic assignment of ER 5339 rests entirely on the subjective argument presented below.

The first step is to determine whether ER 5339 could belong to some extant genus of viverrid. Given the size of the specimen the only genus that is truly relevant is *Civettictis*, the skull of which is ca 15% shorter than ER 5339. Comparisons with this or any other taxon are, however, made difficult by the distortion of ER 5339 – although not entirely flattened, ER 5339 has suffered some dorsoventral flattening leading to changes in proportions and displacement of some features relative to each other. Nevertheless, there appear to be both similarities and differences between ER 5339 and *Civettictis* in skull morphology. Anteriorly the two are quite similar, with similarly arching incisor rows. However, the palate of ER 5339 flares laterally much more abruptly than in *Civettictis*, where the broadening of the palate at the carnassials is quite gradual. The opposite is true at the posterior end of the zygomatic arches. The opening for the temporalis muscle enclosed by the zygomatic arches appears to be more squared-off in *Civettictis* and is rounded in ER 5339. In dorsal view the lyriform crests are much more prominent in ER 5339 and the sagittal crest is not fused into a single crest until posterior to the postorbital constriction. In *Civettictis* the single sagittal crest extends anterior to the postorbital constriction.

Differences in the morphology and proportions of the teeth are also evident between *Civettictis* and ER 5339. The teeth of the latter are generally more robust than those of the extant genus, especially the P4. These
differences are quite distinct and require no elaboration. However, there are also differences in the position of the teeth relative to the skull. The P1 is smaller in ER 5339 than in *Civettictis* and the diastemas separating it from C and P2 are larger. The P2 and P3 are both larger than in the modern genus and imbricated, although this may be an age-related trait. The P4 is set much further posteriorly in ER 5339 than in *Civettictis*, resting almost entirely on the anterior root of the zygomatic arch. This suggests that the missing M1 and M2 of ER 5339 would have been smaller than those of *Civettictis* to fit in the skull. We conclude from this that ER 5339 is unlikely to be congeneric with *Civettictis* or any other extant viverrid.

As for the specific relationship to *Pseudocivetta* there is little to go on. As noted above, Petter and Howell (1977) and Morales and Pickford (2011) suggest that the m1 O33-354 and P4 L338 Y15, from the Omo deposits represent the lower and upper carnassials of *Pseudocivetta*, respectively. We have dealt above with why we feel that this is incorrect with regard to the m1. Here we will consider the P4. The P4 of ER 5339 and the P4 L338 Y15 (Fig. 6.7) are quite different in morphology, although both could plausibly be derived from the P4 assigned by Morales and Pickford (2011; Morales et al. 2005) to *Pseudocivetta howelli*. The main differences lie in the straight buccal face of the Omo specimen, the position of the protocone, which extends mesial to the parastyle in ER 5339 but is distinctly distal to it in the Omo specimen, and the shape of the protocone, which is rounder but buttressed by ridges in ER 5339 and oval and smooth in the Omo specimen. The Koobi Fora specimen has a lingual shelf extending distally from the protocone to the carnassial notch that is not seen in the Omo specimen. However, the latter is damaged in this area and may plausibly have had such a shelf, although it would have been less prominent than in ER 5339. Finally the Omo specimen is considerably smaller than the ER 5339 P4.

How much smaller is best visualized through a crude but illustrative analysis of the relative sizes of the upper and lower carnassials. The major difficulty with any such analysis is that given the identification by Petter and Howell (1977) and Morales and Pickford (2011) of O33-354 as an m1 of *Pseudocivetta* there is no universally accepted carnassial known of the genus, since, as noted above, the Omo and Melka Kunturé (Geraads et al. 2004) lower carnassials (to which can be added ER 2134 described herein) can hardly belong to the same taxon. Fortunately, however, they are not too different in size, and the unpublished Olduvai m1 that we here consider to belong to *Pseudocivetta* is close in size to the Omo specimen. Using a small \((N = 12)\) sample of *Civettictis civetta* we regressed m1 length against P4 length using the reduced major axis regression. We used this method because the question of dependent/independent variable is moot, and because we wanted to obtain estimated lengths in both directions. The regression equation for P4 is

\[
f = 1.087X - 2.693, \quad (\text{Eq. 1})
\]

while for m1 it is

\[
f = 0.920X + 2.478, \quad (\text{Eq. 2})
\]

and \(r^2 = 0.392\). The latter is not very high, indicating a good deal of scatter in the regression. Two here accepted lower carnassials of *Pseudocivetta* have lengths of 20.5 mm (Olduvai; measurement by Werdelin) and 18.4 mm (Melka Kunturé; measurement from Geraads
et al. [2004]) (ER 2134 described above is unfortunately damaged distally and no accurate length measurement can be obtained.) Using Eq. 1 above, the estimated P4 lengths of these individuals would be 19.6 mm and 17.3 mm, respectively. Both of these estimates are much greater than the Omo P4 L338 Y15 (16.0 mm; measurement by Werdelin). The estimated length of the m1 of the latter would be 17.2 mm, which is not only smaller than either of the above mentioned specimens but also much smaller than L39-13 (Fig. 6.8) from Omo (length 20.1 mm; measurement by Werdelin), which is a morphological match for O33-354 suggested by Petter and Howell (1977) and Morales and Pickford (2011) to be an m1 of *Pseudocivetta*. We conclude from this that unless the range of variation in carnassial length in *Pseudocivetta ingens* is much greater than expected given the available specimens and/or the length proportions between the carnassials in *Pseudocivetta* differ drastically from those of *Civettictis*, L338 Y15 is unlikely to belong to *Pseudocivetta* (though not entirely impossible given the low $r^2$ of the *Civettictis* regression). In terms of size, the P4 of ER 5339 is better matched with the existing m1 of *Pseudocivetta ingens*, as the matching m1 would have a length of 19.2, i.e., intermediate between the two existing specimens. As noted above, there is nothing in the morphology of the ER 5339 P4 that would contradict derivation from something like *P. howelli*. We thus tentatively suggest that ER 5339 is the skull of *Pseudocivetta ingens*, though this is based entirely on circumstantial evidence and could be falsified by finding associated upper and lower dentition specimens.

**Genus Genetta Cuvier, 1817**

*Generic diagnosis:* Small-sized viverrid with dental formula I 3/3, C 1/1, P 4/4, M 2/2; pleiomorphic dental anatomy; M2 present; m1 talonid developed; m2 well developed. (From Gaubert et al. 2004)

*Stratigraphic range in Africa:* Late Miocene – Recent based on FAD in the Lower Nawata Fm., Lothagam (<7.5 Ma; McDougall and

---

**Fig. 6.7:** Omo, Shungura Fm., Mb. E3 specimen L338 Y15, right P4 in occlusal view.

**Fig. 6.8:** Omo, Shungura Fm., Mb. F1 specimen L39-13, right dp4 or m1 (see text) in occlusal view.
The FAD is tenuous; even more tenuous is the identification of *Genetta* from the Middle Miocene of Beni Mellal, Morocco (Ginsburg 1977). A more definite FAD is the Kanapoi Fm. (<4.3 Ma; Feibel 2003).

**Stratigraphic range at Koobi Fora:** Early Pleistocene based on FAD in the Upper Burgi Mb (≤ca 2.0 Ma) and LAD in the Okote Mb (≥1.38 Ma).

**REMARKS**

*Genetta* is a well-known and, in the modern fauna, speciose genus whose relationships have recently been extensively revised by Gaubert and colleagues (e.g., Gaubert et al. 2002, 2004, 2005). The genus is evidently of African origin and its modern distribution is exclusively African, except for populations of the common genet (*G. genetta*) occurring in the southwestern part of the Arabian and Iberian peninsulas, the latter introduced by humans in historic times (Gaubert et al. 2008, 2011).

The fossil record of *Genetta*, as of all small carnivorans, is limited. It has somewhat of the status of a wastebasket taxon and has therefore been cited as present at a number of sites without adequate comparative analysis. Thus, for example, *Genetta* sp. is cited as present in the Middle Miocene of Beni Mellal, Morocco (Ginsburg 1977), but in reality this material is probably not diagnostic and unlikely to belong to *Genetta* in any case. The same may be true of the records of *Genetta* from Lothagam (Werdelin 2003b), which are also based on limited material. The oldest material that is clearly diagnostic of the genus *Genetta* is from Kanapoi (Werdelin 2003a). This material is, however, significantly different from extant species of *Genetta*, although it appears close to *G. genetta*. The only extant species of *Genetta* to have been described from the fossil record are *G. genetta*, reported from Koobi Fora and Sterkfontein (Werdelin and Peigné 2010), and *G. tigrina* from Swartkrans Mb 3 (as cf. *G. tigrina*) and Plovers Lake in South Africa (Hendey 1974; Turner 1993).

**Genetta genetta** (Linnaeus, 1758) or **Genetta maculata** (Gray, 1830)

Fig. 6.9

**Stratigraphic range at Koobi Fora:** Early Pleistocene based on FAD in the Upper Burgi Mb (≤ca 2.0 Ma) and LAD in the Okote Mb (≥1.38 Ma).

**REMARKS**

The two species here listed are indistinguishable based on features present in the material available from Koobi Fora. Their modern ranges also overlap, and include the Turkana Basin. Other species of *Genetta* differ in size and/or morphology from these two, or have ranges and habitat requirements that are not compatible with their presence in the Early Pleistocene of Koobi Fora. In addition, unlike material from Kanapoi (Werdelin 2003a), the Koobi Fora specimens placed here show no features to distinguish them from all extant species of *Genetta*. Therefore, we assign the specimens below to *Genetta* and to either *G. genetta* or *G. maculata*, but we cannot determine which of these species is present (or if both are).

**KOOBI FORA MATERIAL**

ER 3123 is a maxilla fragment with P4 and emerging P3. The P3 is long and slender, with a tall main cusp and very small distal acces-
sory cusp that is essentially just a bump on the distal margin of the main cusp. The P4 is also long and slender. The protocone extends mesially well beyond the paracone and is a large, trenchant cusp separated from the paracone by a deep notch. There is no parastyle in evidence. The paracone is tall but not very elongated. The carnassial notch is deep. The metastyle is long and slender. The protocone, paracone, and metastyle are all nearly aligned on a straight line that, judging from the position and orientation of P3, is set at an acute angle to the main mesiodistal axis of the tooth row.

Specimen ER 979 is a palate with right P1-M1 and broken left P2-P4. The P1 is minute and slightly longer than wide. The P2 has a broken tip and is long and slender. The P3 is very similar to P2, but larger. It has a small buccal cingulum cusp. The P4 is long and slender. The parastyle is very low but has a distinct cusp. The protocone is small, about level with the parastyle and with a cusp that is somewhat crest-like. The paracone is tall and pyramidal. The metastyle is long and slender. The M1 is very short and broad. The paracone is located buccal to a wide parastyle wing. The metastyle wing is reduced and the metastyle indistinct. The M2 is minute, but with a distinct paracone and protocone.

ER 44365 (Fig. 6.9) is a mandibular ramus with worn m1. The ramus is broken and damaged, leaving no diagnostic features except the m1. Though worn, the paraconid and protoconid are low and long, with the paraconid the longer and probably lower (when unworn). The paraconid is set at about 15 degrees to the long axis of the tooth. The protoconid and metaconid are set at the same level, with the latter so worn as to be almost lost. The notch between them can only be vaguely discerned. The talonid is low and slender with no distinct cusps remaining.

ER 44716 is a maxilla fragment with damaged P3, roots of P4, and complete M1. The P3 is slender, with a low mesial cingulum, a small lingual accessory cusp and a small distal accessory cusp set in a low, narrow shelf. The main cusp is slender and tall, though broken apically. The roots of P4 indicate a slender tooth. The M1 is triangular. The parastyle wing is larger than the metastyle wing. The paracone is small but distinct, as is the metacone. The protocone is the largest cusp. The maxilla fragment shows a large infraorbital foramen, but no other features are preserved.

*Genetta nyakitongwer* sp. nov.

Fig. 6.10

Specific diagnosis: Species of *Genetta* of the size of, or slightly larger than, the extant giant forest genet, *Genetta victoriae*. Considerably larger than other known species of the genus. Dentition more robust and broader than that of *G. victoriae*, especially p3. Accessory

Fig. 6.9: *Genetta genetta* or *G. maculata* specimen ER 44365, fragmentary left mandibular ramus with m1. a) buccal view; b) lingual view; c) occlusal view.
cusps on premolars strongly developed both mesially and distally. Talonid of m1 distinctly narrower than trigonid, unlike in *G. victoriae*.

**Holotype**: KNM-ER 46408, left mandibular ramus with p1 alveolus, broken p2, p3-m1, broken m2 (Fig. 6.10).

**Horizon and locality**: ?KBS Member of the Koobi Fora Fm., Area 104 of the Koobi Fora Ridge. Age probably between 1.87 Ma (KBS Tuff) and 1.56 Ma (Morutot Tuff) (Brown 1994).

**Hypodigm**: Holotype only.

**Etymology**: Nyakitongwer, meaning ‘genet’ in the Dassenech language.

**KOOBI FORA MATERIAL**

Ramus tall and slender, deepest just posterior to the m1. There are three mental foramina. Anteriorly there is a small foramen below the p1 and a larger one directly ventral to that; a third, larger foramen is situated below the posterior root of p3. The coronoid process ascends nearly vertically posterior to m2. The symphysis is directed from anterodorsal to posteroventral at about 30 degrees. The root of the canine was large and mediolaterally compressed. The p1 was small and single-rooted. The p2 is two-rooted but does not preserve crown morphology. The p3 is robust, with a small mesial accessory cusp, a tall main cusp that makes up 2/3 of the crown length, and a small distal accessory cusp that is situated some way up the distal margin of the main cusp. The p4 also has a small mesial accessory cusp. Its main cusp is about equal in height to that of p3, but makes up only about 2/5 of the length of the crown. The distal accessory cusp is large and low, and there is a small distolingual shelf. The m1 has three subequal trigonid cusps. The protoconid is slightly taller than the paraconid and metaconid, and the latter two are subequal in height. The trigonid is nearly equilateral in occlusal view, with the angle between paraconid-protoconid and paraconid-metaconid approaching 45°. The talonid is low and short, with three small cusps at its distal margin: entoconid (largest), entoconulid and hypoconid. The m2 preserves only the roots, but was clearly longer than wide.

**REMARKS**

The identification of this specimen as a new species of genet is quite straightforward. It is the largest known genet, and the dentition is considerably more robust than the second largest, *G. victoriae* (Fig. 6.11), so that it is not reasonable that ER 46408 should represent a large fossil individual of the extant taxon. In view of the fact that the material is limited to a single specimen, however, it is not possible to say anything about the relationships of *G. nyakitongwer* sp. nov.

**Viverridae indet. aff. Civettictis sp.**

Specimen ER 878 is a partial left mandibular ramus with roots of p4 and m1 and the alveolus for m2. The ramus is very robust, with a massteteric fossa that extends anteriorly to just in front of the anterior end of m2. The p4 is elongated. Its anterior root is much larger than the posterior one. The m1 gives the impression of being relatively short, especially in its trigonid part. The m2 is large and two-rooted.

ER 7726 is a posterior part of a left m1 with talonid, metaconid and part of protocon-
id. The protoconid was low. The metaconid is set slightly posterior to the protoconid and is considerably lower. There is a broad notch between these two cusps. The talonid is long and low, with little relief. The hypoconid is the largest cusp, but the entoconid is slightly taller and sharper. There is also an indication of the presence of a hypoconulid, but the slight wear obscures some relief on the talonid.

Specimen ER 44717 is an upper carnassial of moderate size. The protocone is very large and protrudes anteriorly well beyond the anterior part of the paracone. It is large and conical in shape. There is no parastyle. The paracone is tall. Its anterior face is strongly angled towards distal. The carnassial notch is shallow and the metastyle is short.

Viverridae indet. aff. Genetta sp.

Specimen ER 5677 includes three fragments. The first is a neurocranium of a medium sized carnivore in which the sagittal crest is very low, as is the nuchal crest, while the occipitals are rounded. The second is a maxilla fragment with a possible anterior premolar. Both specimens are damaged and abraded, but the rounded appearance of the neurocranium is strongly reminiscent of that of genets and we suggest that the affinities of ER 5677 may lie there.

The third specimen is a small right scapula including much of the blade, although it is broken off before the neck (Fig. 6.12). The origin of the spine on the blade is
present, although the spine is missing. The epiphysis appears to be missing from the blade. The anterior and posterior borders of the blade are reasonably well-preserved.

These specimens represent a small carnivoran, most likely a genet, but are not diagnostic of any specific taxon.

**Viverridae indet. sp. A**  
Fig. 6.13

Specimen ER 702 is a left humeral shaft belonging to a large species of viverrid (Figure 6.13). The head and most of the distal end are missing. The morphology of this specimen is unlike that of felids, such as ER 2009A. The entepicondylar foramen is preserved in this specimen. In general, the specimen is short and stout. Although much larger in overall size, the proportions are similar to *Civettictis* with the exception that the shaft is much more robust. This specimen shows the characteristic flaring of the distal shaft seen in viverrids.

**Viverridae indet. sp. B**  
Fig. 6.14

ER 3754 is a proximal left femur that is the size of a cheetah or leopard, but is clearly not a felid, hyenid, or canid (Figure 6.14a1-d1). The intertrochanteric fossa is deep and does not extend very far inferomedially. The lesser trochanter is large and projects far from the shaft. In medial view, there is a slight hollow medial to the lesser trochanter before the curve of the shaft begins. Unfortunately, the top of the greater trochanter is broken off. The head slopes posteriorly onto the neck. The small size of the head also precludes this specimen being a felid. In short, this speci-
men is exactly what one would expect of a large viverrid.

This femur is very similar to that of *C. civetta*, but on a much larger scale. The fovea capitis is not mediolaterally elongate, as in ER 78, ER 80, ER 1347, or ER 2034. In fact, it looks slightly taller than it is wide. It appears to be from a larger taxon than is the humerus ER 702.

**Viverridae indet. cf. sp. B**

Fig. 6.14

ER 3797 is a proximal left femur that most likely belongs to a large viverrid (Fig. 6.14a2-d2). The head is eroded, but the greater and lesser trochanters are well-preserved. The intertrochanteric region appears relatively smaller in all proportions than in *Civettictis*. The intertrochanteric fossa is deep. The intertrochanteric crest forms a straight line from the top of the greater trochanter that proceeds distally and slightly medially before stopping and moving laterally to the lesser trochanter. The whole crest almost has a backwards checkmark look to it. The head is eroded, but the fovea capitis is preserved with its cortical bone. It lies on the superomedial surface in the midline of the head. The head extends far superiorly beyond the level of the superior end of the greater trochanter. There is a groove running at an angle demarcating the bottom of the greater trochanter on the lateral side.

This specimen is similar in size to ER 3754 and may be a geologically younger representative of the same species or lineage. The morphology of the neck is somewhat different, although this is difficult to evaluate given the fragmentary nature of the head. ER 3754 also has a lesser trochanter that projects to a much greater degree.

**Viverridae indet sp. C**

Fig. 6.14

The large left proximal femur ER 2034 (Fig. 6.14a3-d3) is missing the superior end of the greater trochanter. What is present of the greater trochanter flares laterally from the shaft. The lesser trochanter is very large and projecting, as in viverrids. The head is small and round. However, just as in ER 3797, this specimen has a small, but deep intertrochanteric fossa. In addition, the neck appears relatively short. These two conditions give the specimen an overall compressed look, unlike in modern viverrids. The intertrochanteric fossa appears to have been partially covered by a bulky medial lip from the greater trochanter. The neck projects anteriorly as in modern viverrrids. The area of attachment of the capsular ligament can clearly be seen.

This specimen has the mediolaterally
Fig. 6.14: Proximal femora of Viverridae indet. a) posterior view; b) anterior view; c) proximal view; d) medial view. a1-d1) ER 3754; a2-d2) ER 3797; a3-d3) ER 2034; 4) a4-d4) ER 1347.

elongate fovea capitis seen in ER 78, ER 80, and possibly ER 1347. ER 3754 lacks this feature. Other differences from ER 3754 are that the greater trochanter does not begin as medially on the superior surface of the neck in ER 2034, the wedge-like lesser trochanter in medial view, while the low lesser trochanter of ER 2034 is also a little less robust.

cf. Viverridae indet. A

Fig. 6.14

The large proximal left femur ER 1347 (Fig. 6.14a4-d4) is not particularly well-preserved as the head and greater trochanter are eroded. The lesser trochanter, however, is large.
CHAPTER 6: FAMILY VIVERRIDAE

Overall, this appears to be a large viverrid. This specimen is similar in morphology to ER 3754 and ER 2034, but is much larger and probably a different species.

Once again, the specimen follows the general viverrid pattern. However, as in ER 3754, the greater trochanter, flares more laterally than in extant *Civettictis*. In *Civettictis*, the lateral side of the greater trochanter is flatter. The anterior projection of the head and posterior projection of the lesser trochanter seem more accentuated than in the smaller specimens.

**DISCUSSION**

The viverrid fossil record from Koobi Fora can be said to substantially increase our knowledge of the group during the Plio-Pleistocene, but not to enhance our understanding of it.

If the identification of ER 5339 as the skull of *Pseudocivetta* is correct, this is, of course, a major advance in our understanding of this aberrant viverrid (and would make it somewhat less aberrant). However, definitive proof of this must await additional material from this or other sites.

The major obstacle to a better understanding of Viverridae in the Plio-Pleistocene is the large number of isolated postcranial specimens from Koobi Fora that cannot be related to any known taxon. These specimens (a humerus and a number of femora) all appear too large to belong to any of the taxa at Koobi Fora that are known from craniodental material. This is true even of *P. ingens*, which would be expected to have a postcranium that was smaller than indicated by any of these specimens.

There are two known African viverrid taxa that are large enough to have postcrania of the size of the Koobi Fora specimens described above. These are *Viverra leakeyi* and *Sahelictis korei*. The former was originally described from the Upper Laetolil Beds (Petter 1963) and subsequently from the Shungura Fm., Mbs C and G (Howell and Petter 1976), although the Mb. G specimen, a P4, is unlikely to belong to the taxon (Werdelin, personal observations). It thus has a stratigraphic range from 3.85 – 2.52 Ma (Brown 1994; Deino 2011). *Sahelictis korei* is an older taxon, known from Toros-Menalla in Chad and probably Langebaanweg, South Africa, with a stratigraphic range of ca 7 – 5 Ma (Peigne et al. 2008). Given this, it is possible that *V. leakeyi* is represented by postcrania at Koobi Fora, while the presence of *S. korei* is unlikely. This accounts for one (or possibly two if *V. leakeyi* can be equated with the two possible Viverridae indet. sp. B specimens) of the Koobi Fora femora, but the remaining specimens must belong to taxa that are entirely unknown from craniodental remains. This unsatisfactory state of affairs can, of course, only be remedied through new fossil finds that will be crucial to the understanding of viverrid evolution.

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The family Hyaenidae originated in western Eurasia in the earliest part of the Miocene (Turner et al. 2008; Werdelin and Solounias 1991). The earliest forms were small, viverrid-like omnivores such as Protictitherium and Plioviverrops, while more carnivorous forms such as Thalassictis did not evolve until the middle Miocene. The first hyenid with distinct adaptations to bone-cracking (sensu Werdelin 1989) appeared in Eurasia in the early late Miocene in the form of Adcrocuta eximia (Werdelin and Solounias 1990). However, the vast majority of hyenas of the Miocene were small- to medium-sized, dog-like forms (Werdelin and Solounias 1991, 1996).

The Hyaenidae suffered a mass extinction in the latest part of the Miocene – earliest Pliocene and subsequently, the ecomorphological composition of the family changed (Werdelin 1996). The dog-like forms were gone and hyenas of the Pliocene - Recent have, with the exception of the insectivorous Proteles, been either more or less bone-cracking, scavenging forms related to the living genera Hyaena, Parahyaena, and Crocuta, or members of the ‘hunting-hyena’ lineage, mainly the genus Chasmaporthetes. The reasons for this change in ecomorphological emphasis have been debated, but clearly relate in some way to the immigration of Canidae into Eurasia from North America in the late Miocene (Van Valkenburgh 1999; Werdelin 1996).

The history of Hyaenidae in Africa is quite different from that in Eurasia. The earliest representatives of the family are not recovered from Africa until the middle Miocene of Beni Mellal, Morocco. Species of Hyaenictis and Protictitherium were described from this site by Ginsburg (1977), but these identifications require further confirmation. The earliest sub-Saharan Hyaenidae are from the Namurungule Fm. of the Samburu Hills, Kenya (≤10 Ma). The material was described as Ictitherium, but in size and morphology it more closely matches Protictitherium (Nakaya et al. 1984; Werdelin and Peigné 2010).

In the latest Miocene, the African record of hyenas becomes increasingly diverse, with the majority of species belonging to mainly Eurasian genera such as Hyaenictitherium and Chasmaporthetes. However, the first endemic genera also appear, notably Ikelohyaena and Werdelinus (Bonis et al. 2010; Werdelin and Solounias 1991; Werdelin et al. 1994). Most remarkable about the African fossil record of Hyaenidae in the Miocene, however, is the absence of any species with specialized bone-cracking or scavenging adaptations in sub-Saharan Africa. Adcrocuta is present at Sahabi, Libya in the latest Miocene (Howell 1987), but apparently never migrated further south. Since the late Miocene hyenid record in sub-Saharan Africa is extensive, it is unlikely that this absence reflects sampling and the natural
assumption is that some other group of animals assumed the role of bone-eating scavengers. Which group of animals that might have been is, however, open to conjecture.

The Pliocene history of hyenas in Africa matches that of the rest of the world, with increasing loss of taxonomic and ecomorphological diversity. It is noteworthy that the fossil record clearly points to Africa as the place of origination of all four extant lineages. *Hyaena* and *Parahyaena* derive from *Ikelohyaena*, which was subsequently replaced by primitive members of the extant genera (*H. makapani* and *P. howelli*, respectively). *Crocuta* appears in Africa nearly 1.5 million years before appearing in Asia, and three million years before its first appearance in Europe, clearly showing its African origin. The origin of *Proteles* some 10 million years ago (Koepfli et al. 2006) is shrouded in mystery, but the genus has never been recovered outside Africa and must for lack of other information be assumed to have originated there. *Proteles* is not known from Koobi Fora and will not be further discussed herein.

**Subfamily Hyaeninae Gray, 1821**

**Genus Crocuta Kaup, 1828**

*Generic diagnosis:* Hyaenidae of large size; premolars massive, P4 paracone weak, metastyle blade greatly elongated; m1 trigonid elongated, metaconid vestigial or lost, talonid greatly reduced. (Emended after Kretzoi 1938.)

*Stratigraphic range in Africa:* Early Pliocene – Recent based on FAD in the Upper Laetolil Beds (≥3.85 Ma).

*Stratigraphic range at Koobi Fora:* Late Pliocene – Early Pleistocene based on FAD in the Lokochot Mb. (≤3.58 Ma) and LAD in the Chari Mb. (≥0.74 Ma).

**REMARKS**

Like the other genera of living hyenas, *Crocuta* first evolved in Africa, though its antecedents there are not known at present. The first record of *Crocuta* is *C. dietrichi* from the Upper Laetolil Beds (Werdelin and Dehghani 2011), although the West Turkana record of *C. eturono* from the Upper Kataboi Mb. of the Nachukui Fm. is only slightly younger (Werdelin and Lewis 2008).

Subsequent to this early origin from yet to be discovered ancestors, *Crocuta* evolves through a sequence of distinct morphotypes that we will here consider species (a more in-depth study of the evolution of the genus *Crocuta* is in progress), taking it from more striped hyena-like morphology to the modern day hunter/scavenger morphology. The origin of the extant species is not precisely known. All eastern African fossil *Crocuta* differ in diagnostic features from the extant species, suggesting that the latter is a very young species. This agrees with assessments of the behavioral ecology and physiology of extant *C. crocuta*, which show that certain aspects of its biology are under very high selection pressure, indicating that they cannot have been evolving for very long.

**Crocuta eturono** Werdelin and Lewis, 2008

*Fig. 7.1 – 7.3, 7.16*

*Synonyms:* Pachycrocuta brevirostris (*partim*) (Werdelin 1999)

*Holotype:* KNM-WT 40181, left mandibular corpus fragment with p4–m1, associated
isolated left p2, p3, right P3, partial left and
right P4, two lumbar vertebrae. Housed in
the National Museums of Kenya, Nairobi,
Kenya.

Type locality: Locality LO 6s, uppermost
Kataboi Mb., Nachukui Fm., West Turkana,
Kenya.

Specific diagnosis: Crocuta of a size equal to
or greater than the extant C. crocuta. Man-
dibular corpus very robust and deep. Lower
carnassial very long, especially compared to
the length of p3 and p4. Length ratios p3/m1
and p4/m1 well outside the range of all other
Crocuta.

Stratigraphic range in Africa: Late Pliocene
based on FAD in the Kataboi Mb., Nachukui
Fm. (≤3.4 Ma) and LAD in the Tulu Bor. Mb.,
Koobi Fora Fm. (≥2.62 Ma).

Stratigraphic range at Koobi Fora: Late Plio-
cene based on FAD and LAD in the Tulu Bor
Fm. (≤3.44 Ma – ≥2.62 Ma).

KOOBI FORA MATERIAL

CRANIODENTAL

KNM-ER 3748 (Fig. 7.1) includes a partial
p4 with a damaged posterior shelf and a dam-
aged m1. This specimen was identified as a
possible Pachycrocuta in Werdelin (1999).
The ramus is very deep, despite missing a
substantial part of its ventral side. The mas-
soteric fossa ends just posterior to the distal
end of m1. Too little is preserved of p4 to
enable statements regarding its morphology.
The m1 is long and massive. The paraconid
is longer than the protoconid. The tooth is
heavily worn and somewhat damaged and its
original dimensions cannot be determined
precisely. There is a small, broken metacon-
id closely appressed to the protoconid. The
talonid is broken, but appears to be short and
wide, with two cusps developed. Although
broken distally, the length and width of m1
can be approximated quite closely. The spec-
imen differs considerably from all other Cro-
cuta m1 from Koobi Fora in its much greater
size, approaching that of large C. spelaea.
However, it has a longer talonid than any
specimen of that species, which is accentu-
ated by the fact that, if anything, the talonid
length of KNM-ER 3748 is slightly under-
estimated due to the broken distal end of the tooth.

**POSTCRANIAL**

The second metacarpal ER 2119 has been described previously (Werdelin and Lewis, 2008) and assigned tentatively to *C. eturono* based on its size and possible age. Although similar to the second metacarpal of *C. ultra* ER 970, it is much longer, but within the range of modern *Crocuta*. In proximal view, the dorsal edge is narrower than in *Crocuta ultra* ER 970 or ER 2115, but the articular surface is much longer dorsoventrally. (Fig. 7.2a; 7.16d)

Only one other hyenid specimen falls within the size range of ER 2119, the left fourth metacarpal ER 699 (Fig. 7.3). Although it is possibly much younger (KBS Mb.) than ER 2119, it is rather large in comparison to the other *Crocuta* specimens from this member. However, the morphology of the carpal articulation is most like *Crocuta* in terms of the large breadth relative to dorsoventral height. In comparison to the Langebaanweg *Chasmaporthetes australis* (PQ-L 22204), another hyenid with relatively long metacarpals, this specimen is clearly shorter.

**REMARKS**

Both of the tentative referrals of postcranal material to *C. eturono* have been based on the large size and *Crocuta*-like morphology of those specimens. Both ER 2119 and ER 699 are longer relative to their articular surfaces than ER 970 (*C. ultra*) or ER 721 (*C. dietrichi*). If they are indeed *C. eturono*, it would indicate that this species was more cursorial than other species of *Crocuta* at this time and more like modern *C. crocuta* in terms of its manual morphology.

The recognition of *C. eturono* as a distinct early species of *Crocuta* has made the interpretation of the early evolution of the genus more complex. Previously, it was thought that *Crocuta* evolved from smaller, more generalized (but still clearly *Crocuta*) forms, such as *C. dietrichi*. The presence of *C. eturono* makes an evolution from larger, more hypercarnivorous forms plausible. These possibilities are discussed further in Werdelin and Lewis (2008).

*Crocuta dietrichi* Petter and Howell, 1989

*Fig. 7.4 – 7.7, 7.14*

**Synonyms:** *Crocuta* sp. (Barry 1987).

**Holotype:** LAET 79-2953, left mandibular
CHAPTER 7: FAMILY HYAENIDAE

**KOIOBI FORA MATERIAL**

**CRANIODENTAL**

The KNM-ER 3109 ramus is tall and robust, with a large mental foramen located beneath p2. The masseteric fossa does not reach the distal end of m1. The p2 is small and slender. Wear makes the mesial part of the tooth difficult to characterize, but there is a small distal accessory cusp. The main cusp is set mesial to the center of the tooth and the distal shelf is long but only slightly transversely expanded. The p3 appears to have been relatively slender. The p4 is small. Wear has obliterated most occlusal features, but there must have been a relatively large distal accessory cusp. The m1 is long and slender and has heavy buccal wear.

KNM-ER 3753 is a small and slender tooth lacking a mesial accessory cusp, though the main cusp continues mesially as a blunt crest. The main cusp is set mesial to the center of the tooth. The distal shelf is long but not transversely expanded, at least on the buccal side. The distolingual part is broken.

The KNM-ER 721 mandible (Fig. 7.4) is robust but not very deep. There is a single mental foramen beneath the distal root of p2. The coronoid process is robust and the masseteric fossa deep. The latter ends level with the distal end of m1. The p2 is moderately slender, with a distinct waist as seen in occlusal view. There is no mesial accessory cusp, but the crest that runs from the apex of the main cusp to the mesial end of the tooth is strong. The main cusp is not tall and is set somewhat mesial to the center of the tooth. The distal accessory cusp is well developed and set on a moderately expanded distal shelf. The p3 has no mesial accessory cusp, but the mesial crest
is strong. The main cusp is conical. The distal shelf is short and wide and probably held a small distal accessory cusp, but the area has been damaged on both sides, so it is difficult to judge the exact degree of development of this cusp. The p4 is short and robust, with a small mesial accessory cusp. The main cusp is tall and conical. The distal accessory cusp is tall but short. The distolingual cingulum crest forms an incipient cusp. The m1 is typical of Crocuta, with a tall and long paraconid and lower and shorter protoconid. The talonid is short. The specimen can be seen to have a relatively broad p4 and m1. The latter tooth is also relatively long. The extensive postcranial material belonging to this specimen is described below.

Fig. 7.4: C. dietrichi, ER 721H, mandible. a) occlusal view; b) left lateral view.

POSTCRANIAL

Specimen ER 721 preserves numerous postcranial elements. Within the axial skeleton (Fig. 7.5), a large portion of the cervical region is preserved. The atlas (ER 721L) differs from extant Crocuta in that the transverse processes are smaller relative to the overall size of the bone. These transverse processes are directed more ventrally, as in Hyaena. The dorsal surface of the atlas is much wider in comparison to the ventral surface in the midline. On the ventral surface there is an absolutely wide space between cranial articulations despite the small size of this specimen. In dorsal view, there is a smaller space between the transverse processes. The transverse processes are relatively wider, but not as rounded as in extant Crocuta.

The axis (ER 721K) differs from extant Crocuta in having a craniocaudally shorter body (Fig. 7.5a, b). The spinous process is on the same level as the zygapophyseal articulation for C3. In extant Crocuta, the distal end of the spinous process lies more cranially.

The ER 721 thoracic vertebrae (Fig. 7.5c-g) include T4 (D), T5 (R), T7/8 (G), T10 (P), T11 (F), T12 (A), T13 (U), and T16 (AD). T4 and T5 are similar to extant Crocuta in size. The spinous process is oriented at a more caudal angle and is slightly more gracile in both T4 and T5 than in extant Crocuta. In the midthoracic vertebra (T7/8), the spinous process is at a smaller angle and is quite long, although it is the right size and morphology to be a part of the skeleton. The articular facets, size and angle suggest that it is somewhat cranial to ER 721P. Vertebra ER 721G does not articulate with P or R.

The T10-12 (ER 721P, F, A) vertebrae have shorter bodies and are more gracile than in extant Crocuta. In addition, the spinous processes form a smaller angle with the axis of the
Fig. 7.5: Selected elements of the axial skeleton of *Crocuta dietrichi* partial skeleton ER 721. Note the gracile, elongated spinous processes. a-b) axis ER 721K, in a) left lateral and b) dorsal view; c) thoracic vertebra ER 721D, lateral view; d) thoracic vertebra ER 721R, lateral view; e) thoracic vertebra ER 721G, lateral view; f) thoracic vertebra ER 721F, lateral view; g) thoracic vertebra ER 721A, lateral view; h) lumbar vertebra ER 721E, lateral view (right side shown in mirror image); i) lumbar vertebra ER 721C, lateral view; j-k) sacrum ER 721O in j) left lateral and k) dorsal view.

vertebral column than is seen today in *Crocuta*. The small angles of the spinous processes suggest that the thoracic region may have had more curvature to it to accommodate longer processes at a smaller angle. In comparison to extant *Hyaena hyaena*, the fossil has longer transverse processes and is slightly more robust.

T13 was identified by the shape of the zygapophysis and is very similar to extant specimens. The posterior zygapophysis is not preserved. T16 looks like a lumbar vertebra, but still has anterior costal facets. It is clearly the last thoracic vertebra and articulates with L1 (ER 721B).

Four ER 721 lumbar vertebrae (Fig. 7.5h, i) are known: L1 (B), L2 (E), L4 (C), and L5 (S). The lumbar vertebrae are similar to extant *Crocuta* with the exception of the ends of the spinous processes. In extant *Crocuta*, the ends of T15 through L3 are flattened with large muscle insertions. The fossil specimens, as can be seen in E and C, are not quite as flattened at the end and are much less robust. The curvature of the lumbar region is roughly similar to extant *Crocuta*. The transverse processes are, for the most part, not preserved, but appear to have been smaller. There is some osteophytic growth all around the perimeter of the cranial surface of the centrum of L4. This not seen on the caudal surface. Unfortunately, L3 is not preserved.

The sacrum (ER 721O) is somewhat similar in general shape to *Crocuta* with one
major difference: the spinous processes are unusually long (Fig. 7.5j, k). Even the third sacral vertebra has an elongated process, an occurrence not seen in modern Crocuta. The craniocaudal length of the sacrum is shorter, while the width is equivalent to modern Crocuta. The sacral foramina are, therefore, angled and tucked into the bone. The caudal centrum is small compared to the cranial centrum, as is to be expected in an animal with a relatively short tail.

Four caudal vertebrae have been found (ER 721V, AG, AB, AF). ER 721V may be a second caudal vertebra as it does not seem to fit the sacrum and is slightly too small. In extant Crocuta, the first caudal vertebra may be partially fused to the sacrum. The transverse processes in the caudal vertebrae are much more robust in extant individuals than in the fossil. The caudal vertebrae are much more like those of a striped hyena, but with even shorter transverse processes than extant Hyaena.

The thoracic limb is not as well preserved as the axial skeleton. The left scapula (ER 721N) has a broken blade and the acromion is missing. The base of the spinous process, however, is visible along the part of the blade that is preserved. The glenoid fossa (Fig. 7.6a) is relatively pear-shaped, coming to a rounded point anteriorly on the lateral edge. The fossa is relatively narrow for its length, but is still rounder than in extant Crocuta and much more rounded than in extant H. hyaena. The supra-glenoid tubercle is curved as in extant Crocuta. In this respect, it is unlike H. hyaena, which is less curved. The fossil is different from C. crocuta and more like H. hyaena in that the tubercle extends less from the fossa than in Crocuta. The fossa itself is less deep than in H. hyaena. The inferior end of the glenoid is barely buttressed. The neck is angled such that the glenoid is directed slightly medially. The entire infraspinous fossa is preserved and is narrow and striped hyena-like. Although the end of the blade is broken, the area of attachment for teres major is preserved. This area is angled, with a portion falling on the vertebral border and the majority running along the end of the posterior

Fig. 7.6: Thoracic limb of Crocuta dietrichi partial skeleton ER 721. a) ER 721N, left scapula, view of glenoid; b) ER 721Q left distal humerus, anterior view; c-d) ER 721W proximal right metacarpal 4 in c) dorsal view and d) proximal view; e-f) ER 721X proximal right metacarpal 5 in e) dorsal and f) proximal view, note unusual morphology; g) ER 721Z, distal right metacarpal 5, note healed injury.
CHAPTER 7: FAMILY HYAENIDAE

The scapula is larger than that of *H. hyaena* and slightly smaller than in *C. crocuta*. Overall, the scapula is larger than that of *H. hyaena* and slightly smaller than in *C. crocuta*. The capitulum of this specimen is more rounded than in *C. crocuta* or *C. ultra* ER 970 and is more like that of *H. hyaena*. The fossil is also intermediate in size between *C. crocuta* and *H. hyaena*. The trochlea extends more posteriorly than in *H. hyaena*, but is not as high proximodistally as *C. crocuta*. In distal view, the trochlea is more narrow and “waisted” in appearance than that of ER 970. Although ER 721Q is broken, it does appear to have had a supratrochlear foramen.

The proximal and distal ends of metacarpal 4 (ER 721W, Y) and metacarpal 5 (ER 721X, Z) also appear to be halfway in morphology between *H. hyaena* and *C. crocuta* in shape (Fig. 7.6c-f). In metacarpal 4, the carpal articulation is much more narrow mediolaterally in all areas than in later unpublished *Crocuta* material from Olorgesailie. However, the articulation extends more ventrally than in the Olorgesailie specimen. The narrowness suggests a more narrow, tightly compacted manus than in the Olorgesailie material. The fifth metacarpal (Fig. 7.6g) differs in morphology from *Crocuta ultra* ER 970. The groove between the tuberosity and the articular surface is larger in this specimen than in ER 970, particularly on the ventral surface. This may be related to the healed trauma found on the distal end of this metacarpal and resulting osteoarthritis.

Only a few elements of the pelvic limb remain. The right os coxae (ER 721I) is missing the pubic portion, but is otherwise well preserved (Fig. 7.7a). The pelvic inlet seems somewhat narrow dorsoventrally with respect to modern *Crocuta*. The shape of the obturator foramen cannot be assessed due to the missing portions. The acetabulum is slightly shorter and wider than in extant *Crocuta*. The ilium is quite unlike that of extant *Crocuta* and is more gracile for its size. The neck of the ilium is also longer than in *Crocuta*. Like *H. hyaena*, this specimen has a blade that is straighter and less curved laterally at the tip than in extant *Crocuta*. A unique feature among hyenids, however, is that the iliac blade is more compressed and triangular in shape, as seen in this specimen. The angle formed by the ilium and ischium in this specimen is similar to extant *Crocuta*. In *Hyaena*, the blade is angled more posteriorly, thus forming a more acute angle. The ischium is unlike *Hyaena*, which has much more curvature than in this specimen. This specimen also has less flaring in the ischium than in *C. ultra* ER 794 from the Okote Mb (Fig. 7.15e).

The proximal left tibia (ER 721J; Fig. 7.7b, c) is also reasonably well preserved. This specimen has a more gracile shaft than in extant *Crocuta* and is smaller. In comparison to the possible *Parahyaena* tibia, ER 872, this specimen is smaller overall. Despite its gracility, ER 721J is more similar to *Crocuta* than *Hyaena* in morphology. However, in medial view, the proximal end is even flatter than that of extant *Crocuta*. In posterior view, there is not as much lateral expansion of the proximal end as there is in extant *Crocuta*. In lateral view, the proximal end does not extend as far posteriorly. The tuberosity is also narrower relative to the size of the proximal end and is slightly more elongated than in extant *Crocuta*.

The right calcaneum (ER 721T; Fig. 7.7d, e) is very similar to *C. crocuta*, but smaller. It differs from both *C. crocuta* and *H. hyaena* in that the articulation for the cuboid is less sloped across the surface and rounder in circumference. It is similar to *C. ultra* ER 970, but is much better preserved. The cuboidal facet is relatively round. The tuber calcanei has
the medial projection seen in Crocuta, but not Hyaena. In medial view, the proximal half of the specimen is more tapered than in the possible C. ultra calcaneum ER 3765K and the medial projection of the tuber calcanei is larger. This specimen is not as robust as ER 3765K.

REMARKS

Overall, Crocuta dietrichi material is smaller and more gracile than modern Crocuta. While the similarity to other species of Crocuta is clear, some features are quite Hyaena-like. The vertebrae, in particular, suggest a more extant Hyaena-like posture and form of locomotion than a modern Crocuta one. The gracile, elongated spinous processes and their orientation, along with that of the transverse processes, suggest a lack of carcass carrying adaptations and a lack of the unique sloping posture of extant Crocuta, as noted previously (Lewis, 1995, 1997). This hypothesis is currently being tested.

The feet are also unlike extant C. crocuta in that C. dietrichi lacks the more elongated metacarpals of extant Crocuta and in some ways tends to resemble Hyaena in the manus. The pes, however, seems more like modern Crocuta, although metatarsals are not preserved.

Crocuta cf. C. dietrichi

Fig. 7.1, 7.8

KOOBI FORA MATERIAL

CRANIODENTAL

The P3 of ER 1541 is large and pyramidal in shape. There is a crest running from the apex of the main cusp to the mesiolingual corner of the tooth and another from the apex of the
main cusp distally, where it meets a low distal accessory cusp. The cingulum runs around the base of the tooth except on the central part of the buccal side, but is best developed on the lingual side. The P4 is long and slender, with a low protocone. The paracone and metastyle are both tall. This specimen had a relatively broad P4 blade, though not as broad as that of KNM-ER 10078.

KNM-ER 3745 is a mandibular ramus with a large mental foramen located below the mesial part of p2. The diastema is short. The teeth are difficult to assay, though the anterior premolars appear to have been relatively slender.

The neurocranium KNM-ER 361 lacks everything anterior to the postorbital processes, as well as the zygomatic arches and the sagittal crest. The specimen is heavily worn. It can be identified as Crocuta on the basis of the morphology of the basisphenoid and its size, which is considerably less than that of Pachycrocuta.

POSTCRANIAL

A variety of postcranial elements have been referred tentatively to C. dietrichi based on Crocuta-like features, overall gracility, and, to a lesser degree, age.

The second metacarpal, ER 3761 (Fig. 7.2b), is similar to extant Crocuta, but differs slightly in morphology and is smaller and more gracile, particularly in the articular surfaces. The proximal morphology and orientation of the shaft suggest that the metacarpals were more closely compacted than in C. ultra (ER 970). Although it is the smallest, most gracile specimen of Crocuta at Koobi Fora and is within the size range of extant striped hyenas and Ikelyhaena abronia, the morphology seems more Crocuta-like than Hyaena-like. However, the attribution to this genus remains tentative.

The distal left femur, ER 3745A (Fig. 7.8a), associated with the mandible described above is smaller than extant Crocuta, but larger than Hyaena. It is similar in morphology to C. ultra ER 3765, but is not as robust. The patellar groove with parallel sides is like the remnants of what is seen in ER 3765. That, along with age and robusticity (relative to Hyaena) of the specimen led to the current taxonomic designation.

Two tibial specimens are known. The left tibial shaft, ER 654, includes a large nutrient foramen. A small amount of the distal articular facet is preserved. The sharp medial

Fig. 7.8: Selected elements referred to Crocuta cf. C. dietrichi. a) distal left femur ER 3745A, anterior view; b-c) distal half of tibia ER 3103 in b) posterior and c) distal view.
edge of the shaft is most similar to the *C. dietrichi* ER 721J tibia. However, it differs from ER 721J in not having a sharp lateral edge.

The distal right tibia, ER 3103 (Fig. 7.8b, c), is one of only two specimens of *Crocota* from the Lokochot member (the other being ER 3100, a robust proximal phalanx assigned to *Crocota* sp.). The morphology is more like *Crocota* than *Hyaena*. It is distinguished from extant *Crocota* by being narrower anteroposteriorly.

**Crocota ultra** Ewer, 1954

*Fig. 7.9 – 7.16*

**Synonyms**: *Crocota spelaea capensis* (Broom 1939); *Crocota ultra ultra* (Ewer 1954a); *Crocota crocuta latidens* (Ewer 1954a); *Crocota venustula* (Ewer 1954b); *Crocota crocuta angella* (Ewer 1954b).

**Holotype**: KA 58, anterior part of skull with rt damaged C, P2, M1, occipital part of skull, rt and lt mandibular fragments with lt p2-m1, rt p3-m1, lt c, lt i2, i2, first thoracic vertebra, various limb elements (Ewer, 1954a, p. 571, Figs 3, 4). Housed in the Ditsong National Museum of Natural History (formerly the Transvaal Museum), Pretoria, South Africa.

**Type locality**: Kromdraai A, South Africa.

**Specific diagnosis**: A medium-sized *Crocota* with a broad low skull, relatively short snout with compressed incisor region; premaxillae and frontals not in contact; postorbital processes small; P4 with long metacone and anteriorly sloping protocone; M1 small and situated internal to P4; mandible shallow with horizontal lower border; p4 with anterior cusp reduced; M1 with long blade and metaconid absent or at most appearing as a minute vestige. (Ewer 1954a).

**Stratigraphic range in Africa**: Late Pliocene – Early Pleistocene based on FAD in the Lomekwi Mb., Nachukui Fm. (<3.35 Ma) and LAD in Olduvai, Bed II (>1.2).

**Stratigraphic range at Koobi Fora**: Early Pleistocene based on FAD in the Upper Burgi Mb. (<ca 2.0 Ma) and LAD in the Okote Mb. (>1.38 Ma).

**KOOBI FORA MATERIAL**

**CRANIODENTAL**

The ramus of ER 896 (Fig. 7.9) is robust, with a single mental foramen located beneath the distal root of p2. The canine, as judged from the root, must have been robust and moderately flattened. The distal shelf of p2 was expanded both lingually and buccally and there was a low distal accessory cusp. The p3 is large and pyramidal in form. The mesial cingulum cusp is minute. The main cusp of p3 is large and is angled distally. The distal shelf is short, with a small distal accessory cusp. The p4 is large and more slender than p3. The mesial accessory cusp is large and low. The main cusp is pyramidal and the distal shelf long. The distal accessory cusp is large, while the distolingual cingulum crest is very low. As judged from its mesial part, the m1 was very robust.

All teeth on KNM-ER 4387 are heavily worn, especially the canine. The ramus is robust, with a single mental foramen located beneath the distal root of p2. The c is relatively small, but wear has obliterated all other features of interest. The p2 is small and slender, with a narrow distal shelf and small distal accessory cusp. The main cusp is set mesial to
the center of the tooth and there is no mesial accessory cusp. The p3 is short and pyramidal. The mesial cingulum cusp is very small. The main cusp is broad and the distal shelf short. There must have been a relatively well developed distal accessory cusp, but it has been worn down along with the main cusp. The p4 is slender. The mesial accessory cusp is very small and the main cusp large. The distal shelf is long and must have had a substantial distal accessory cusp, though this is now worn flat. The distolingual cingulum crest is low.

The inferior border of the orbit of ER 940 is preserved and ends level with the posterior root of P3. This tooth is large and robust, with a wear facet that is inclined from buccal to lingual, and extends dorsoventrally along the mesiolingual face of the tooth to the cingulum. There is a very small distal accessory cusp that is essentially an extension of the cingulum. The cingulum runs around the entire base of P3 except for the central part of the buccal face. The P4 is long and slender. It has a low but well developed protocone. The metastyle is very long. There is an extensive wear facet from the mesial end of the para-syle to the distal end of the metastyle, extending dorsoventrally to the lingual cingulum.

The ramus of KNM-ER 4967 is fairly robust. The p3 is large and robust with a main cusp that has crests running mesially to the mesiolingual part of the tooth and distally to a small distal accessory cusp. The distal shelf is very compressed and the distal cingulum crest oriented nearly vertically. The p4 is large. It is broken mesially but would appear to have had a mesial accessory cusp. The main cusp is pyramidal and the distal shelf large but narrow and tapering distally. There is a substantial distal accessory cusp.
The ramus of KNM-ER 10078 (Fig. 7.10) is robust, with a single mental foramen set beneath the middle of p2. The canine is rather small, with clear antero- and posteromedial crests. The diastema is short and the p2 large but relatively slender. The distal shelf is only expanded on the lingual side. There is no mesial accessory cusp, but a blunt, well-developed distal accessory cusp is present. The p3 is large but relatively slender. There is no mesial accessory cusp, nor any distinct cingulum cusplet. The main cusp is tall and pyramidal. The distal shelf is short and the distal accessory cusp small and more separated from the main cusp than in other Koobi Fora specimens. The p4 is large. The mesial end is damaged, but the mesial accessory cusp must have been either very small or non-existent. The main cusp is pyramidal and the distal shelf is long and tapering. The distal accessory cusp is long and somewhat crest-like, while the distolingual cingulum crest is very

Fig. 7.10: *C. ultra*, ER 10078, partial cranium and ramus. a-c) damaged cranium in a) ventral, b) right lateral, and c) anterior view; d-f) partial left ramus in d) occlusal, e) buccal, and f) lingual view.
low. The m1 is long and robust with a small talonid with two distinct cusps, which may be identified with the entoconid and hypoconid.

The skull consists of only a small part of the frontals and nasals, the dentary parts of the maxillae and premaxillae, the zygomatic arches, mastoids and occipitals. The I1 and I2 are small and very worn. The I3 is large and robust, with a prominent medial cingulum. The upper canine is small and moderately transversely flattened. The P1 is small and nearly round in occlusal view, with a short, crest-like cusp. The P2 is large. There is no mesial accessory cusp. The main cusp is large and conical, while the distal accessory cusp is small and low. There is a short distolingual shelf. The P3 is large and pyramidal. There is no mesial accessory cusp, but a crest runs from the apex of the main cusp to the mesiolingual corner. The main cusp is very large, while the distal shelf is very short and has a low distal accessory cusp. The P4 is long and slender. The parastyle is large, while the protocone is low and relatively small. The paracone is tall and conical, while the metastyle is long.

The p4 of KNM-ER 897 has a well developed mesial accessory cusp from which a strong crest runs to the apex of the main cusp. The main cusp is tall and conical. The distal accessory cusp is well developed and trenchant in morphology. The distolingual cingulum crest is broad. The main cusp in this specimen is short relative to the length of the accessory cusps.

The ramus of ER 358 (Fig. 7.11) is robust. There is a single mental foramen set beneath the mesial root of p2. The ramus is thickest beneath p3. The canine is only slightly recurved and has distinct antero- and posteromedial crests. The diastema is short. The p2 is short and robust. There is no mesial accessory cusp and the main cusp is set anterior to the center of the tooth. The distal shelf is wide, with a low but distinct medially placed distal accessory cusp. The distal shelf is expanded both lingually and buccally. The p3 is a pyramidal tooth. There is no mesial accessory cusp, only a small bulge of the cingulum mesial to the main cusp. The main cusp leans distinctly distally. The distal shelf is very short, with a small distal accessory cusp closely appressed to the main cusp. The p4 is large. The mesial accessory cusp is small and appressed to the main cusp, which is tall. The distal accessory cusp is large and the distolingual cingulum crest is reduced to a cusplet. The m1 is too broken to assess.

ER 1659 lacks a mesial accessory cusp, but a crest runs from the mesialmost point of the tooth to the apex of the main cusp. The latter is pyramidal in shape and set mesial to the center of the tooth. There is a small distal accessory cusp set in a large distal shelf that expands distally.

ER 723 includes left i2, right i3, left c, and left and right p2-m1 of a single individual. The p2 is short. It lacks an mesial accessory cusp, but the mesial crest leading to the apex of the main cusp is strong. The main cusp is situated somewhat mesial to the midline of the tooth. The distal accessory cusp is well developed and located in a strongly expanded distal shelf. The p3 has a strong mesial crest. The main cusp is pyramidal, while the distal shelf is well developed, but worn, so that the condition of the distal accessory cusp cannot be determined. The p4 is long, with well developed mesial and distal accessory cusps. The distolingual cingulum crest is low. The m1 is low and long, with a short, incipiently two-cusped, talonid. The associated postcrania of ER 723 will be described below.

ER 694 is a partial right maxilla frag-
ment with P3 and roots of P4. The infraorbital foramen is set just mesial to the mesial root of P3. The P3 is relatively slender, with a crest running from the apex of the main cusp to the mesiolingual corner of the tooth. The main cusp is pyramidal in shape. There is a small distal accessory cusp. The cingulum runs around the base of the crown except in the central portion of the buccal face.

The ramus of ER 330 is not particularly robust. There is a single mental foramen beneath p2. The masseteric fossa does not quite reach the distal end of m1. The p2 has a large, expanded distal shelf, housing a small distal accessory cusp.

The anterior part of the ER 360 ramus is small and the individual must have been relatively young. The canine is moderately flattened. The diastema is very short. The p2 is short and moderately wide. The distal shelf is mostly expanded on the lingual side. The distal accessory cusp is well developed and set towards the buccal side of the tooth. There is no mesial accessory cusp. The p3 is short and robust, with a small mesial cingulum cusp, a tall, pyramidal main cusp, and a short distal shelf with a low distal accessory cusp pressed to the main cusp.

In ER 367 the buccal side of the ramus is worn away, exposing the roots of the premolars. The ramus was not very robust. The p2 is small, with a minute anterior cingulum.
cusp, a tall, pyramidal main cusp set mesial
to the midline of the tooth, and a large dis-
tal shelf that expands distally and holds a low
distal accessory cusp. The p3 is robust but not
very wide. There is a very small mesial cingu-
lum cusp from which a low crest leads to the
apex of the main cusp, which is pyramidal in
shape. The distal shelf is short, with a small
distal accessory cusp and a low, blunt lingual
cingulum crest separated from the main cusp
by a narrow valley. The p4 is broken distally
and on the mesial face of the main cusp. It
has a low mesial accessory cusp and a slightly
better developed distal one. The main cusp is
tall.

ER 4421 does not retain enough of
the orbital border to determine its position
relative to the tooth row. The P3 is not fully
erupted. It is a large, pyramidal tooth with a
low crest running from the apex of the main
cusp to the mesiolingual corner of the tooth.
Another crest runs from the apex of the main
cusp to the distal end of the tooth. The extent
of the basal cingulum cannot be determined
due to the state of eruption of the tooth. The
P4 is long and slender, with a low but well
developed protocone and tall paracone and
metastyle, but lower parastyle. There is a
strong lingual cingulum. The tooth shows no
evidence of wear.

The ramus of ER 667 is relatively slen-
der. The p3 is large and slender. It is less
compressed than in other specimens, such as,
e.g., KNM-ER 358 and 360. There is no me-
sial accessory cusp and the mesial part of the
cingulum is relatively weak. The main cusp
is tall and pyramidal. The distal shelf is short,
though slightly less vertically oriented than
in KNM-ER 358 and 360. The distal acces-
sory cusp is short and robust.

The ER 44485 mandible is robust and
curved. It increases in depth to a point be-
neath the distal root of m1. There is a single
large mental foramen beneath p2/p3. The
masseteric fossa reaches to the distal end of
the m1 protoconid. The p4 is robust, with a
moderately large mesial accessory cusp ap-
pressed to the main cusp, a large, pyramidal
main cusp and a low, somewhat crest-like
distal cusp. The distolingual shelf is broad
with a crest-like margin but no cusp. The
m1 is long and low, with a long and robust
paraconid and shorter, lower and more slen-
der protoconid. The talonid is small and two-
cusped, set somewhat to the lingual side of
the protoconid. There is a mesial cingulum
that runs from the middle of the buccal side
of the paraconid to the middle of the lingual
side of that cusp. The p3 is a robust, pyrami-
dal tooth with a small mesial shelf lacking a
cusp, but with a distinct crest that runs from
the mesial end of the tooth to the apex of the
main cusp. The latter is tall and pyramidal.
The distal shelf is broad, with a small distal
accessory cusp. The canine is slender and re-
curved. Only the crown is present.

In specimen ER 40417, the P2 is ro-
 bust, with a small mesiolingual cingulum
cusp, a conical main cusp, and a small distal
cusp that is moderately appressed to the main
cusp. The mesiobuccal part of P3 is broken,
as is part of the mesiolingual side including
the mesial accessory cusp. The main cusp
is tall and conical and the distal accessory
cusp (also broken) small. This material also
includes a canine root and other bone frag-
ments.

ER 44433 is a complete and unworn
p3. There is no mesial accessory cusp, but a
strong crest runs from the apex of the main
cusp to the mesial end of the tooth. The main
cusp is tall and pyramidal. The distal shelf is
short and has a small distal accessory cusp.

The very worn maxilla with roots of P3,
ER 40418, is not diagnostic below the family level, but see postcranial, below.

POSTCRANIAL

Associated with the cranium ER 10078 are some nondescript rib fragments (ER 10078D-J).

The ER 970 partial skeleton (Fig. 7.12) is robust and relatively complete but shows signs of moderate age-related arthritis. For example, the lateral astragalar facet on the calcaneum shows clear signs of lipping. Similar signs are seen throughout the skeleton. The skeleton overall appears to be of an older individual that has gone through osteoporotic degeneration, which means that measurements of this specimen should not be considered typical for *C. ultra*.

The ER 723 skeleton (Fig. 7.13) is quite fragmentary. The few well-preserved specimens are similar in size in morphology to ER 970. Some of the well-preserved specimens are commented on below.

A tiny fragment of the axis, ER 723Y, is known and includes the dens and atlantoaxial articular facet. In addition, four caudal vertebrae have been preserved: ER 723Q, R, S, T.

What little is known of the thoracic limb of *C. ultra* is quite fragmentary. The few well-preserved specimens are similar in size in morphology to ER 970. Some of the well-preserved specimens are commented on below.

A nearly complete left ulna of *C. ultra* is known (ER 2008; Fig. 7.15a, b). This specimen is only missing the olecranon process and the distal end. On the medial surface there is a large ridge for the attachment of biceps brachii and brachialis. Other specimens of *Crocuta* from Koobi Fora do not have this region preserved. This specimen has been assigned to *C. ultra* based on its similarity to fragmentary material from the ER 970 skeleton, the proximal portions of the right and left ulnae (ER 970A, B; Fig. 7.12c, d) and the distal right shaft (ER 970AM). The ER 970 specimens are the same size as ER 2008, although the ER 970 specimens are more robust. The only other difference is in the amount of lipping of the semilunar notch onto the medial side. The medial coronoid process may be slightly more rectangular than in ER 2008. The ER 970 material has a short, sloped olecranon as in large *Crocuta*, such as *C. spelaea*.

A well-preserved left proximal ulna (A) and shaft (C) of ER 40418 (Fig. 7.15c, d) have been recovered. The proximal specimen is missing a little of the anteromedial end of the medial coronoid process, although it looks like the very anteriormost end is only slightly eroded - just a small portion of the medial side is missing. Thus, the medial coronoid process may be wider anteriorly than it appears. This specimen is larger than the ER 970B (*Crocuta ultra*) ulna. The morphology is typically *Crocuta* and robust. It looks like ER 2008, but with a more complete proximal end.

A small portion of the ulnar shaft, ER 723Z, is also known. The ulnar shaft is similar to that of ER 970.

A complete left radius (ER 970D, E;
Fig. 7.12: Appendicular skeleton of *Crocuta ultra* partial skeleton ER 970. a-b) distal right humerus ER 970F in a) posterior and b) anterior view; c-d) proximal left ulna ER 970B in c) lateral and d) anterior view; e-f) proximal left radius ER 970D in e) anterior and f) proximal view; g-h) distal left radius ER 970E in g) anterior and h) distal view; i) dorsal view of right calcaneum ER 970G; j) proximal view of right scapholunar ER 970L; k) proximal view of right navicular ER 970H; l) dorsal view of right cuboid, ER 970I; m) dorsal view of right metacarpal 5 ER 970N; n) dorsal view of distal half of left metacarpal 1 ER 970A1; o) medial view of proximal phalanx 1 ER 970AE; p) medial view of terminal phalanx 1 ER 970Z.

Fig. 7.12e-h) in pieces and two proximal right radii (ER 970E and ER 7230) are known. The ER 7230 specimen (Fig. 7.13a, b), although fragmentary, is similar in morphology to the ER 970 specimens. All are very similar to extant *Crocuta* in morphology, but the ER 970 specimens show clear degenerative changes. The material is more robust than ER 6077 and ER 44425. The shaft is fairly long and straight. The ER 970 radius is from an individual that is approximately the same size as the ER 2008 ulna. The anteroposterior curva-
Fig. 7.13: Selected elements of the partial postcranial skeleton of *Crocuta ultra*, ER 723. a-b) proximal right radius ER 723O in a) anterior and b) proximal view; c) anterior view of patella ER 723W.

Fig. 7.14: Distal view of *Crocuta* humeri demonstrating that *C. ultra* and *C. dietrichi* do not differ greatly in size, but do differ greatly in morphology. a) ER 721Q *C. dietrichi*, note that the lateral side of the olecranon fossa is broken off; b) ER 970F *C. ultra*, note the anteroposteriorly thicker trochlea.

structure of the shaft is slightly greater than *Crocuta* sp. specimens ER 6077 and ER 44425.

Portions of both the left and right manus of ER 970 are known, including the left and right scapholunar (ER 970K, L; Fig. 7.12j), cuneiform (Q) and pisiforms (AD, AH). The right scapholunar is complete, but the left is broken and not measurable. The morphology of these specimens clearly that of *Crocuta*.

The ER 970 right metacarpals all articulate. This individual shows what looks like age-related osteoarthritis around the proximal and distal joints and slightly in the shaft. The most obvious changes occur in the head. The bones seem a little gracile, particularly in comparison to the larger metacarpals of *C. ultra* (ER 2119, 699). They are much shorter than in modern *Crocuta* and *C. eturono*.

One of the more unusual finds is the presence of the distal halves of the right (ER 970AU) and left (ER 970AJ; Fig. 12n) first metacarpals; elements that are usually not preserved due to their small size and overall gracility. ER 970AJ articulates well with phalanx ER 970AE. In fact, the entire first digit is known (see below), even if the bones are not all complete. ER 970AU is a little more arthritic than ER 970AJ, with a lot of osteophytic lipping and a large arthritic growth on the dorsal surface.

The second right metacarpal, ER 970P/AA (Fig. 7.16c), looks very much like living *Crocuta* in its straight shaft and triangle-shaped carpal articulation. The articulation is deeply indented. The lateral surface of the shaft and articulation is extremely flat. This metacarpal is slightly longer than the fifth metacarpal, as expected, and the head is more robust.

The right third metacarpal, ER 9700/S, has a straight shaft and is moderately robust with the blocky head typical of *Crocuta*. The ventral part of the sagittal crest appears to be affected by arthritic changes.

The proximal and distal thirds of right metacarpal 4 (ER 970A1, AC) also look similar to modern *Crocuta*. Despite the missing shaft, the length of this metacarpal can be estimated based on the typical proportions amongst *Crocuta* metacarpals. It has a reconstructed total length of approximately 79.5 mm when all of the metacarpals are placed in articulation. The head is only slightly less ro-
CHAPTER 7: FAMILY HYAENIDAE

Fig. 7.15: Additional postcranial material referred to *Crocuta ultra*. a-b) left ulna ER 2008 in a) lateral and b) anterior view; c-d) proximal left ulna ER 40418A in c) lateral and d) anterior view.; e) lateral view of left os coxae ER 794.

bust than that of the third metacarpal.

A complete right (ER 970N/AB; Fig. 12m) and proximal left (ER 970M) fifth metacarpal are known. Once again, the head shows more degenerative arthritis than the proximal end. There is more arthritis, however, in the proximal fourth and fifth metacarpals than in the second and third. The fifth metacarpal is approximately 2/3 the length of the third metacarpal, but similar in robusticity. These proportions are typical for *Crocuta*. The proximal end has a large groove bisecting it, as in other *Crocuta*. The lateral tuberosity is not particularly robust. The proximal end is not very robust.

The ER 970 phalanges clearly show the individual’s age, as they are osteoporotic and arthritic despite their robusticity. The terminal phalanges are robust and chunky and look like typical hyenid terminal phalanges: little curvature and relatively blunt.

Several manual phalanges are known. The tiny manual first proximal phalanx, ER 970AE (Fig. 7.12o), articulates with the tiny terminal phalanx ER 970Z (Fig. 7.12p). ER 970Z is robust, but short. The ER 970AF middle phalanx is robust and articulates with terminal phalanx ER 970X. Both appear to be from the second manual digit. The terminal manual phalanx, ER 970R, is the largest of the preserved terminal phalanges. It may articulate with ER 970AF, but seems too large for it. The claw support is chunky, but somewhat more curved and pointed than the other preserved terminal phalanges.

Pedal phalanges from either the third or fourth digit of ER 970 are known: proximal (AG), middle (T), and terminal (Y). Although the proximal phalanx is poorly preserved, the middle and terminal phalanges are better preserved and clearly articulate.

In addition to the ER 970 phalanges,
A third proximal phalanx, ER 897G, is also known. This specimen is missing part of the base. A proximal phalanx (P) from ER 723 has also been recovered.

The left os coxae, ER 794 (Fig. 7.15e), is mostly complete and includes a portion of the pubic symphysis and a little of the right pubis. The pelvic inlet appears narrower in this specimen than in extant *Crocuta*. The obturator foramen still retains a distinct division between the superior and inferior portions of the foramen. The small superior portion is distinguished from the larger inferior one not only by bony projections for the obturator ligaments, but also by a narrowing of the foramen in this region. This narrowing gives the foramen the appearance of a bottom-heavy pear. In extant *Crocuta*, this distinction between superior and inferior portions is much less clear. In extant *H. hyaena*, the distinction is greater than in extant *Crocuta*, but the superior portion is relatively small relative to the fossil and extant *Crocuta*. The acetabulum is similar in size to extant specimens of *Crocuta*, but the tubercle superior to the acetabulum is much smaller than in extant individuals. The ischium is less flared than in *Hyaena*, but more so than in *C. dietrichi*, ER 721I. The ilium and pubis are indistinguishable in shape from modern *Crocuta*. However, in superior view, the iliac crest is slightly more s-shaped than in ER 721I.

Only fragments of the ilium of the ER 970 and ER 723 individuals are known, including a right ilium fragment (ER 970AK), a fragment of the iliac blade (ER 723V), a portion of the left acetabulum and ilial neck (ER 723V), and a fragment of ischial tuberosity (ER 970AL). These fragments are similar to ER 794 in robusticity and in the curvature of the ilium leading to the sacral articulation.

ER 897C includes the head and neck of a right femur. It does not seem to differ from ER 953, ER 1569, or ER 1539, material that has been assigned tentatively to *C. ultra*. The ER 723 femoral head (U) is also similar to these specimens in size and morphology. From ER 970, only a fragment of the greater trochanter (V) is present. It does not differ substantially from ER 953 except that it is much more robust.

The patellae of the different species of *Crocuta* are not particularly distinct in morphology from one another. A complete patella, ER 723W (Fig. 7.13e), is typical for *Crocuta*. As with most hyenids, the articular surface takes up the entire posterior surface.

The ER 897F tibia is so fragmentary that it is barely recognizable. The distal right fibula, ER 970AO, looks like other specimens of *Crocuta*.

Several tarsals from the right pes of ER 970 have been recovered and articulate. The right calcaneum, ER 970G (Fig. 7.12i), is missing the medial process of the tuber calcanei, but is otherwise complete. It is about the same size as *C. dietrichi*, ER 721T, but is more robust and thickened for its size. The cuboidal facet slopes in a manner similar to *C. crocuta*. The facet is ovoid, as in *C. crocuta*, and can be distinguished from the round facet in ER 721T. However, there are osteoarthritic changes in the cuboidal facet, so the shape may be due to age-related changes. In comparison to ER 721T, the distance from the sustentaculum tali to the tuber calcanei is roughly similar. The medial process is broken off, however. The right navicular, ER 970H (Fig. 7.12k), is not unlike the other navicular, ER 3765G, from Koobi Fora, even though that specimen belongs to *C. dietrichi*. In contrast, the right cuboid, ER 970I (Fig. 7.12l) is like modern *Crocuta* in size and proportions. Although the ectocuneiform (ER 970AV) is
incomplete, the mesocuneiform (ER 970U) is well-preserved and is similar to modern Crocuta.

The ER 970 partial skeleton includes the proximal third of a right third metatarsal (J) and proximal end of a right fifth metatarsal (W). Both specimens show the typical Crocuta morphology. Other material includes ER 723N and M, the distal halves of right third and fourth metatarsal, respectively, and ER 897H, a distal metatarsal probably belonging to the third digit. Epiphyseal lines are still visible on the ER 723 material, although the epiphyses are well-fused.

REMARKS

While ER 970 had noticeable arthritis and the healthy ER 723 is quite fragmentary, some generalizations about Crocuta ultra morphology can be made. In comparison to C. dietrichi, C. ultra may not necessarily have been larger in terms of overall height or head to tail length, but it certainly was much more robust. The robusticity is similar to that of extant Crocuta, but C. ultra was a smaller, or at least shorter-limbed, animal.

One great difference between C. dietrichi and C. ultra is the morphology of the distal humerus (Fig. 7.14). C. ultra is much thicker anteroposteriorly in distal view. This type of thickness is associated with heavy loading of the elbow (Lewis, 1995; see Chapter 9 for a similar discussion of Homotherium vs. other machairodonts) and may indicate a move towards a more modern Crocuta-like forelimb. This may indicate the beginning of the ability to carry larger carcasses by mouth.

A second hint at the beginnings of modern Crocuta posture is the changes in the os coxae from C. dietrichi to C. ultra. The ilium is broader and more curved as in C. crocuta, rather than narrower and straighter as in C. dietrichi. Could this slightly more bowl-like pelvis reflect a change in the center of gravity such that the gluteal muscles have been reoriented to provide more force in extension/stability, while the pelvis is lower and more accommodation must be made for the weight of the viscera?

With the well preserved manus ER 970, it is clear that the digits were much shorter relative to the overall size of the animal than in extant C. crocuta. Examination of the carpal articulations of the metacarpals suggests less compaction of the metacarpals than in C. dietrichi.

Crocuta cf. C. ultra
Fig. 7.17 – 7.19

KOOBI FORA MATERIAL

CRANIODENTAL

The juvenile mandible KNM-ER 28520 has an m1 with a short, though incipiently two-cusped, talonid. There is a small but well developed metaconid on this tooth.

The jaw of KNM-ER 3765 was very broad and robust. The relative sizes of the teeth must have been as in other Crocuta, though the p4 appears to have been comparatively small.

ER 44346 is a worn and abraded lower canine. There is a strong wear facet on the lingual face and another one on the buccal face, slightly medially situated relative to the mid-line.

Specimen ER 44530 consists of an m1 and sieving fragments. The sieving fragments are very broken and abraded. The carnassial is missing the distal part of the protoconid. The paraconid is tall and relatively short, with a strong mesiobuccal cingulum.
POSTCRANIAL

A small collection of material can only be tentatively assigned to *C. ultra* due to the fragmentary nature of the specimens. The proximal radius associated with ER 44530 is so fragmentary that little can be said except that it matches the size of the tooth.

The ER 3765 partial skeleton is extremely fragmentary and eroded. Elements are similar to ER 970, hence the taxonomic designation. However, this partial skeleton is so fragmentary that it is difficult to assign it to a taxon with any assurance.

What little is known of the ER 3765 axial skeleton includes a cervical vertebra fragment (L) and rib fragments (M). In the vertebral fragment, the transverse foramen is preserved along with a portion of the zygapophysis.

Very little of the thoracic limb of ER 3765 is preserved. The proximal radius ER 3765F is fragmentary, but consistent in morphology and robusticity with ER 970D even though it is slightly smaller. It is also not unlike ER 723Q. The proximal right ulna, ER 3765J, is broken and the olecranon is missing. Most of the semilunar notch is preserved, but only a portion of the medial coronoid process is present. The proximal left metacarpal 2, ER 3765H, is smaller than ER 970P/AA but clearly has a *Crocuta* carpal articulation. The proximal shaft is clearly diseased.

The right distal radius ER 44709 (Fig. 7.17a, b) is relatively abraded. It is clearly *Crocuta* and most likely *C. ultra* due to its size.

The proximal portion of the left second metacarpal ER 2115 is within the size range for ER 970. However, the shaft is a little less robust than that specimen. Note that the shape of the proximal articular surface is different from *C. eturono* ER 2119. If both specimens are oriented with the ventralmost point of the proximal articular surface downwards, ER 2115 (Fig. 7.18a) has a much greater slope to its dorsal edge such that the medial point is much further below the lateral point than in ER 2119 (Fig. 7.16d).

With a few exceptions, the pelvic limb of material referred to *C. ultra* is only slightly better preserved than the thoracic limb. Little can be said based on the fragment of left ilium and acetabulum, ER 3765E, as not enough of either portion is preserved. The acetabular fossa is deep and round, as in all *Crocuta*. This specimen is more robust than ER 721I.

In contrast, the right femur ER 953 (Fig. 7.17c-e) is the most complete *Crocuta* femur found from Koobi Fora and is within the size range of modern *Crocuta* and known specimens of *C. ultra*. There is little to distinguish it morphologically from extant *Crocuta*. It is eroded at the anterosuperior portion of the condyle. A portion of the medial condyle is missing. The distal end of this specimen does not show any appreciable morphological differences from the ER 3765 distal femur. As with other distal femora of *Crocuta* at Koobi Fora and Olduvai Gorge, the attachment of the lateral head of gastrocnemius crosses almost half of the posterior surface of the shaft. The intercondylar distance is great. The patellar groove is poorly preserved, but seems to have the wide, parallel sides seen in ER 3745 and ER 3765.

The proximal left femur, ER 1569 (Fig. 7.17e, g), like ER 953, is similar in size to modern *Crocuta*. There is little to distinguish it morphologically from extant *Crocuta* with the exception of having a somewhat shorter neck. In contrast, the other proximal left femur, ER 1539, is slightly less robust than ER 1569 and ER 953.
Unfortunately, only the distal femur and shaft fragments (ER 3765A-C) are preserved in the partial skeleton ER 3765. The distal specimen (A) is eroded with the exception of part of the patellar groove and shaft. What little can be seen is consistent with Crocuta.

A complete tibia, ER 695 (Fig. 7.18a), is also known. In comparison to the other complete hyenid tibia from Koobi Fora, ER 872, a possible Parahyaena, this specimen is much shorter, yet has similarly sized articular surfaces. What is preserved of the proximal articular surface is similar to C. crocuta, but slightly more gracile. The tibial tuberosity is more robust and extends more anteriorly. The distal articular morphology is similar to C. crocuta. ER 695 differs from ER 872 in not having the increased anteroposterior width seen in that specimen, although it does seem to be relatively wider anteroposteriorly than the smaller and much older ER 3103.

The proximal tibia, ER 3765D, is so eroded that the edges are worn off. Only the articular surfaces and intercondylar eminence are somewhat preserved. What little can be seen is similar to that of ER 695, as well as C. dietrichi, ER 721J.

In contrast, many of the tarsals of ER 3765 are well-preserved. The right astragalus (ER 3765N; Fig. 7.19b) is well-preserved.
and articulates beautifully with the navicular and calcaneum. This specimen is superficially similar to cf. *Parahyaena*, ER 1185 (Fig. 7.19c), although ER 3765N is more robust. One of the primary differences is that the mediolateral width of the head in ER 3765 is relatively greater even though the neck is about the same size relative to the body. Note, however, that the head of ER 3765 is not as wide and robust as indeterminate hyenid ER 1184 (Fig. 7.19a). In inferior view, the calcaneal facets are very similar to the other hyenid specimens. In medial view, the neck may be slightly longer relatively than in ER 1185, but not to a significant degree.

The right calcaneum, ER 3765K (Fig. 7.17h, i), is even better preserved than ER 970G. There is a slight navicular facet blending into the round cuboidal facet. The facet for the head of the astragalus is large and continuous with the navicular facet, although not in the same plane. This region is not well-preserved in ER 970G. The groove for the flexors ventral to the sustentaculum tali is large and deep, as in ER 970G. The tuber calcanei is also better preserved and includes the proximal projection from the medial side. This projection does not extend very far, a condition seen in all large hyenids. However, in this specimen there is less projection than in ER 970G or ER 721T. In comparison to *C. dietrichi*, ER 721T, this specimen is more robust. The calcaneal tuberosity flares less medially and laterally than in ER 721T and is thicker. The sustentaculum tali is more robust and seems to project relatively less medially than in ER 721T. All in all, this specimen appears to be an undamaged version of ER 970G.

The right navicular, ER 3765G (Fig. 7.17j), is also well preserved. This specimen is similar to ER 970H. However, this specimen is not as wide dorsoventrally, even though the mediolateral width is relatively similar. ER 970H is much more robust, with larger processes than this specimen.

Although the proximal left fourth metatarsal, ER 1664, is similar to ER 699 in size and shape, its incomplete nature makes it difficult to assess. It is a little larger and more robust than ER 723, but might be within the size range of ER 970 based on comparison to ER 970 J, a proximal third metatarsal.
Fig. 7.19: Comparison of hyenid astragali. a-d) dorsal view of a) Hyaenidae indet. ER 1184; b) *Crocuta* cf. *C. ultra* ER 3765N; c) cf. *Parahyaena* sp. ER 1185; d) Hyaenidae indet. sp. A ER 40416A. Note the enlarged tubercle on the neck and the evidence of pathology along the margins of the trochlea in ER 1184.

**REMARKS**

This postcranial material supports the conclusions drawn from the ER 970 and ER 723 skeletons of *C. ultra*. This was a robust species of *Crocuta* similar in many respects to modern *Crocuta*, but with shortened paws. The calcaneum ER 3765K indicates that much of the short, stocky nature of the ER 970G calcaneum is not wholly due to arthritic changes. Likewise, the tibia, ER 695 indicates a relatively short-limbed *Crocuta*, with a tibia shorter than extant *Crocuta*, and only slightly more gracile.

**REMARKS ON C. ETURONO, C. DIETRICH, AND C. ULTRA**

We will treat the evolution of *Crocuta* in detail in a separate contribution (Lewis and Werdelin in prep.). Here we will just make a few comments and describe some preliminary analyses that are directly relevant to the taxonomic status of the Koobi Fora *Crocuta*. As far as the craniodental evidence is concerned, most information relevant to species-level distinctions within *Crocuta* is derived from metric analysis of the teeth. We shall not be directly concerned with distinctions between Koobi Fora material and extant *C. crocuta*, but will confine ourselves to analyses relevant to distinctions within the Koobi Fora material and the question of which taxon or taxa they belong to.

The taxa of relevance to Koobi Fora are *Crocuta eturono* (Werdelin and Lewis 2008), *Crocuta dietrichi* (Petter and Howell 1989), *C. ultra* (Ewer 1954a), and of course the extant *C. crocuta* (Erxleben 1777). We are not here concerned with whether these are valid biological species or not, which is an issue for another time. However, we are concerned with
whether they are identifiably distinct morphological units and if so, what their functional adaptations might be.

In their original description, Petter and Howell (1989) stated that the main characteristic distinguishing *C. dietrichi*, then known only from the Upper Laetolil Beds, from extant *C. crocuta* was the reduced size and especially the smaller premolars. Barry (1987) had listed other characters as possibly distinguishing the Laetoli material from the extant species, but refrained from naming it at that time. Werdelin and Dehghani (2011) added the relatively wide p4 to this list. A problem with the characterization of *C. dietrichi* has been the relatively small sample of specimens from Laetoli, as well as the fragmentary nature of most of these. However, Geraads (1997) described a large sample of *Crocuta* from Ahl al Oughlam in Morocco (dated ca. 2.5 Ma; Geraads 2002, 2006) under the name *Crocuta dbaa*. This species matches the Laetoli *C. dietrichi* in all particulars and there is little doubt that they are conspecific, despite the Ahl al Oughlam material being more than a million years younger than the Upper Laetolil Beds specimens. These two samples together provide an excellent characterization of *C. dietrichi*, at least as far as the lower dentition goes, as this is better represented in the available material than the upper.

*Crocuta dietrichi* is, indeed, smaller on average than later *Crocuta*, just as originally stated by Petter and Howell (1989). Among the cheek teeth, p2 is longer relative to p3 than in the extant species. Both p4 and m1 are broader than in the extant species, and the trigonid of the latter tooth is shorter relative to the total length of the tooth (i.e., the talonid is longer). We carried out a principal components analysis of some cheek teeth measurements (Table 7.11). This clearly separates *C. dietrichi* from other *Crocuta*. It does not distinguish between *C. ultra* and *C. crocuta*, however. The former is, as would be expected of a geologically younger species, less distinct from *C. crocuta* than is *C. dietrichi*. However, some characters of the dentition separate them quite clearly. This includes an m1 talonid that is still longer than in *C. crocuta* and a p4 that is relatively broad. Unfortunately, too few specimens are complete enough to make a principal components analysis useful.

Nevertheless, with this information in hand we can attempt to place the Koobi Fora *Crocuta* specimens in their proper taxa. Most telling in distinguishing the fossil specimens from extant *C. crocuta* is the relationship between p3 and p4 widths. Figure 20a shows that all the fossil specimens have a p4 that is broad relative to p3 width compared to *C. crocuta*. The trigonid length serves to reinforce this distinction (Fig. 20b), although the differences are smaller here. Thus far, however, neither comparison serves to show whether there is more than one species at Koobi Fora. The principal components analysis provides a partial answer to this question (Fig. 20c). Thus, when the full cheek-tooth row (except p2) is taken into account, ER 721H clearly falls some distance away from ER 723, ER 896A, and ER 44485. The latter cannot be distinguished from *C. crocuta* in these metrics, but ER 721H falls outside the modern species and near *C. dietrichi*. We therefore consider the latter specimen to belong to *C. dietrichi*, taking into account that since it comes from the Upper Burgi Mb. it is younger than any previously identified *C. dietrichi* and can therefore be expected to have evolved away from the type series. Metrics such as the relative length of the trigonid further suggest that this and other possible later *C. dietrichi* are trending towards the condition seen in *C. ultra*. Koobi Fora specimens such as ER 721H may thus be showing an intermedi-
Fig. 7.20: Metric analyses of Crocuta spp. Koobi Fora specimens labeled. a) bivariate diagram of widths of p3 and p4; b) bivariate diagram of m1 length against m1 trigonid length (i.e., a measure of the relative length of the talonid). Note the relatively short trigonid (long talonid) of C. dietrichi. The position of specimens ER 721H and ER 723 is equivocal; c) bivariate diagram of a principal components analysis of the lower cheek dentition. In this analysis ER 723 lies comfortably within the scatter of C. crocuta and with other Koobi Fora C. ultra, while ER 721H falls closer to C. dietrichi, though not within the scatter. Numerical details of this analysis are given in Table 7.1.

With this information in hand it is easier to place the specimens ER 3753 and ER 3109 (the former from the Upper Burgi, the latter of uncertain provenance but likely from the Upper Burgi) in C. dietrichi. Both are quite small and especially ER 3109 is close to ER 721H in metrics. The maxilla specimen ER 1541 is not distinguishable from C. dietrichi on preserved features and is here referred to C. cf. C. dietrichi on the basis of its Upper Burgi age.

On the same basis, the remaining measurable Koobi Fora craniodental specimens can be referred to C. ultra. The oldest of these

Table 7.1: Principal components analysis of selected Crocuta specimens.

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</tr>
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</table>

ate stage in the evolution from C. dietrichi to C. ultra, while still remaining identifiably the former.
may be ER 896, which is from the Upper Burgi or KBS Mbs. The remaining specimens are from the KBS or Okote Mbs.

Specimens that are not measurable are usually not well preserved in other respects either. These are difficult to assign to a species. Here, they have been referred to C. cf. C. dietrichi or C. cf. C. ultra on the basis of their age, with Upper Burgi specimens referred to the former and younger specimens to the latter. Specimens with ambiguous dates have been left as Crocuta sp.

In terms of ecological differences, C. eturono represents a large and possibly more modern-like cursorial species if metacarpals are properly assigned. In contrast, C. dietrichi is smaller and more Hyaena-like in many ways. It lacks features indicating a sloping posture and carcass carrying. Crocuta ultra may have overlapped in time with C. dietrichi and was much more robust and heavily muscled. However, the paws still were shortened, even though other aspects of the postcrania begin to indicate a shift in posture via changes in the distribution of weight and reorientation of muscles. Crocuta ultra does not appear to have been as cursorial as modern C. crocuta or possibly C. eturono and is likely a descendant of C. dietrichi.

**Crocuta sp.**

Fig. 7.21

**KOOGI FORA MATERIAL**

**CRANIODENTAL**

KNM-ER 2126 can be identified as Crocuta on the basis of the size and shape of the posterior shelf of p4.

ER 16029 includes cranial fragments but no teeth. Characters of the basicranium identify this specimen as Crocuta.

ER 44383, upper canine. The root is short and relatively straight, being only slightly curved in the mediolateral direction. The crown is damaged and broken.

ER 40419 is a broken left P3 of Crocuta. The mesial face is broken off, but the mesial accessory cusp is located towards the lingual side. The main cusp is tall, conical and robust. The distal accessory cusp is short and appressed to the main cusp. There is a strong distolingual cingulum crest.

**POSTCRANIAL**

Several postcranial specimens are attributable to undetermined species of Crocuta. The ER 44425 left proximal radius (Fig. 7.21) includes much of the proximal half of the shaft and is in good condition. The morphology is somewhat similar to ER 970D (C. ultra) and to modern C. crocuta. Differences from ER 970D include the fact that this specimen is more gracile and there is slightly less proximal projection of the medial side of the anterior edge of the head. The bicipital tuberosity/ridge also appears to be slightly higher relative to the size of the shaft. All in all, there are not enormous differences amongst the C. ultra radii found at Koobi Fora (ER 3765F, ER 723O, ER 970D). This specimen is nearly identical to ER 6077.

ER 6077 is similar in size and morphology to modern Crocuta. The head is oval with the central depression falling medially. The shaft is flat and has the bicipital tuberosity on the lateral edge of the shaft, as in all hyenids. As with all hyenids, there is no extension of the head over the shaft as there is in felids. This specimen is more similar to ER 44425 than it is to ER 970D.

The distal right fifth metatarsal, ER 4432, belongs to a medium-sized Crocuta. The proximal end is eroded and not much can be
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Fig. 7.21: Proximal half of left radius ER 44425 assigned to *Crocuta* sp.; a) anterior view; b) posterior, view; c) proximal view.

Two proximal phalanges are attributable to *Crocuta*: ER 3100 and ER 6113. ER 3100 is a robust proximal hyenid phalanx that is one of the oldest hyenid specimens from Koobi Fora (Lokochot Mb.). ER 6113 is also a proximal phalanx.

* cf. *Crocuta* sp.

KOOBI FORA MATERIAL

CRANIODENTAL

ER 44524 includes one complete and one fragmentary incisor. The complete incisor is probably i2. It is heavily worn, with the crown having lost more than half its height.

ER 44608, m1. This tooth is exploded from within by sediment expansion, so the shape and size are distorted. The protoconid is broken and the talonid lost.

POSTCRANIAL

An eroded distal right femur, ER 44720, is the right size for *Crocuta*. The condyles seem a little short, like a mustelid, but that could be due to erosion. The height of the patellar groove is *Crocuta*-like.

Genus *Hyaena* Brisson, 1762

*Synonyms*: *Euhyaena* Falconer, 1867

*Generic diagnosis*: Large-sized Hyaenidae with moderate bone-cracking adaptations; limbs slender with elongated metapodials; skull robust: dental formula I 3/3, C 1/1, P 4/3, M 1/1; premolars with some bone-cracking adaptations; P4 short, with metacrista shorter than paracone; m1 with short but well-formed talonid, metaconid usually present.

*Stratigraphic range in Africa*: Late Pliocene – Recent based on FAD in the Lokochot Mb., Koobi Fora Fm. (≤3.58 Ma).

*Stratigraphic range at Koobi Fora*: Late Pliocene – early Pleistocene based on FAD in the Lokochot Mb. (≤3.58 Ma) and LAD in the Okote Mb. (≥1.38 Ma).

REMARKS

*Hyaena* is a much rarer genus in the fossil record than *Crocuta*. In Africa it is best known from Makapansgat Mb. 3, where a minimum of 43 individuals have been recovered (Reed 1996). *Hyaena* clearly evolved from *Ikelohyaena* (Werdelin and Solounias 1991) and there is a distinct evolutionary gradient from the lat-
The genus, best known from the type locality, Langebaanweg (Hendey 1974), via Hyaena makapani from Makapansgat (Toerien 1952), to the extant species, the first occurrence of which may be in Olduvai, Bed I, while the record of ‘Hyaena hyaena praecursor’ from Aïn Brimba in Tunisia at ca. 3 Ma (Arambourg 1979) requires renewed investigation.

**Hyaena cf. H. makapani**

Fig. 7.22 – 7.25

KOobi Fora Material

Craniodental

One of the best preserved and most complete of all Koobi Fora carnivores is ER 1548, a skull with complete dentition and associated postcrania. The cranium (Fig. 7.22a, b) is smaller and relatively more slender than that of modern *H. hyaena*. The premaxillae are slender and extend dorsally about half way along the nasals, which is similar to the condition in extant specimens examined. The palatine fissure is small, while the premaxillary-maxillary suture is set further posteriorly in the fossil than is usual in the extant form, almost at the extreme posterior end of the fissure.

The nasals are long and slender, with their greatest posterior extent just anterior to the anteriormost point of the orbit. This is in contrast to the usual condition in the extant form, in which the nasals extend further posteriorly.

The maxillae are slender, with prominent bulges for the canine alveoli and marked, thumbprint-sized depressions anteromedial to the orbits. The maxillary-frontal suture lies about 10 mm posterior to the anterior end of the orbit, i.e., well posterior to the nasal-frontal juncture, which is in keeping with the condition in the extant species. The major palatine foramina are located level with the main cusp of P2, and the anteriormost point of the maxillary-palatine suture lies level with the distal accessory cusp of P3. The lateral maxillary-zygomatic suture is obliterated, but within the orbit it is clear that the lacrimal is entirely bounded by the maxillary, i.e., there is no lacrimal-palatine suture, but instead a wide suture between the frontal and maxillary. Inside the orbit the maxillary forms a wide shelf that continues up on the medial side of the zygomatic arch, to the dorsal margin of which the maxillary therefore contributes, just as in the extant form.

The frontals are very short in their anterior extent, ending level with the large, single infraorbital foramen of the maxillary. This leaves a broad suture between the maxillary and nasal, unlike the condition in the extant *H. hyaena*, in which the frontal reaches the premaxilla and there is no maxillary/nasal contact. Further posteriorly, the frontals are slightly inflated and lack the distinct median valley seen in many extant specimens. The postorbital processes are broken, but were probably quite short. The lyriform crests originate at the postorbital processes as distinct crests and join at the midline just anterior to the suture between the frontal and parietal. The zygomatic is a relatively small bone with a broad orbital component as in the extant form. Its postorbital process is short and narrow.

The zygomatic component of the temporal is more arched and more dorsoventrally expanded than in many extant specimens. This is unexpected in view of the overall gracile appearance of ER 1548. On the other hand, the posterior part of the zygomatic arch is much less laterally expanded than in the extant form and the temporal forms a narrow groove between the braincase and the zygo-
Fig. 7.22: H. cf. H. makapani, ER 1548, complete cranium and mandible. a-b) cranium in a) ventral and b) left lateral view; c-d) mandible in c) occlusal and d) left lateral view.
omatic arch.

The parietals are much as in the living species, although there does not appear to have been a parietal-sphenoid suture, but instead a suture between the frontal and temporal.

The posterior orbital foramina are not visible in the fossil, nor are the sutures between the sphenoid, pterygoid, temporal and other bones of this region. The basisphenoid and basioccipital are flat, as in modern *H. hyaena* (but unlike in *Crocuta*). The auditory bullae are complete and unbroken. They are small in size. Except for the tympanooccipital fissure and hypoglossal canal, which are situated as in the extant form, the foramina of the basicranium are indistinct. The paroccipital processes are short and robust.

The occipital curves ventrad in its posterior extremity. The nuchal crests are low, as is the occipital crest. The processes for the nuchal ligaments are prominent, more so that is typical of the extant form. There is a second pair of processes, of uncertain function, on the dorsal rim of the foramen magnum, medial to the occipital condyles.

The central incisors (I₁-I₂) are set in a more or less straight line, while I₃ is set somewhat distolateral to them. The size relationships, with I₂ somewhat larger than I₁, and I₃ considerably larger than I₂, are as in the extant species. The I₁ and I₂ both have distinct, paired buccal cusps. The right I₁-I₂ are broken, while the left are complete, though the tips are worn flat.

The canines are very short and slender and are more laterally compressed than is usual in the extant species. They have low but indistinct mesial and distal crests. The tips are slightly worn.

The P₁ is slender. It lacks accessory cusps, but has a distinct cingulum that extends around the tooth except for the mesialmost part.

The mesial accessory cusp on P₂ is very small. The main cusp has slightly convex mesial and distal faces. The distal accessory cusp is relatively large and more appressed to the main cusp than in the extant form. There is a prominent lingual cingulum, but no or only a small mesiolateral one. The P₃ shows the same characteristics as P₂ in having a very small mesial accessory cusp, appressed distal accessory cusp and distinct lingual cingulum.

The P₄ is relatively small, with a prominent parastyle that is more trenchant than in the extant form. There is a small but fairly tall protocone that is separated from the paracone by a short but deep valley. The paracone itself is tall and conical. The metastyle is shorter than the paracone, as in the living species, and distinctly curved. There is a distinct cingulum on the lingual side of the tooth.

The M₁ is mesiodistally very short, and has a distinct metastyle wing. The paracone is low, while the buccal paracone shelf is broad and low. The paracone and metacone are united by a low ridge. The broadest point of this tooth is at the metacone after which it tapers gradually towards the protocone, which is low and indistinct.

Like the cranium, the mandible (Fig. 7.22c, d) is smaller and more slender than the mandible of extant *H. hyaena*. The symphysis is gracile and does not show any sign of a ventral chin, unlike the situation in many individuals of the living species. There is a single, large mental foramen beneath the center of p₂. The masseteric fossa is relatively smooth, but is deeply incised. Its anterocentral extremity runs smoothly into the corpus, while the anterior face of the ramus, bounding the anterior end of the masseteric fossa, forms a very tall ridge that curves around medially
CHAPTER 7: FAMILY HYAENIDAE

and posteriorly to partly enclose the anterior end of the masseter. The angular process is well developed and its posterior part forms a medial shelf. This shelf is more substantial than commonly seen in the extant form. The condyles are transversely relatively short in relation to their height.

The lower incisors increase in size from i1 to i3. They are set in a gently curving arch. None of the incisors has a buccal accessory cusp. The i3 is broad and short and has a well developed and semi-independent lateral accessory cusp that is much larger than average for the extant form. There is a 2.5-3 mm diastema between i3 and the lower canine.

The lower canines are short, though not as short relatively as the upper canines. They are angled outwards relative to the main axis of the ramus, as is normal for hyenas. The mesial and lateral sides are rounded, while the medial side is almost flat, giving the tooth a somewhat triangular cross-section. The mesial and distal crests are strongly developed. The post-canine diastema is about 9 mm long.

The p1 is absent as in most derived hyenas. The p2 is small and relatively broad. The mesial accessory cusp is very small, leading straight into a distinctly convex mesial face of the main cusp. The distal accessory cusp is also very small and is more in the form of a low crest than a distinct cusp. The distal basin is relatively wide.

The p3 is short and slender. It has a very small mesial accessory cusp, the transverse grooves for which are weakly distinct. The mesial face of p3 is convex, as is the distal face. The distal accessory cusp is small and distinct, while the distal basin is well developed, as in the extant form.

The p4 is a very slender tooth. The mesial accessory cusp is short and low, and there is no trace of a mesial cingulum cusp such as is often seen in the extant form. The main cusp is relatively long and slender and has convex mesial and distal faces. The distal accessory cusp is large and narrow. The distobuccal cingulum shelf is very low and narrow and has no distinct cusp on it.

The m1 is short, with a short talonid. The paraconid is slightly longer than the protoconid and at the stage of wear of the specimen they are of about equal height. The metaconid is low and set close to the protoconid, with only a shallow groove separating them. The talonid has two cusps, identifiable as the entoconid and hypoconid. There is no m2 present.

The Koobi Fora carnivore assemblage includes a second skull of *H. cf. H. makapani*, ER 3766 (Fig. 7.23). The cranium (Fig. 7.23a, b) of this specimen is slender but robust. It is cracked and worn so that it is a mosaic of small pieces. It is, however, only moderately distorted, being sheared somewhat from left to right, with the right side compressed and pushed slightly dorsad relative to the left side. Thus, the cranium appears slightly taller and narrower than in life. The cracking into small pieces has obliterated all signs of sutures between bone elements, as well as all foramina. The left and right zygomatic arches are missing from the skull, as well as parts of the basicranium. The mandible is lacking both condyles, the right coronoid process, a piece of the ramus beneath p4 and the right p3, together with the left angular process.

The premaxillae are slender and the anterior ends of the maxillae as well, with only moderate bulges for the upper canine alveoli. The infraorbital foramina are large and positioned above the middle of P3. The frontals are moderately inflated and there is a slight depression in the maxillae anterodorsal to the orbits, marking the extent of the inflation. The
Fig. 7.23: *H. cf. H. makapani*, ER 3766, damaged cranium and mandible. a-b) cranium in a) ventral and b) left lateral view; c-d) mandible in c) left lateral and d) occlusal view.

Lyriform crests are blunt and meet to form a low sagittal crest near the frontal-occipital suture. The sagittal and nuchal crests meet at the occiput, which is only moderately extended beyond the occipital condyles. The nuchal region is U-shaped.

The upper dentition is complete except for the right P1, which may have been lost in life, and the tip of the main cusp of the right P2, which has been broken off. All teeth have only slight wear. The I1-I2 are small, spatulate teeth, placed in a gentle arch, with the I1s slightly anterior to the I2s. Both have distal accessory cusps that are probably double,
though post-mortem damage makes this difficult to determine. There is a diastema of about one mm between I2 and I1. The I3 is a caniniform tooth with a sharp cusp. The diastema between I3 and the upper canine is about 10 mm. The canine is straight and moderately flattened. It has distinct mesial and distal crests. The postcanine diastema is very small (about 1-2 mm) on the left side, where P1 is retained.

The P1 is a small, rounded, single-cusped tooth. The cusp is set slightly mesial to the middle of the tooth. The P2 is robust, with a distinct mesial accessory cusp placed somewhat mesiolingually. The main cusp is tall and conical, while the distal accessory cusp is about twice the size of the mesial one. There is also a slight distolingual swelling and incipient cingulum.

The P3 is a tall, conical tooth. The small mesial accessory cusp is placed mesiolingually. The main cusp is tall, and the distal accessory cusp appressed to it. The distolingual cingulum crest is low and blunt.

The P4 is short and broad. There is no preparastyle. The parastyle is a tall, robust cusp that is somewhat crest-like. The protocone is large and located level with the mesial end of the parastyle. The paracone is the tallest cusp. The metastyle is short and slender and slightly mediolaterally curved. The M1 is small, with a very reduced metastyle wing, but a distinct protocone.

The mandibular corpus (Fig. 7.23c, d) is robust throughout its length, but relatively mediolaterally narrow. It is tallest beneath the distal part of m1. There is one mental foramen, located beneath the mesial root of p2. The coronoid process is tall and slender.

The lower incisors are situated in an interrupted arch, interrupted because the left i1 is located slightly anterior to the right i1. Both are very small, two-cusped teeth. The i2s are similar to I1, but have a single distinct cusp. Both i1s and i2s are placed facing anterodorsally. The i3 has a large medial cusp and a smaller lateral one. There is no diastema between i3 and the lower canine.

The lower canine is robust, with mesio- and distomedial crests. It faces slightly lingually. The postcanine diastema is about 15 mm long. The p2 is a short, robust tooth. The mesial accessory cusp is very small and appressed to the main cusp. The main cusp is low and robust and situated slightly mesial to the midline of the tooth. The distal accessory cusp is low and somewhat crest-like.

The p3 is similar to p2, but is larger. The mesial accessory cusp is very small, just a bump on the mesial face of the tall and conical main cusp. The distal accessory cusp is also small and appressed to the main cusp. There is a low and blunt distolingual cingulum crest.

The p4 is a slender tooth. The mesial accessory cusp is small and appressed to the main cusp, which is tall and conical. The distal accessory cusp is large and somewhat crest-like. The distolingual cingulum crest is prominent and sharp.

The m1 is short. The paraconid is the longest and broadest cusp, but the protoconid is slightly taller. The metaconid is small but set more or less free of the protoconid. The talonid is short and has prominent entoconid (larger) and hypoconid (smaller).

ER 669 is a mandibular fragment with p3. The p3 of this specimen matches that of ER 1548 in all respects. It is intermediate in size between the p3s of ER 1548 and ER 3766.

Specimen ER 1666 consists of many separate but associated elements of both craniodental and postcranial origin. Specimen ER 1666J is a left P4 with a broken protocone. There is a small preparastyle bump. The
parastyle is robust, with strong oblique wear. Part of the apex is broken off. The paracone is tall and conical with strong wear on its distolingual face. The metastyle is short. The lingual cingulum is prominent. ER 1666K is a left p4. The mesial accessory cusp is small, and the main cusp tall, conical, and situated mesial to the tooth's midline. The distal accessory cusp is large but low, and somewhat crest-like. The distolingual cingulum crest is moderately developed. ER 1666L is a distal fragment of a right p4 with a strong distal accessory cusp and small distal cingulum cusp. ER 1666M is a damaged left m1. The crown is low and long, with a paraconid that is longer and more massive than the protoconid. The metaconid is broken off, along with the lingual part of the talonid. The latter is short and has a prominent hypoconid. ER 1666 N is a (probable) lower canine fragment with a broken tip. ER 1666O is a fragment of the talonid and distalmost part of the trigonid of a right m1. The entoconid and hypoconid are present, while the metaconid is well developed. ER 1666P includes two probable lower incisors with strong apical wear. ER 1666Q is an indeterminate tooth fragment. ER 1666R is an indeterminate tooth fragment. ER 1666S is a fragment of ?p4 that includes a basal cingulum. ER 1666V is a fragment of the right mandibular ramus with a remnant of the distal alveolus of m1. It is identical to ER 1666Y in most respects. ER 1666W is a fragment of left mandibular condyle. ER 1666Y is a fragment of left mandibular ramus with the distal root of p4 and roots of m1. The ramus is robust but not broad. It is tallest beneath the distal part of m1. The masseteric fossa does not quite reach the distal end of m1. ER 1666AJ is an anterior fragment of the right p3. There is a crest running from the mesiobuccal part of the tooth towards the tip of the (broken) main cusp. ER 1666AW is a right upper third incisor. The crown is somewhat caniniform and recurved, with a prominent medial ridge. ER 1666AX is a fragment of cranium with occipital condyle. ER 1666AY is an incisor, probably i2. ER 1666AZ is a broken, indeterminate incisor. ER 1666BB is a fragment of a premolar. ER 1666BC is an central incisor, probably i1.

**POSTCRANIAL**

ER 1548 is a well-preserved specimen that is much smaller than modern *Hyaena hyaena*, but is more similar to this species than to any other extant hyenid. However, as one might expect given the craniodental morphology, the postcranial morphology does differ from *H. hyaena*. The thoracic limb is probably the best preserved region of the body and includes portions of almost all of the bones of this region.

ER 3766 includes vertebral elements in matrix and shaft fragments, including the atlas, axis and at least the third cervical vertebra. There may be some caudal vertebrae. Not much can be said about the postcrania at present and not all fragments in the matrix belong to Carnivora.

The ER 1666 partial skeleton includes some material that is quite robust, although not as robust as smaller *Crocuta* such as *C. dietrichi*. Limb material is not well preserved in this specimen.

The axial material is distinct in morphology from extant *Hyaena*, although not much axial material is known. One of the best preserved pieces is the atlas (ER 1548C; Fig. 7.24a). In this specimen, the body is elongated anteroposteriorly. The transverse processes are drawn more caudally and angle ventrally as one moves towards the tips in comparison to *H. hyaena*. The transverse processes are ori-
Fig. 7.24: Postcranial material of partial skeleton ER 1548 *Hyaena* cf. *H. makapani*. a) ventral view of atlas ER 1548C; b) lateral view of C5 vertebra ER 1548J; c) glenoid of right scapula ER 1548D; d-e) left humerus ER 1548F in d) anterior and e) posterior view; f) left ulna ER 1548G in lateral view; g-h) proximal left radius ER 1548E in g) proximal and h) anterior view; i-j) distal right radius ER 1548AS in i) anterior and j) distal view.

...ented more towards the midline, a condition seen also in *Proteles*. The tips of the processes are more rounded than those of *Proteles*, but less rounded than in *H. hyaena*. The foramina on the dorsal surface are larger and more mediolaterally separated. Caudal to each vertebral foramen is a very large fossa. The ventral surface of the body is relatively flat in com-
parison to the more rounded ventral surface in *H. hyaena*. The atlanto-occipital articulation extends further cranially, suggesting a difference in the range of cranial extension between this species and the extant striped hyena. The articular surface area is narrower mediolaterally, yet the ventral surface is relatively wider than in extant *Hyaena*.

Other axial material includes three articulating cervical vertebrae (ER 1548H through K; Fig. 7.24b) that probably represent C3 through C6. There are also several caudal vertebrae (ER 1548L through P, BL), all of which are middle to terminal caudal vertebrae. More fragmentary material includes vertebral fragments (ER 1548BM) and rib fragments (ER 1548Q through Z, AA, AV).

Within the ER 1666 specimen, associated axial material includes fragments of an axis (ER 1666G, AG), cervical vertebrae (ER 1666AA, AB, AC, AF), thoracic vertebrae (ER 1666H, T, BE), lumbar vertebra (ER 1666BF), and additional more fragmentary material. Three rib fragments, including two heads and a dorsal fragment (ER 1666D) are also preserved.

Unfortunately, most of the ER 1666 vertebral material is quite fragmentary. Portions of the spinous process (ER 1666AG) and lamina (ER 1666G) are preserved from the axis. The small size suggests that it is *Hyaena* rather than *Crocuta*. Another cervical vertebra (ER 1666AB) is roughly the size of *H. hyaena*, but shorter craniocaudally. This specimen includes the cranial and caudal zygapophyses of C4 or C5.

The right scapula (ER 1548D; Fig. 7.24c) includes the glenoid, part of the spine and all of the acromion. In lateral view, the acromion angles in the same direction as the superior portion of the glenoid and lacks caudal curvature anteriorly and posteriorly. The tip of the acromion process is elongated. There is a deep supraspinous fossa. The inferior surface of the neck is grooved. There is a relatively robust attachment for the teres minor, although not to the degree seen in *H. hyaena*. The position of the glenoid relative to the blade is like modern *Hyaena*. The glenoid is slightly narrower mediolaterally relative to length than in modern hyenids. The only other scapular material is a fragment of the glenoid of a right scapula (ER 1666F).

The left humerus (ER 1548F; Fig. 7.24d, e) includes most of the shaft, as well as the distal end. This specimen is slightly smaller than modern *H. hyaena*. There is greater waisting of the trochlea anterosexteriorly than in *H. hyaena*. The trochlea is narrower relative to the width of the capitulum, which corresponds to the narrower coronoid process of the ulna. A second distal humeral specimen (AT) is fragmentary and includes only the distal portion of the right humeral shaft.

The fragment of the proximal left ulna (ER 1548G; Fig. 7.24f) includes the radial notch. In extant *Proteles*, the radius is oriented more anteriorly on the ulna than in *H. hyaena*. The fossil is more like *H. hyaena* in orientation, but not to the same degree. As in *Hyaena*, the medial coronoid process juts out prominently from the shaft. Its triangular shape is roughly like that of *Hyaena*. However, the tip does not deviate laterally as in *H. hyaena*. The broken lateral coronoid process, however, appears to have extended further than in *H. hyaena*. Whether this feature is as prominent as in *Proteles* is unknown. In *H. hyaena*, the articular surface slopes distally as one moves medially. In the fossil, the surface is flatter and less sloping. That of *Proteles* is even flatter. A distal right ulna (ER 1548BW) has also been preserved.

The proximal ulna and shaft fragment
ER 2239 is similar in morphology to ER 1548G. The olecranon and anconeal processes are missing. The medial coronoid process and radial notch are eroded, although the general shape can be seen. However, the erosion means that the extent of the lateral coronoid process cannot be assessed.

The left distal ulna with partial shaft (ER 1666X) is a typical hyenid and falls within the size range of a small species of *Crocuta* or modern striped and brown hyenas. Like these hyenids, it is robust, with robust muscle markings. The morphology is consistent with the more poorly preserved distal ulna ER 1548BW. The shaft has an anteroposterior curvature. The shaft as preserved extends past the midshaft. A slight posterior expansion of the shaft can be seen, but not enough to be near the proximal end of the ulna.

As with the rest of the skeleton, the radius (ER 1548E, left proximal; ER 1548AS, right distal; Fig. 7.24g-j) is smaller than modern *H. hyaena*. The head is relatively flat and flares from the shaft more than is typical for modern *H. hyaena*. The proportion of maximum mediolateral width to maximum anteroposterior width of the distal articular surface falls within the range of modern *H. hyaena*. However, the proportions of the keyhole-shaped surface are slightly different. The narrower end of the “keyhole” does not comprise quite as much of the mediolateral width as in extant *Hyena*. The shape of the articulation, however, still is more like that of *H. hyaena* than like other hyenids.

The right manus of ER 1548 is relatively complete and includes numerous carpals. In the scapholunar (ER 1548AB; Fig. 7.25e), the extensor groove is deeper in extant *H. hyaena* than in this specimen, causing a more dorsally

![Fig. 7.25: Postcranial material of partial skeletons ER 1548 and ER 1666 referred to *Hyena cf. H. makapani*. a-d) dorsal views of right metacarpals: a) second ER 1548AI; b) third ER 1548AH; c) fourth, ER 1548AG; d) fifth, ER 1548AJ; e) proximal view of right scapholunar ER 1548AB; f) proximal view of right metatarsal 3 ER 1666C; g) dorsal view of left metacarpal 5 ER 1666B; h) dorsal view of right metatarsal 2 ER 1666AD.](image-url)
curled medial process. The process in the fossil specimen is only slightly dorsally angled and has only a slight curvature. The distal surface is similar in morphology to *H. hyaena*. Other right carpals included in this skeleton are the magnum (AD), trapezoid (AE), unciform (AC) and a possible trapezium (AF).

Metacarpals from the right manus of ER 1548 are well-preserved and are clearly from the same individual (Fig. 7.25a-d). They are much smaller in all dimensions than those of extant *H. hyaena*. The third metacarpal (ER 1548AH) is the longest, followed in length by the fourth (ER 1548AG), second (ER 1548AI) and fifth metacarpals (ER 1548AJ). In extant *H. hyaena*, the third metacarpal is just barely longer and slightly more robust than the fourth. In extant *Crocuta*, the third metacarpal is longer in comparison to the fourth metacarpal length than in the fossil. The fossil is more similar to *H. hyaena* than *Crocuta*.

Two left metacarpals from ER 1666 are also known. The second metacarpal (ER 1666AE) is quite robust relative to *Hyaena*. It includes a well-preserved distal end and distal third of the shaft. The robusticity and size of the specimen fits with the associated fifth metacarpal, ER 1666B, but it is not as robust as that of *Crocuta* ER 970. The squared-off distal articular surface clearly indicates that it is a hyenid, although the size and robusticity seem a little great for *H. cf. H. makapani*.

The fifth metacarpal (ER 1666B; Fig. 7.25g) is much more gracile and slightly shorter than ER 970N. However, it is not as gracile as ER 1548AJ. The morphology is *Crocuta*-like, but much less robust. For example, the lateral side of the shaft is more curved, resulting in a mediolaterally wide shaft supporting the head. The lateral side of the shaft also flares laterally resulting in a greater flare leading to the lateral tuberosity on the proximal end.

ER 45541 is the proximal half of a right metacarpal 4. The ventral end of the carpal articulation and the dorsomedial edge are both broken off. This makes the carpal articular surface look much shorter dorsoventrally than ER 1548AG, but that is a false impression. However, it does seem more robust than ER 1548, but not to the degree seen in *C. dietrichi* and, of course, it is smaller overall. It is otherwise similar in size and morphology to ER 1548.

In both *Crocuta* and *Hyaena* fossil metacarpals, the main carpal articulation is set at much more of an angle than in other cursorial carnivorans, such as canids. The ER 45541 specimen is angled more than canids, but does not seem to be as angled as ER 1548. The ventromedial surface in hyenids has a projection not found in canids, which have a smooth carpal articulation. This projection serves to limit rotation.

In *Crocuta*, the proximal and distal ends of the metacarpals are large and robust and the bones are only somewhat appressed. In *Proteles*, the shafts are tightly appressed and the proximal articulations are tightly interlocked. *Hyaena hyaena* represents the middle ground where the bones are less splayed than in *C. crocuta*, but not as tightly bound as in *Proteles*. In the fossils referred to *H. cf. H. makapani* above, the shafts are more tightly appressed than in *H. hyaena* and approach the condition in *Proteles*. However, the distal ends are more flared than in *Proteles*.

A large number of phalanges have also been recovered, including left proximal phalanges from digits 2 through 5 (ER 1548BQ, AO, BS, BU, respectively) and a set from the right (ER 1548BP, BR, BT, BV, respectively).
Middle phalanges are also represented, including those from the second (ER 1548AZ, BB), third (ER 1548AY, BA), fourth (ER 1548AW, AX), and fifth digits (ER 1548BC, BO). Numerous terminal phalanges are also present (ER 1548BD through BK).

The os coxae (ER 1666AH, AI) includes a fragment of the ischium with part of the acetabulum preserved. This specimen is smaller and less robust than extant *Hyaena*. ER 1666AI is a fragment of the superior portion of the acetabulum, including the tubercle. It does seem to articulate with AH, although this is through a tiny connection along the articular surface that may not be a true conjoin. The crucial difference between this specimen and *C. dietrichi* (ER 794) is that the ischium is relatively short in comparison to the size of the acetabulum. In all other respects, the two os coxae fragments seem very much like the *Crocuta* os coxae. The ischial spine also seems larger relative to overall size than in ER 721I and ER 794 and there is more of an obvious crest running from it to level with the acetabulum.

A left distal fibula (ER 1666E) is missing the posterior portion of the distal end and shaft. It is similar to *Crocuta* 970AO, but much smaller and more gracile. The anterior portion of the distal end is rounded with the groove for the flexor tendons, as expected.

A right metatarsal 2 (ER 1666AD; Fig. 7.25h) is complete and very gracile. The morphology is clearly hyenid and the length relative to the amount of robusticity suggests that it is *Hyaena*. As one would expect in a second metatarsal, the head slopes medially in ER 1666AD. The proximal articulation is wide dorsally, but extremely narrow mediolaterally. As one would expect, the proximal articulation is triangular.

The right metatarsal 3 includes only the proximal half (ER 1666C; Fig. 7.25f). This specimen is more robust than *Hyaena*, but not as robust or large as the ER 970 *C. ultra*. The proximal articulation is more mediolaterally compressed than in ER 970 and there is a greater ventral expansion of the articular surface. The specimen overall seems rather robust for *H. cf. H. makapani*, but not as robust and wide mediolaterally as *Crocuta*. It seems rather large relative to 1666AD, but they seem to articulate.

Other materials from the ER 1548 skeleton not attributable to manus or pes include distal metapodial fragments (ER 1548AK through AN) and the ubiquitous unidentified fragments (ER 1548BN). Seventeen sesamoids have also been recovered (ER 1548AU).

The pelvic limb is very poorly represented in the ER 1548 individual. Specimens include a distal femoral fragment (ER 1548AR), left proximal tibial shaft fragment (ER 1548AP), and a shaft fragment that may belong to the fibula (ER 1548AQ). Very little can be said about these fragments.

**REMARKS**

The ER 1548 individual is small, but clearly *Hyaena*. The postcrania material associated with the ER 1548 skull represents the most complete set of material yet assigned to an extinct species of *Hyaena*. In contrast, material of *H. makapani* from Makapansgat includes postcranial elements that are not associated with craniodental material.

ER 1666 is most similar to *H. makapani*, but seems relatively robust, particularly within the forelimb. Unfortunately, so little of the limbs are preserved that it is difficult to get a true understanding of proportions and robusticity in this specimen.
**Hyaena cf. H. hyaena**

Fig. 7.26 – 7.27

KOObI FORA MATERIAL

CRANIODENTAL

ER 23094 (Fig. 7.26) is a broken left mandibular ramus found at the archeological site FxJj24. It retains a broken c, complete p2, broken p3-p4 and nearly complete though cracked m1. The corpus is robust, very robust compared to the size of the teeth, and tallest beneath m1. There is a single, large mental foramen beneath the middle of p2. The masseteric fossa does not reach the distal end of m1, but was deep and well defined. The coronoid process is broken at the level of the occlusal surfaces of the cheek tooth row.

The lower canine is robust, and likely had a distomedial crest though this part of the tooth is damaged. The tooth is, as in most Hyaenidae, set at an angle to the main axis of the mandible.

The p2 is a robust tooth. There is no mesial accessory cusp, but a blunt crest runs from the apex of the main cusp mesially to the mesialmost point of the tooth. The distal accessory cusp is low but long. It is appressed to the main cusp and is terminated by a small distal cingulum cusp that turns into a very small cingulum on the buccal side of the distal accessory cusp.

The p3 was a comparatively slender tooth with a small mesial accessory cusp and shelf. The main cusp has been nearly entirely broken off and retains only the distalmost portion. The distal accessory cusp was low and set in a short distal shelf. There is a very indistinct distal cingulum.

![Fig. 7.26: H. cf. H. hyaena, ER 23094, damaged mandibular ramus. a) buccal view; b) lingual view; c) occlusal view.](image-url)
The p4 is a slender tooth with mesial and distal accessory cusps that are larger than those of p3. The main cusp is elliptical in cross-section and broken apically so its height cannot be determined. The distal shelf is long and low with a small lingual crest.

The m1 has paraconid and protoconid about equal in length and height, with the former slightly the longer. The metaconid is low and appressed to the protoconid. The talonid is short. Its occlusal surface is worn but appears to have had two cusps, an entoconid and a hypoconid.

**POSTCRANIAL**

The calcaneum ER 5482 (Fig. 7.27) is not quite as long as that of modern *Hyaena*, but is relatively larger than what one would predict for *H. cf. H. makapani* at Koobi Fora. It is also larger than *H. makapani* from Makapansgat. However, in comparison to *Ikelohyaena abronia* from Langebaanweg, this specimen is relatively small. This difference is not surprising as the lengths of the *I. abronia* calca-

nea from Langebaanweg are within the upper range of extant *Hyaena* and *Parahyaena*.

The sustentaculum tali is oriented in the same manner as in other *Hyaena*. There is no distinct projection from the tuber calcanei, although the medial end projects further posteriorly than the lateral. As in all *Hyaena*, the tuber slopes from the medial to the lateral end without any groove between them. The cuboidal facet is eroded. There is no lateral shelf off of the manubrium, but there normally is not in hyenids.

Overall, ER 5482 resembles *Hyaena* in morphology and not *Crocuta* and therefore is not *C. dietrichi* or any other small *Crocuta*. The possibility remains that this may be a relatively small *Ikelohyaena*.

**REMARKS**

Because of the scarcity of material, the genus *Hyaena* has been much less studied than its larger relative, *Crocuta*. For this reason, the taxonomic conclusions drawn here are very tentative and we will treat *H. cf. H. makapani* and *H. cf. H. hyaena* together while trying to pinpoint the distinction between them and what their relationship to other African material of the genus *Hyaena* might be.

A confounding factor in the study of the fossil record of the genus *Hyaena* is its common use in the past as a waste-basket name for a variety of fossil hyenids. Thus, material now assigned to *Crocuta, Pachycrocuta*, and *Pliocrocuta* has at one time or another been placed in *Hyaena*. Most of these incorrect assignments have been winnowed out over the years, but a few remain. Thus, e.g., *Hyaena hyaena praecursor* (Arambourg 1979) needs further study, although Howell and Petter (1980) suggest that it belongs in *Pliocrocuta*.

The main African fossil sample of *Hy-
aena is the extensive material from Makapansgat referred to *Hyaena makapani* (Toerien 1952). Most authors have considered this material conspecific with the extant *H. hyaena*, but there are distinct differences, the taxonomic implications of which are moot, however. The Koobi Fora *Hyaena* material will in the following discussion be compared with this South African sample, as well as with samples of extant *H. hyaena* from Africa and Asia. Because of the fragmentary nature of all of the fossil material, with the exception of the two skulls from Koobi Fora described above, the comparisons will be carried out using ratio diagrams (Simpson 1941). It is well to remember that the ratio diagram itself is not a statistical method *per se* but a visual aid, although we will be utilizing statistics on individual variables in our assessments.

The ratio diagram for the lower dentition is shown in Fig. 7.28. The upper dentition material is too limited to make a similar diagram useful. Before this diagram was made, it was determined that the African and Asian samples of extant *H. hyaena* were so similar (their respective means lay within the 95% confidence intervals of both samples for all variables) that they could be combined into a single sample.

The first thing to note is that the means for *H. makapani* lie outside the 95% confidence interval of extant *H. hyaena* for 9 of 11 variables (with the two deviating variables being the length and width of m1) and that the respective confidence intervals only show overlap for 5 out of the 11 variables. Further,
the ratio diagram indicates that the lower carnassials of *H. makapani* were larger relative to the size of the other teeth than in extant *H. hyaena*. We take this combination of size and shape differences as strong indication that *H. makapani* should be separated from *H. hyaena* at some taxonomic level and since we consider the subspecies rank to be biologically meaningless in a temporal context we will here consider them as separate species.

Of the Koobi Fora specimens, ER 3766 is broadly similar to *H. makapani* though it is overall considerably smaller dentally, and has a long but slender m1. By itself it could plausibly be included in a local eastern African population of *H. makapani*. However, the inclusion of ER 1548 makes any such interpretation suspect. This specimen is quite different from both *H. hyaena*, *H. makapani*, and ER 3766. Overall it is even smaller than ER 3766, has a very small lower canine, broad p2 and p3, and a slender p4, while the m1 was small and, though damaged and not measurable, likely to have been slender like that of ER 3766. Thus, despite the fact that they both come from the Upper Burgi Mb., ER 3766 and ER 1548 are as different from each other as either is from extant *H. hyaena*.

Of the less well preserved specimens, ER 1666 and ER 669 are both specimens in the size region of ER 3766 and ER 1548 and should be grouped with them. ER 23094, on the other hand, is very similar to *H. hyaena* in both size and proportions, except that the p2 is on the small side for that taxon. Clearly, however, it differs considerably from the other Koobi Fora specimens and cannot be grouped with them. ER 23094 comes from the lowermost KBS Mb., so that its differences from the other specimens cannot be accounted for by a younger stratigraphic age.

In summary, the fossil history of *Hyaena* in Africa is a confusing one. Around 3 Ma in South Africa there existed a taxon, *H. makapani*, which was smaller than extant *H. hyaena* and had some differences from it in dental proportions. Then, around 2 Ma there existed in eastern Africa one or more taxa of *Hyaena* that were smaller than, and more different from, *H. hyaena* than the older *H. makapani*. Specimens from eastern Africa also differ amongst themselves as much as they differ from *H. makapani*. In view of this, it is at this time not possible to say how many taxa were present in eastern Africa during the Pleistocene, nor what the affiliations of the respective specimens might be. It is in light of this that we place the smaller specimens in *H. cf. H. makapani* to highlight their differences from *H. hyaena*. In view of this, these designations should not be seen as definitively indicative of phylogenetic affinities, however.

*Hyaena* sp.
Fig. 7.29

**KOBO FORA MATERIAL**

**CRANIODENTAL**

In addition to the material discussed above, there are a small number of specimens that can be assigned to *Hyaena*, but that cannot be confidently assigned to either of the groups identified above. These do not represent a distinct group or taxon, but are either too fragmentary to assign to group, or are intermediate in size or shape between them.

Specimen ER 44713 includes a fragmentary corpus and p4, roots of c and p3, and alveoli for p1-p2. The corpus is robust
and curved. It is broken dorsally behind the canine, where a piece of bone is missing that would otherwise have been perforated by the mental foramen. The corpus appears to be deepest beneath p4, but since it is also broken dorsal to m1 and 15 mm from the anterior end of the masseteric fossa, it may have been deeper there. The canine was robust, with its root mediolaterally compressed. The p1 appears to have been single-rooted and the p2 two-rooted. The p3 was large to judge from the roots preserved. The p4 is robust and relatively short. There is a substantial mesial accessory cusp, a conical main cusp (strongly worn) and a large posterior shelf (also worn) with a distinct distolingual crest. The shape of the m1 is indeterminate. The measurements of the p4 place it as intermediate between the H. cf. H. makapani and H. cf. H. hyaena groups.

Specimen ER 40415 is a broken right P4 of *Hyaena*. The protocone is missing. The parastyle is robust and strongly worn in an oblique direction from mesiodorsal to distoventral. The paracone is tall and conical with strong wear. The metastyle is short and worn. The basal cingulum is prominent along the lingual face of the tooth.

**POSTCRANIAL**

ER 3095 is a complete right radius (Fig. 7.29a). It is much shorter than that of H. hyaena and the shaft is relatively straighter. Although this specimen is much larger than the ER 1548 H. makapani radius, it is still outside the range of modern *Hyaena*. The length of this specimen is about 85% of the average modern *H. hyaena* and closer to *H. makapani* in size. It is still much larger, however, than *Proteles cristatus*. This specimen is much smaller than the *Parahyaena* from Kanapoi and *I. abronia* from Langebaanweg. It comes from the Lonyumun member. If the specimen does belong to *H. makapani*, this may indicate a slight reduction in size in the species by the Upper Burgi.

A second radius (ER 707; Fig. 7.29b) is that of a juvenile and is missing the distal epiphysis. The shaft appears to be very long. This specimen was found in the same area as metacarpal ER 709 and metatarsal ER 715. The field numbers of these specimens are in sequence. The epiphyses of these gracile specimens ER 709 and ER 715 are fully
fused. Although metapodial epiphyses tend to fuse before that of the distal radial epiphysis in mammals, their timing is relatively close (e.g., Kohn et al. 1997; Sumner-Smith 1966). While they are not likely to be associated, a relationship cannot be completely ruled out.

This third metacarpal (ER 709; Fig. 7.29c) falls near the lowest end of variation in length in extant *H. hyaena*. Although more elongated than the ER 1548AH third metacarpal, this specimen is only slightly more robust. This can be seen in the fact that the midshaft of this much longer specimen is almost identical in mediolateral and anteroposterior widths to that of ER 1548AH. This gracility may be explained if epiphyseal fusion had occurred relatively recently. In addition, the carpal articulation is more mediolaterally compressed than in ER 1548. There is a slightly more massive ventral expansion of this articulation, as well.

The relatively gracile metatarsal 4 (ER 715; Fig. 7.29d) includes only the proximal and distal ends. The proportions seem relatively unusual and gracile for *Hyaena*. The proximal articulation is very mediolaterally compressed, as is the entire specimen.

**REMARKS**

The ER 709 metacarpal seems a bit long in proportion to the ER 1666 and ER 1548 material and thus may not belong to *H. makapani*, as it represents a significant difference in function due to its elongation. Perhaps this is evidence that the metapodials, or at least metacarpals, were becoming more elongated resulting in an increase in cursorial ability in the Ōkote relative to the *H. makapani* of the Upper Burgi.

The main interest of the two craniodental specimens discussed above is that they represent definite occurrences of the genus *Hyaena* in the Ōkote Mb. That the genus is much rarer in this Member may be due to a subtle change in the environment, but may also simply be due to sampling effects.

**Genus Parahyaena Hendey, 1974**

Generic diagnosis: Large-sized Hyaenidae with moderate to strong bone-cracking adaptations; limbs slender with elongated metapodials; premolars robust; P3 and p3 with strong bone-cracking ability; dental formula I 3/3, C 1/1, P 4/3, M 1/1; P4 with large protocone, metastyle longer than paracone; m1 short with short but well-formed talonid, metaconid commonly lost.

Stratigraphic range in Africa: Early Pliocene – Recent based on FAD at Kanapoi (≥4 Ma).

Stratigraphic range at Koobi Fora: Late Pliocene – Early Pleistocene based on FAD in the KBS Mb. (≤1.87 Ma) and LAD in the Chari Mb. (≥0.74 Ma).

**REMARKS**

*Parahyaena* is the genus used by us for the brown hyena (*P. brunnea*). The genus is known from a number of eastern African sites of the early Pliocene, e.g., Kanapoi and Laetoli (Werdelin 2003; Werdelin and Dehghani 2011). These records all belong to the primitive species *P. howelli*. The extant species is endemic to southern Africa, but has been recorded from the Middle Pleistocene at West Magadi, Kenya (Werdelin and Barthelme 1997). Since the Koobi Fora specimens described here are from the Early Pleistocene, they bridge this temporal gap. Unfortunately, they are too fragmentary to show whether they
belong to either of these species, or neither.

**cf. Parahyaena sp.**
Fig. 7.18 – 7.19, 7.30

KOOBI FORA MATERIAL

CRANIODENTAL

ER 872C is a short canine that is moderately recurved and has anteromedial and posterior crests. The P3 (ER 872B) is large, with a small mesiolingual cusp with distinct crest running from it to the apex of the main cusp. The latter is massive, while the distal shelf is very short with no distinct cusp.

POSTCRANIAL

The complete left tibia, ER 872A (Fig. 7.18b; 7.30a, b), has proximal and distal articular surfaces that are the size of modern Crocuta tibiae. In anterior view, this specimen is like an unusually elongated version of extant Crocuta. The proximal and distal ends are large, yet the shaft is longer and less robust than in extant Crocuta. This specimen is the length typical of a striped hyena, but much more robust, as one would expect for Parahyaena. It is too long relative to the size of its articular surfaces to be Crocuta. The proximal and distal ends are large, yet the shaft is longer and less robust than in extant Crocuta. The proximal and distal articular surfaces are C. crocuta-like although the lateral condyle is more curved than in C. crocuta or H. hyaena and extends further anteriorly. The articular surfaces are C. crocuta-like although the lateral condyle is more curved in lateral view. The posterior extension of the lateral condyle is similar to C. crocuta. The distal end is narrower mediolaterally than in extant individuals, yet is wider anteroposteriorly than in C. dietrichi (e.g., ER 3103). Both this specimen and H. hyaena have more relief in the contours of the distal end than is seen in extant Crocuta.

The partial manus, ER 44999, includes a distal second metacarpal (A; Fig. 7.30c), and two proximal phalanges (B, C; Fig. 7.30d, e). The metacarpal has the rectangular head of hyenids but is small in comparison to C. cf. C. dietrichi (ER 3761) and very large and robust in comparison to all specimens of Hyaena from Koobi Fora. The morphology of these specimens is most consistent with Parahyaena.

The right astragalus, ER 1185 (Fig. 7.19c), is more similar to ER 3765 than to ER 1184 or the small ER 40416. However, there are some differences, as discussed in the description of ER 3765N. It is much larger than known specimens of Ikelohyaena or H. makapani. In terms of size, this specimen
is within the upper range of extant specimens of *H. hyaena* and *P. brunnea*, but smaller than *C. crocuta*.

**Hyaenidae indet. sp. A**

![Fig. 7.19](image)

**KOOBI FORA MATERIAL**

**POSTCRANIAL**

Specimen ER 40416 includes an astragalus and a third metacarpal. The third metacarpal (ER 40416B) has a relatively flat shaft with parallel sides that extends proximally just beyond what is probably the midpoint. The distal end is not preserved. In dorsal view, the head is squared off, as in all living hyenids. The shaft has the elongated feel of *Hyaena* and *Proteles*, but is very small in comparison to modern *Hyaena* metacarpals. The shaft is also wider mediolaterally than ER 1548 or ER 709.

The astragalus (ER 40416A; Fig. 7.19d) is that of a typical hyenid. The trochlea is mediolaterally compressed relative to felids. The head is rotated and oval in shape. Along the long axis of the head, the most lateral portion is almost pointed. In ventral view, the medial facet is very narrow and is about as wide as the groove between the facets. The neck is less angled relative to the long axis of the trochlea than in *Parahyaena* specimen ER 1185 and the trochlea itself is more compact. The trochlea is smaller relative to the size of the head than is seen in *Crocuta*.

In terms of size, the ER 40416A astragalus is smaller than the smallest extant *H. hyaena*, as well as extant and extinct forms of *Parahyaena*, and is in the lower range of the extinct forms *H. makapani* and *I. abronia*. In contrast, it is roughly 1/3 larger than extant *Proteles cristatus*.

There is evidence of osteophytic lipping on the dorsolateral edge of the articular surface of the head and the general condition of this bone and the associated metacarpal suggests age-related degeneration.

**REMARKS**

While in the lower end of the size range of a small extinct *Hyaena* or related genus, these specimens show some subtle differences from taxa such as *H. makapani*. While it is certainly possible that this is some form of *H. makapani* or similar-sized taxon, the lack of known *H. makapani* astragali from Koobi Fora makes this difficult to assess. Other possibilities include a form of *Ikelohyaena* or even a large form of the very rare *Proteles*.

**Hyaenidae indet.**

![Fig. 7.19](image)

**KOOBI FORA MATERIAL**

**CRANIODENTAL**

Specimen ER 44712 is a distal part of the m1 of a hyenid, broken just mesial to the metaconid. The latter is well developed and robust. The talonid has two well-developed cusps, an entoconid and a hypoconid, with the latter being slightly the larger. The morphology clearly identifies this specimen as belonging to the *Hyaena* lineage. However, given its age (Lokochot Mb.), it is plausible that the specimen might be *Ikelohyaena*, as this genus is present in approximately coeval sediments at Laetoli (Werdelin and Dehghani 2011). This would be the first record of *Ikelohyaena* from Koobi Fora, but unfortunately this genus cannot be distinguished from *Hyaena* on the basis...
of such a fragment.

Specimen ER 5345 includes two tooth fragments, a hyenid third incisor that is more likely to be a lower than an upper incisor but is so worn and cracked that definite identification is precluded, and the anterior part of a possible hyenid P1. Neither of these is identifiable below the family level.

Specimen ER 44163 is a slightly damaged p2. The tooth is low, with a minute mesial accessory cusp, a robust main cusp, and a large but low distal accessory cusp.

A P4, ER 44385 is very damaged. The metastyle appears short. Size and robustness make assignment to Hyaenidae plausible.

Specimen ER 362 is a left upper canine. The crown is short and moderately flattened with weak mesial and distal crests. The root is robust and straight with its broadest part just beneath the crown.

POSTCRANIAL

ER 1184 (Fig. 7.19a) differs from ER 1185 (Parahyaena) and ER 3765N (Crocuta ultra) in several ways, some of which are probably due to pathology. One of the most noticeable features is the large tubercle on the neck anterior to the groove for the medial malleolus. This tubercle on the medial surface of the neck is much more enlarged than anything seen in other hyenids. For example, ER 3765 has a moderate tubercle, while ER 1185 has only a slight scar. This enlargement may indicate a tear or strain in the ligament that attaches here. It might restrict anterior movement of the medial malleolus. There is some osteophytic lipping on the medial side of the trochlea as well as a little troclear eburnation, in addition to the large tubercle.

Other differences from ER 1185 and ER 3765 include having a head and neck that is wider mediolaterally. This is similar to the difference seen between Homotherium and other felids (see Chapter 9), but unlike in Homotherium, the morphology of this specimen may be partially due to injury.

The medial side of trochlea is shorter anteroposteriorly and the inferior side of medial trochlea forms a wider, gentler curve. The lateral side of trochlea is more tightly curved; the lateral projection is more posterior resulting in tighter, deeper curve on inferior side to accommodate lateral side of calcaneum.

REMARKS

The specimens listed above can be assigned to Hyaenidae with varying degrees of confidence. With better sample sizes some may in the future be assigned to genus and/or species, but for now all are best left as Hyaenidae indet.

Although ER 1184 is similar to Crocuta, its morphology is enigmatic due to pathology. It is also of unknown provenience and age. This specimen is larger than extant H. hyaena, but smaller than C. crocuta. It is most similar in morphology to C. crocuta and may be a large C. dietrichi or small C. ultra.

DISCUSSION

The diversity of hyenids at Koobi Fora is fascinating. Our previous research (Werdelin and Lewis 2008) provided a brief scenario of how the region could support so many hyenids. Briefly, we hypothesized that these taxa can be broken down into groups reflecting their distribution in space and time across eastern Africa, each with different ecologies. The first group consisted of broad hunting/scavenging generalists not unlike Crocuta today (e.g., Pachycrocuta, C. ultra, and C. eturono)
and was more common across West Turkana, while the second group had more disparate ecologies and could partition the habitat along a hunting/scavenging/size spectrum (e.g., *Ikelohyaena, Parahyaena, Chasmaporthetes*) thus gaining a wider distribution. Finally, a third group, consisting only of *Hyaena*, is found at a relatively restricted range of localities, including not only Koobi Fora, but also Omo. *Crocuta dietrichi* can be found with all groups, suggesting that it was much more of a generalist than some other hyenids.

The present work expands some of the ranges of the above taxa in time, so that there is more overlap. There is also some material that is unidentified and may add taxa to the Koobi Fora faunal list, including a tantalizing hint of a large form of *Proteles*.

The diversity of hyenids, with somewhat modern-like specimens found slightly earlier than expected (e.g., *Hyaena cf. H. hyaena*), also hints that there are other unusual or unexpected hyenid species, like *C. eturono*, waiting to be discovered.

REFERENCES


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Werdelin, L., Turner, A., and Solounias, N.
The family Felidae has its origin in the latest Eocene or beginning of the Oligocene, with its likely center of origin being in western Eurasia (Hunt 1998; Peigné 1999). Its extant sister taxon is the Asian linsangs, genus Prionodon (Gaubert and Véron 2003), though the morphological differences between this genus and recognized Felidae leave ample room for a stem lineage, to which the genera Stenogale and Haplogale may belong (Hunt 1998). The earliest definitive felid is, however, Proailurus, known from the Oligocene – early Miocene of western Europe (Peigné 1999). This genus is superseded by the paraphyletic Pseudaelurus, which gave rise to the major lineages of Miocene – Recent Felidae. An overview of felid evolution can be found elsewhere (Werdelin et al. 2010).

Proailurus is not known from Africa. The paraphyletic genus Pseudaelurus has in the past erroneously been reported from the continent (e.g., Savage 1965), but is not known with certainty. The earliest true felid known from Africa is instead Asilifelis coteae from the early Miocene of Rusinga Island, Kenya (Werdelin 2011). Overall, the pre-late Miocene record of Felidae is very limited and difficult to interpret. A case in point is the records of Diamantofelis and Namafelis from Arrisdrift, Namibia (Morales et al. 1998, 2003). The relationships of these genera to other Felidae (if they are Felidae at all) are unclear.

In the late Miocene, however, the typical Eurasian lineages of Felidae migrate into Africa. Thus, Machairodus is first known from the Beglia Fm., Tunisia, Amphimachairodus from Toros-Menalla, Chad, and Dinofelis from the Lower Nawata Fm., Lothagam, Kenya. The earliest known African member of the Felinae, to which all extant cats belong, is also from Toros-Menalla. A review of the African fossil record of Felidae and other carnivores is available in Werdelin and Peigné (2010).

Subfamily MACHAIRODONINAE Gill 1872

This subfamily includes the so-called saber-toothed Felidae. The end members of the lineages included within the subfamily (Homotherium, Smilodon, Megantereon) are highly distinctive in most aspects of morphology and remain iconic members of the extinct faunas of the “ice ages” in the public’s eye. However, the diagnosis of the entire subfamily Machairodontinae is far from straightforward. Early members of the subfamily, such as Paramachaerodus, are less readily distinguished from the Felinae (Christiansen 2008; Salesa et al. 2005), while genera commonly assigned to the tribe Metalurini (Metalurus, Dinofelis) show few diagnostic features of the Machairodontinae (Werdelin et al. 2010). Members of the former genus are very generalized in their morphology, while the latter show clear convergences with the living genus Panthera (Werdelin and Lewis 2001).

Most authorities cite the mediolaterally compressed upper canines as a synapomorphy
of the Machairodontinae. However, some species of Dinofelis do not conform to this model, and have canines that are no more compressed than those of living lions and tigers (Werdelin and Lewis 2001). Similar arguments apply to other characters of the feeding and prey-procurement apparatus of Machairodontinae, which is much less uniform in morphology than that of living cats. Werdelin and Lewis (2001) identified two features that allied Dinofelis with all other Machairodontinae available to them: the size differential between the upper and lower canine, which is much greater in Machairodontinae than in Felinae (and due to a reduced lower canine rather than an enlarged upper one), and the presence of a deep pit or groove superomedial to the troclear notch of the ulna (reduced in Homotherium) that is absent in Felinae. Recovery of a skeleton of Metailurus parvulus from Euboia, Greece (Roussiakis et al. 2006), showed that no such groove is present in that genus, however. We are left with the canine size differential as a diagnostic feature of Machairodontinae. A similar conclusion was reached by Christiansen (2012). Thus, Machairodontinae as a group is very poorly diagnosed and basal forms such as Paramachaerodus retain a primitive skull structure, presumably inherited from ancestral forms within Pseudaelurus (sensu stricto; see Werdelin et al. 2010). It may be noted that Christiansen (2008) uses the similarity in skull morphology between Paramachaerodus and Neofelis (clouded leopard) to argue that the latter is incipiently sabertoothed. However, it seems more likely, following Prevosti et al. (2010) and Slater and Van Valkenburgh (2008), that the two genera are similar because of shared primitive traits that have nothing to do with functional convergence.

In Africa, Machairodontinae have been present since the earliest Late Miocene with Machairodus robinsoni from the Beglia Fm., Tunisia. Miocene machairodonts of this genus, as well as Amphimachairodus and Lokojiria are poorly known (see (Sardella and Werdelin 2007). In the latest Miocene Dinofelis and Metailurus appear, and shortly thereafter, in the early Pliocene, Homotherium and Megantereon.

Genus Homotherium Fabrini, 1890

Synonyms: Epimachairodus Kretzoi, 1929b

Type species: Homotherium crenatidens Fabrini, 1890

Generic diagnosis: Machairodont of large size; dentition serrated and crenulated; incisors robust, I3 caniniform; incisors placed in an arch; C flattened and elongated, crenulations large; c small, subequal to i3; p3 reduced, sometimes lost in derived forms; P4 with completely reduced protocone, preparastyle present; p4 reduced, main cusp large; m1 elongated, metaconid and talonid absent; skull elongated, especially the splanchnocranium; sagittal and lambdoid crests large and robust (emended from Sardella 1994).

Stratigraphic range in Africa: Early Pliocene (∼4.35 Ma) – Middle Pleistocene (ca. 0.8 Ma) based on a first occurrence in the Lonyumun Mb., Koobi Fora Fm., and a last occurrence at Tighenif, Morocco. The latter record needs review and confirmation.

Stratigraphic range at Koobi Fora: Early Pliocene (∼4.35 Ma) – Early Pleistocene (∼1.38 Ma), based on a first occurrence in the Lonyumun Mb. and a last occurrence in the Okote Mb.
**REMARKS**

The tribe Homotheriini, to which *Homotherium* belongs, has a very broad distribution, from southern Africa, through nearly all of Eurasia and North America, down to South America (Werdelin et al. 2010). At least two, and possibly three genera are recognized (*Homotherium*, *Xenosmilus*, and possibly *Dinobastis*). At the specific level, a plethora of species of *Homotherium* have been named (e.g., in Eurasia alone there are *H. crenatidens*, *H. nestianus*, *H. latidens*, *H. nihowanensis*, *H. ultimum*, *H. davitasvili*). Some regional revisions have been attempted, but in the absence of a modern, broad-scale revision, it is impossible to say which of these might be valid.

Four species have been named in Africa: *H. ethiopicum* Arambourg, 1947 from the Omo Group, Ethiopia, *H. problematicum* Collings, 1972 from Makapansgat, South Africa, *H. africanum* Petter and Howell, 1987 from Aïn Brimba, Tunisia, and *H. hadarensis* Petter and Howell, 1988 from Hadar, Ethiopia. The first mentioned is best considered a *nomen dubium*, as the material on which it is based, a partial mandibular ramus with worn teeth, is hardly diagnostic. The others are valid as named. *H. africanum* was originally described as a species of *Machairodus*, but its characteristic skull morphology, as well as its mid-Pliocene age, clearly show that it belongs to *Homotherium*.

It is not clear whether any material outside of these sites belongs to any of these species or some unnamed species, or whether the three species are synonymous and/or synonymous with the Eurasian *H. latidens* (or any other potentially valid Eurasian species of *Homotherium* – see above). Pending a revision of the genus we here retain all Koobi Fora *Homotherium* in open nomenclature as *H.* sp.

**Homotherium sp.**

*Fig. 8.1 – 8.9*

**Stratigraphic range in Africa:** Early Pliocene (≤4.35 Ma) – Early Pleistocene (≥1.38 Ma) based on occurrences at Koobi Fora (see below).

**Stratigraphic range at Koobi Fora:** Early Pliocene (≤4.35 Ma) – Early Pleistocene (≥1.38 Ma), based on FAD in the Lonyumun Mb. and LAD in the Okote Mb.

**KOOBI FORA MATERIAL**

**CRANIODENTAL**

Specimen ER 1540 is an isolated left i3. This tooth is large, with a long, slightly buccally curved root and conical crown. There is a very small medial cusp, a tall, conical main cusp, and a low but distinct lateral cusp. There is a moderately developed wear facet that commences at the tooth apex and continues down on the lateral side of the main cusp to about the level of the apex of the accessory cusp.

The right mandibular ramus ER 931 (Fig. 8.1a-c) is broken anteriorly just behind the canine alveolus and posteriorly just at the base of the coronoid process. The p3 is very small, lacking a mesial accessory cusp but with a minute distal one. The apex of the tooth was broken off post-mortem. The p4 is a large, leaf-shaped anterior accessory cusp. The main cusp and entire distal part of the tooth show extensive, vertical wear facets from attritional wear with the P4 and no longer display any sign of their original morphology. Posterobuccally the enamel is com-
Fig. 8.1: Rami and lower dentitions of *Homotherium* sp. from Koobi Fora. a-c) right ramus ER 931 in a) buccal, b) lingual, and c) occlusal view; d-f) right ramus fragment ER 44606 in a) buccal, b) lingual, and c) occlusal view.
pletely worn away. The m1 is very long, especially the protoconid. The m1 extensively overlaps p4, and together their wear forms a single, long carnassial wear facet. Distobuccally, only a few mm remain of the enamel of the m1. The ramus is extremely robust and thick. There is a small mental foramen below the anterior part of p3. The masseteric fossa reaches the distal end of m1, while the inflected ‘chin’ reaches the mesial part of p3.

The P3, ER 44059 is unworn, with its serrations still clearly visible on the lingual side. There are small mesial and distal accessory cusps that are appressed to the main cusp. The latter is tall and short, with a convex mesial margin and straight-to-concave distal one.

ER 44606 (Fig. 8.1d-f) is broken mesial to p4 and distal to m1. The mesial end of the masseteric fossa is visible and reaches to about the middle of the protoconid. The p4 is nearly unworn. The mesial accessory cusp is very large, tall and free of the main cusp. It is set nearly vertically. The main cusp has a distinct posterad slant. It is very tall and triangular and is also nearly unworn. The distal accessory cusp is of about the same size as the mesial, but closely appressed to the main cusp, to a degree where they can be considered to form a single unit. The m1 overlaps the p4 to about the middle of the distal part of the main cusp. The m1 has some wear on the paraconid, which is long and robust. The protoconid is lower and shorter and more slender. The wear on m1 is not yet so far advanced as to encroach on the distal end of p4. The ramus, though broken ventrally, was relatively deep, though not as deep as some Homotherium, e.g., ER 931, which was presumably a considerably older individual.

ER 3114 includes a number of maxilla and dental fragments, including incisor and canine fragments that are diagnostic of Homotherium. Beyond this, all that can be said about this specimen is that it appears to have had a large and somewhat retracted nasal opening, which is characteristic of Homotherium and most other machairodont felids.

ER 3093P is a small fragment of upper canine. By itself it is not diagnostic, but the associated postcrania can be definitively assigned to Homotherium (see below).

ER 46409 is a set of four upper incisors, including right I3, left and right I2 and a possible I1 that can’t be assigned to a side.

POSTCRANIAL

Postcranial material of Homotherium will be presented by member. While there is no evidence that there are multiple species of Homotherium, there are some differences through time within this lineage. Discussion will be reserved until all the specimens of Homotherium have been described, rather than at the end of each section.

Lonyumun Member

The axial skeleton of ER 3093 is extremely fragmentary and consists mostly of vertebral centra (Q, R, Z, AA, AE). Thoracic vertebral centra include ER 3093Q, R, and AA. These specimens are robust and the centrum is very rounded. They seem rather short in length for their width relative to other felids. Lumbar centra include ER 3093Z and AE. Although much of ER 3093Z is broken or eroded on the edges, the dorsal part of the centrum is well preserved. A deep, almost V-shaped cleft is present, running down the dorsal surface of the centrum and dividing the posterior part of the centrum into two almost lobe-like portions. This cleft is particularly deep in Homotherium. The lumbar ventral keel can be
seen in ER 3093AE, although the dorsal portion of this vertebra is missing. Caudal vertebrae ER 3093U and W (Fig. 8.2a, b) are complete, while ER 3093AO is the caudal end of the centrum. All are mid-caudal vertebrae. Additional vertebral fragments include ER 3093AG, AJ, AL, and AQ. Ribs are only represented by shaft fragments (e.g., ER 3093AD).

The only vertebral specimens of ER 3111 are extremely fragmentary cervical (E) and lumbar (A) centra. Both specimens are robust, as is to be expected. In contrast, the proximal portion of a rib (ER 3111C) is well preserved and robust.

The scapula fragment ER 3093T (Fig. 8.2c) includes only the inferior portion of the glenoid, which is large and very flat. The infraglenoid tubercle is robust, but does not project greatly. This specimen is similar to that of *Homotherium latidens* from Senèze figured by Ballesio (1963). Another tiny fragment of the glenoid is known (ER 3093AH).

The right humerus, ER 3093H, includes the lateral half of the distal end in poor condition. As not all of the capitulum is included, the anteroposterior trochlear width cannot be assessed. A humeral shaft, ER 3093I, has also been preserved. This large specimen includes the most inferior point of the deltidoid and below and is slightly larger than ER 791 described below. The shaft, as always in *Homotherium*, is robust.

Only the ends of the right radius have been preserved. The proximal end (ER 3093S; Fig. 8.2d, e) is a little cracked. Some of the anterior shaft pieces are missing in the distal end (ER 3093G), but approximately the distal third of the shaft is present.

Radius ER 3093S is much smaller and more gracile than ER 3113 from the Tulu Bor Mb. The head is not round in proximal view, but is more like the oval *Dinofelis* or *Megantereon* heads. The neck is much thinner mediolaterally. However, the anteroposteriorly thin neck relative to the head and shaft is also seen in ER 3113. This means that both specimens have heads that project posteriorly far past the posterior surface of the neck. The anterior surface of the head barely swells anteriorly from the surface of the neck. The bicipital tuberosity is absolutely and relatively lower on the shaft in this specimen. However, the curvature of the head and neck remains the same. Curvature in the proximal shaft cannot be assessed as this has not been preserved.

The distal third of the shaft of ER 3093G (Fig. 8.2f, g) is also gracile and smaller than ER 3113. The shaft is less massive in comparison to ER 3113 as it approaches the distal epiphysis. This specimen shows the beginning of the incredibly thick anteroposterior distal shaft of ER 3113, but this is not nearly as pronounced relative to the size of the distal end. However, the ulnar facet is large. The extremely flat posterior surface of the shaft as it contacts the epiphysis is identical to ER 3113, as is the indentation inferior to the connection. The epiphysis in both specimens seems set slightly anteriorly relative to the shaft. In distal view, the carpal articulation is quite similar to ER 3113. In this specimen, however, there may be slightly less of a posterior extension. In anterior view, the grooves for the extensor tendons are more marked than in ER 3113, but not as much as in *Dinofelis*, *Megantereon* or *Panthera*. The medial flange for the insertion of brachioradialis and for supporting the abductor pollicis longus and extensor pollicis brevis tendons is very small relative to other felids, but is slightly more pronounced in this specimen relative to its size than in later specimens of *Homotherium* from Koobi Fora. A relatively wide groove can clearly be seen for
Fig. 8.2: Homotherium sp. material from the Lonyumun Mb. a) caudal vertebra ER 3093U; b) caudal vertebra ER 3093W; c) inferior portion of glenoid ER 3093T; d-e) proximal radius ER 3093S in d) posterior and e) proximal view; f-g) distal radius ER 3093G in f) anterior and g) distal view; h-i) distal tibia ER 3093C in h) posterior and i) distal view; j-k) astragalus ER 3093F in j) dorsal and k) ventral view; l) dorsal view of distal fifth metacarpal ER 3093L; m) dorsal view of middle phalanx ER 3093X. Note lack of asymmetry; n) dorsal view of metatarsal 3 ER 3093N; o-p) distal fibula ER 3093AB in o) lateral and p) medial view; q-s) distal femur ER 1665 in q) anterior, r) posterior, and s) distal view; t) distal view of distal femur ER 3093B; u) lateral view of os coxae ER 1665B.
these abductor and extensor tendons in comparison to the slight dent in the small flange of ER 3113.

ER 3093D is a proximal left ulna that includes most of the semilunar notch, the medial coronoid process and some of the radial notch. A fragment of left olecranon process (ER 3093Y) includes the medial half of the process and conjoins with ER 3093D. The anconeal process and entire proximal anterior part of the bone is missing. The medial coronoid process is wide and relatively squared off. Although the entire semilunar notch is not preserved, it is clear that it would have been quite large. Its fragmentary nature precludes comparison to the Senèze specimen.

The olecranon process has an anteromedially projecting tubercle at the level of the anconeal process. The medial edge of the olecranon then sweeps back towards the midline as it continues to the proximal end of the bone.

Interestingly, ER 3093Y shows that the width of the shaft posterior to the semilunar notch is not particularly thick anteroposteriorly, and much less so than in the younger West Turkana Homotherium WT 580. Perhaps another trend is the increasing anteroposterior width of the proximal ulna to support the increasing weight.

The right ulnar shaft, ER 3093 J, represents the middle portion of the shaft. The inferior end preserves the proximal half of the larger muscle scar marking the origin of the abductor pollicis longus on the lateral surface.

Only a distal left fifth metacarpal (ER 3093L; Fig. 8.2t) and phalanges are known from the manus of ER 3093. The left metacarpal is relatively gracile. The dimensions of the head are smaller than those of other Koobi Fora Homotherium metacarpals suggesting a smaller individual as Ballesio (1963) indicates that the transverse width of the head does not differ greatly in the second through fifth metacarpals. The articular surface of the head does not slope as far laterally as in other felids and is quite similar to the Homotherium fifth metacarpal figured by Ballesio (1963, fig. 39).

Three proximal phalanges are known, including an incomplete one that is likely from the fifth digit (ER 3093M) and two that only include the proximal ends (ER 3093V and AC). A fourth middle phalanx (ER 3093X; Fig. 8.2m) is well preserved and lacks the asymmetry present in most felids. Homotherium latidens and Dinobastis serus also lack this asymmetry and have been reconstructed as having limited claw retraction (Antón et al. 2005; Rawn-Schatzinger 1992).

The blade of the ilium of ER 1665B (Fig. 8.2u) is well preserved. The blade is long and narrow and the tip curves laterally. The blade of the ilium does not appear to be as wide relative to length as in the Senèze Homotherium, but the Senèze ilium is incomplete and Ballesio (1963) has reconstructed the length. In comparison to modern taxa, the dorsoventral width of the iliac blade relative to the length of the ilium is quite narrow (or to think of it another way, the ilial length is quite long relative to ilial breadth), more like extant cheetahs and pumas rather than lions and tigers. Thus, although some measurements fall within the range of extant large Panthera, the proportions are slightly different.

The neck of the ilium is short and thick, as in the Senèze Homotherium. This feature is more like ursids than large Panthera. The anterior portion of the blade leading to the tip is very thick and heavily buttressed. The posterior part of the blade is thinner and the posteriormost edge curves laterally. The acetabulum is present, but lacks the anterome-
dial wall and a portion of the deepest part. The inner surface of the acetabulum and the surrounding regions curves slightly inward from the ischium to the ilium. The lunate surface is preserved. The acetabulum is relatively round and deep and overall large. The groove anterior to the inferior edge of the lunate surface is very wide and deep, much more so than in *Dinofelis*. Most of the ischium and all of the ilium is preserved. The ischium inferior to the acetabulum is wide and extremely flat. There is no pubis present, although the beginning of the superior ramus is quite thick.

Several fragments of *Homotherium* femora have been recovered from the Lonyumun Mb. One poorly preserved partial right femur includes the head (ER 3093A) and distal end (ER 3093B; Fig. 8.2t). This femur is from a larger individual than ER 1665 (described below), although they are from the same horizon. The intercondylar groove is very similar in shape to other *Homotherium* specimens. The two sides are roughly parallel as they curve. A fragment of femoral condyle, ER 3093AF, is also known.

The femur ER 1665A (Fig. 8.2q-s) includes only the distal third or so. There are rugose ridges from the lateral gastrocnemius attachment to the medial edge. There is no sign of this ridge in other specimens, although the lateral gastrocnemius insertion is usually quite rugose, particularly in *Dinobastis serus*. The edges of the patellar groove might show some signs of age, but there is no osteoarthritic lipping of the condyles. There is, however, pathological pitting similar to that seen in *Dinofelis aronoki* ER 4419. This is seen primarily in the distal femur and to a much lesser degree in the associated os coxae (ER 1665B).

Specimen ER 1665A (with the exception of the ridges) is more typical of other large felids in shape than later *Homotherium* femora. The distal shaft is not particularly flattened anteroposteriorly and it is not very wide. Overall, this specimen, despite being similar in size to the femora from later horizons, is much more gracile. The medial condyle projects further posteriorly than the lateral, as in all later *Homotherium*. However, both the medial and lateral condyles are robust and they are similar in size. This suggests that the lateral condyle is reduced in size as one moves into the Tulu Bor and Upper Burgi. The end-point of this trend can be seen in *D. serus*. The epicondyles are robust and similar to those in later specimens. The patellar groove is narrow and projects far anteriorly from the condyles in distal view. The sides of the groove, however, are not steep and there is not as much curvature as in later specimens. The medial edge of the patellar groove is not very distinct due to the swelling of the shaft on either side of the groove. The groove, therefore, is buttressed.

The eroded right distal femur, ER 3111B, is similar to ER 1665A, but larger. The condyles are too eroded to judge their proportions. It is different from younger specimens of *Homotherium* and more like other large felids in that the patellar groove projects anteriorly to a greater degree, is slightly narrower, and has more relief to it than in younger *Homotherium*. It is larger than any African specimen of *Dinofelis* and similar in size to *H. latidens*.

The proximal tibia (ER 3093E) is extremely poorly preserved. Much of the compact bone is missing or cracked. The tibial tuberosity is present, but damaged and may be slightly crushed. Neither condyle is whole. The intercondylar groove is clearly marked by distinct curvature of the condyles as in all felids. The lateral condyle appears relatively rounded in comparison to the Senèze speci-
men, but the preservation precludes certainty on this point. The small portion of the shaft is compressed and slightly twisted.

The distal specimen (ER 3093C, Fig. 8.2h, i) is also cracked. This specimen is extremely thick anteroposteriorly, as in the Senèze *Homotherium*. *Dinobastis serus* is not as relatively thick anteroposteriorly. The medial malleolus does not project very far distally beyond the level of the articular surface. The articular surfaces are not deeply excavated. The area of the tibia that contacts the astragalar head has a shallow groove running along it. This is the area above the arch on the anterior surface of the tibia.

The distal left fibula ER 3093AB (Fig. 8.2o, p) is smaller than one might expect for an animal the size of *Homotherium*. It appears relatively compressed anteroposteriorly. In contrast, the right distal fibular, ER 3111D, is robust but cracked. The distalmost surface appears relatively flat, but that is due partially to preservation.

The left astragalus ER 3093F (Fig. 8.2j, k) has the typical *Homotherium/Dinobastis* morphology. The head is elongated along the long axis and roughly squared off. The astragalus is short overall and the neck is short and squat. There are a few differences between this specimen and the Senèze *H. latidens* astragalus (as figured in Ballesio 1963). The head of ER 3093F is wider and flatter. If the Senèze drawings are accurate, the lateral calcaneal facet of *H. latidens* is set at a slightly more oblique angle than in ER 3093F, while the medial calcaneal facet is wider than in ER 3093F.

The left distal third metatarsal (ER 3093N; Fig. 8.2n) and proximal fifth metatarsal (ER 3093O) have been recovered from this partial skeleton. The third metatarsal has a very square head and is very robust. The fifth metatarsal looks identical to that of *H. latidens* pictured in Ballesio (1963). It is very narrow mediolaterally.

Another left distal third metatarsal, ER 3111F, is similar to the other *Homotherium* metapodials. The fusion between the epiphysis and shaft is complete, but has the texture of a recent fusion. The head is large relative to the shaft, which is also characteristic of recently fused metapodials.

**Tulu Bor Member**

The atlas and axis of ER 3112 have been recovered. The atlas is made up of three conjoining fragments (ER 3112O, P, X) that include most of the cranial and axial articulations. From what little is preserved, the body seems narrow mediolaterally relative to its height. The transverse processes attach low on the body and must not have been particularly large. The specimen is similar to, but less well preserved than the Senèze *Homotherium* (Ballesio 1963). Only the cranial end of the spinous process of the axis (ER 3112T) has been recovered.

Several additional fragmentary vertebrae of ER 3112 have been recovered including the centra of cervical (B, F, G, R), thoracic (A), and lumbar (E) vertebrae. Specimen ER 3112B is actually two cervical centra fragments in articulation. The cervical centrum ER 3112G is well preserved enough to see that it is quite tall with a ventral keel. The lumbar centrum ER 3112E includes the dorsal groove and the ventral keel. Many other smaller identifiable fragments of vertebrae are present.

The partial skeleton also includes the proximal and distal portions of the left humerus (ER 3112C, H respectively) and a small shaft fragment of the right humerus (ER 3112K). The head is well-preserved (Fig. 8.3a, b). The proximal end is quite large an-
Fig. 8.3: *Homotherium* sp. material from the Tulu Bor Member. a-b) proximal humerus ER 3112C in a) proximal and b) lateral view; c-d) distal humerus ER 3112H in c) anterior and d) distal view; e) dorsal view of distal second metacarpal ER 3112M; f) dorsal view of proximal phalanx ER 3112J; g) dorsal view of distal third metatarsal ER 3112I; h-i) distal femur ER 3112D in h) anterior and i) distal view; j-l) distal femur ER 3750 in j) anterior, k) posterior, and l) distal view.
teroposteriorly. The greater tuberosity makes up more than half of this length, but is not as tall relative to the size of the head as in *H. latidens* from Senèze. The head is rounded and is wide mediolaterally. The proximal humerus is similar in shape and size to Upper Burgi *Homotherium* specimen ER 791, although it is slightly larger than ER 791. The only major difference in ER 3112 is that the head is not anteriorly distinct from the shaft, as in ER 791.

The trochlea of distal humerus ER 3112H (Fig. 8.3c, d) seems anteroposteriorly narrow in distal view, unlike later *Homotherium*. It still seems wider than in *D. aronoki*, the most *Homotherium*-like *Dinofelis*. Only the distal articular surface and the medial epicondyle are preserved. The medial epicondyle projects further medially and is larger than in later *Homotherium*.

The only *Homotherium* radius from the Tulu Bor Member, ER 3113 (Fig. 8.4a-d), is quite large. The head is rounded, but not completely round. The medial side of the head flares slightly from the shaft, while the lateral side is nearly in line with the shaft. This specimen seems slightly larger than the radius that would have been associated with the Upper Burgi humerus ER 791. Specimen ER 3113 was analyzed previously in a study that demonstrated that most machairodontines have a relatively small mediolateral distal articular size (Lewis and Lague 2010), a feature previously assumed to have been just a feature of *Homotherium* and *Dinobastis* (Antón et al. 2005; Ballesio 1963; Rawn-Schatzinger 1992).

The shaft is extremely straight, with only a slight lateral displacement from the neck. The distal end of the shaft is the most robust, as the ulnar side widens in the last third of the shaft. The widened surface is triangular in shape and slightly excavated, as depicted in Ballesio (1963). The ulnar notch at the distal end is therefore quite wide, with an oval bipartite facet. The muscle markings on the shaft are rugose, as described for *H. latidens*.

The proximal half of the shaft is slightly different from that of *H. latidens* as described by Ballesio (1963). The bicipital tuberosity does not lie immediately inferior to the head, as in *H. latidens*. Instead, the insertion for the biceps brachii forms about 12 mm below the head on the lateral side and runs mediodistally for 33 mm as a large, rugose crest. It ends slightly more distal than the distal end of the radial tuberosity. This upside down V-shape formed by the tuberosity and the ridge is seen in the other specimens. This is similar to what is seen in *D. serus*, although the shaft may curve a bit more in *D. serus* from Friesenhahn Cave, Texas (Rawn-Schatzinger 1992).

In the midshaft region, the origin of the abductor pollicis longus is distinct and set off posteriorly by a ridge. It forms slightly above midshaft and runs slightly inferior to it as the shaft begins to widen. The origin of the deep digital flexor is extremely large and rugose as described by Ballesio (1963). The surface of the shaft is flat in this region, and has a pronounced keel along the medial edge for the deep digital flexor and the supinator. Although in modern felids this area is one of curvature in the shaft, this specimen, like other *Homotherium*, has less curvature of the shaft. The posterior surface of the shaft is similar to that of other felids in the proximal half, but the distal half is almost imperceptibly convex in the region of the origin of pronator quadratus.

On the distal end, the groove for abductor pollicis longus is narrow and not very deep. It is quite minimal in comparison to that of ER 3093, *Dinofelis*, and modern large fe-
Fig. 8.4: Left radius of *Homotherium* sp. from the Tulu Bor Mb., ER 3113. a) anterior view; b) posterior view; c) proximal view; d) distal view.
lids. The groove and the supinator flange are located about 1-2 mm more proximally in ER 3113. In contrast to *H. latidens* (Ballesio 1963), there is less flaring of the medial and lateral sides of the shaft. The grooves for the extensors are relatively wide with low, flat ridges between them.

The carpal facet is wide anteroposteriorly in comparison to its mediolateral width. Perhaps the manus has more rotatory ability, since the supinatory abilities of the forearm are reduced in addition to having greater load-bearing ability. The greater anteroposterior width is due mainly to the posterior expansion of the surface. The styloid process is not particularly large, but it is thick.

Metacarpals include the robust distal right second, third and fifth metacarpals (ER 3112M, S, L, respectively). Only the second metacarpal (Fig. 8.3e) is reasonably well preserved. It is broad mediolaterally and relatively flat in comparison to *Dinofelis* or *Megante­reon*. The sagittal keel does not project very far distally in anterior view. Instead, it forms a large, squared-off protuberance when viewed laterally. A single, well-preserved proximal phalanx (ER 3112J; Fig. 8.3f) looks much like the Senèze *Homotherium* (Ballesio 1963).

The right distal femur ER 3112D (Fig. 8.3h, i) is eroded, but the general shape is preserved. This specimen is larger than ER 3750. The patellar groove is in better condition and demonstrates greater relief (i.e., the patellar groove is deeper with higher sides). Thus, this specimen is similar to Lonyumun specimen ER 1665A in having a narrow, deep groove. The groove is relatively wider, though, and the area around the epicondyles is expanded. The condyles appear roughly similar in size. The major difference between this specimen and ER 1665A is the distal shaft and the robusticity of the area around the condyles. The distal shaft is wider and flatter relative to the bicondylar width. Therefore, the changes in the distal shaft and epicondylar region must have evolved before the changes in the condyles themselves.

The femur ER 3750 (Fig. 8.3j-l) is also poorly preserved, such that only the cancellous bone preserves the shape. However, the cancellous bone appears particularly eroded in the posterior projection of the condyles. The shaft fragment does not conjoin with the distal femur, but it is the right size for the shaft slightly proximal to the break. The distal shaft is flattened anteroposteriorly. The condyles are more equal in size than in *D. serus* from Friesenhahn. The patellar groove also is more typical for a felid and does not extend as far anteriorly from the condyles when seen in distal view. The overall appearance of this specimen is a wide condylar and epicondylar region that is flattened anteroposteriorly, but with a patellar groove that is not excessively wide for the size. This is true for all the Koobi Fora *Homotherium*.

A cracked and weathered distal metatarsal 3 (ER 3112I; Fig. 8.3g) is similar to the better preserved *Homotherium* specimens from Koobi Fora. No other pedal elements are known from this member.

**Upper Burgi Member**

The left humerus ER 791A is large, but is not as large as the largest *Homotherium* humerus known from Koobi Fora, KBS humerus ER 704. ER 791A (Fig. 8.5a-e) is similar in size to the humerus of *H. latidens* (Ballesio 1963). The shape of the proximal end is almost identical to that of *H. latidens*. One difference between ER 791A and *H. latidens* is the shape of the olecranon fossa, which is short and squat in *H. latidens*. In ER 791A it is taller and more narrow mediolaterally. This is similar to the
condition in *D. serus* from Friesenhahn Cave, Texas. Previous studies have indicated that this specimen is more similar to the large *Homotherium* from Omo than the smaller *H. hadarensis* from Hadar (Lewis and Lague 2010).

The anteroposterior width of the ER 791A trochlea does not seem quite as thick as in ER 704. Also, the mediolateral width of the trochlea in posterior view seems a little narrower. Granted, this is a slightly smaller specimen. Unfortunately, the head is eroded and the greater tuberosity missing, so its shape cannot be compared to ER 3112C.

Two associated proximal radii have been found (ER 1546A, B). The right proximal radius, ER 1546A (Fig. 8.6a-c), includes the head and neck to inferior to the bicipital tuberosity. The left proximal radius, ER 1546B, includes only half of the head. Comparison of these specimens to the humerus ER 791A indicates that ER 1546 is from a slightly smaller individual.

The head of ER 1546A has a relatively round articular surface, while in most felids it is more oval. There is also less of an angulation of the head and neck from the shaft. Both of these features are typical of *Homotherium*.

A proximal right radius, ER 1580 (Fig. 8.6d-f), will also be described here, although it was found in less securely dated sediments.
that may range from the Upper Burgi to the KBS Members. The head of this specimen is eroded on the anterior border. This specimen appears to be a slightly larger individual similar to ER 3113, but with a slightly more proximally placed bicipital tuberosity. It is larger and more robust than ER 1546.

The unciform, ER 791C (Fig. 8.6g), is robust, as is all of the *Homotherium* material. The metacarpal surface is more triangular than that of *H. latidens* figured in Ballesio (1963), otherwise, they are quite similar. In comparison to *Dinobastis serus*, the distal surface is more sloping. In comparison to *Dinofelis* from Kanam East, this specimen is quite different in several ways. The dorsal surface is very flat and the distal articular surface is elongated and runs the entire dorsoventral length of the bone. In *Dinofelis*, the articular surface stops before reaching the ventral end. In addition, the distal articular surface is also more triangular, while in *Dinofelis* it is more rounded.

Three associated right metacarpals have been found: metacarpal 2, metacarpal 3, and metacarpal 4 (ER 44655A, B, C, respectively; Fig. 8.6h-j). They are from an individual of a size similar to ER 791. These specimens show the robust, elongate morphology characteristic of *Homotherium* and have robust muscle markings. When articulated, metacarpals 3 and 4 are roughly the same length, although the third metacarpal is the more robust specimen. The proximal end of the fourth metacarpal is narrow, such that the metacarpals are more tightly knit than in lions, a feature seen in *H. latidens* (Antón et al. 2005; Ballesio 1963). While the carpal articulation of metacarpal 2 is large, it does not have a large shelf for the metacarpal 3 as in *Panthera* due to the more tightly compressed metacarpals. As in all *Homotherium*, the heads are relatively wide mediolaterally, with the greatest elongation in width seen in the third metacarpal. An additional right second metacarpal, ER 44649 (Fig. 8.6k), looks like ER 44655A, but is more eroded. However, it preserves more of the lateral side of the carpal articulation, a region that is broken off in ER 44655A.

The distal left metacarpal 4, ER 791B (Fig. 8.6m, n), is well-preserved. It is similar in size to the third metacarpals ER 44655B and ER 3112S, but ER 3112S may be from a slightly smaller individual. On the lateral side of the proximal end, there is less lipping than in *Dinofelis* (ER 722V) and less excavation of the articular surface with metacarpal 5, another feature associated with tighter metacarpal compression in *Homotherium*. In lateral view, the distal articulation is also more rounded than in *Dinofelis* and there is a greater distal extension of the plantar surface. The shaft is robust. In cross-section, the shaft is relatively flattened dorsoventrally and is very wide mediolaterally. This differs from the more rounded cross-sectional geometry seen in *D. piveteau*.

The proximal phalanx ER 791D (Fig. 8.6l) is robust, as expected. The head is larger than in any other specimen relative to the size of the shaft. Although similar in length to the proximal phalanx of the third manual digit of *Lokotunjailurus* from Lothagam (LT 26178), it is much more robust, with larger articular ends. The proximal and distal portions of the shaft are roughly equal in size. The interphalangeal facet is relatively wide and the articular surfaces are deep and rounded dorsoventrally. In lateral view, the dorsal surface of the shaft is slightly arched, but the entire shaft does not appear to be curved. The metacarpal articulation is relatively square with a domed top. The ventral processes are more pointed in lateral view than in most felids, including *H. latidens*.  

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Fig. 8.6: Thoracic limb material of *Homotherium* sp. from the Upper Burgi Mb. a-c) right proximal radius ER 1546A in a) anterior, b) posterior, and c) proximal view; d-f) proximal radius ER 1580 in d) anterior, e) posterior, and f) proximal view; g) proximal view of left unciform ER 791C; h-j) dorsal views of associated metacarpals ER 44655A-C including metacarpal 2 (h), metacarpal 3 (i), and metacarpal 4 (j); k) dorsal view of metacarpal 2 ER 44649; l) dorsal view of proximal phalanx ER 791D; m-n) left metacarpal 4 ER 791B in m) proximal and n) dorsal (Q) view.
Fig. 8.7: Pelvic limb material of *Homotherium* sp. from the Upper Burgi Mb. a-c) proximal femur ER 2092 in a) anterior, b) posterior, and c) medial view; d) posterior view of distal femur ER 2125; e-f) distal femur ER 3096 in d) anterior and e) distal view; f) g-h) proximal right fibula ER 45540 in g) lateral and h) medial view; i-j) distal right fibula ER 45540 in i) lateral and j) medial view; k-l) right calcaneum ER 4979 in k) dorsal and l) medial view; m-n) left calcaneum ER 44650 in m) dorsal and n) medial view.
The right proximal femur ER 2092 (Fig. 8.7a-c) is missing the greater trochanter, but is otherwise well-preserved. This is the largest femoral specimen of *Homotherium* housed at the KNM. It is extremely similar to the West Turkana *Homotherium* femur WT 16826, but much larger.

The head is large - much too large for a specimen like the ER 1665 os coxae. It is very rounded with only the slightest hint of a point at the fovea capitis. In medial view, the fovea is located just posterior to the middle of the head, as with extant lions and tigers. The angle of head and neck relative to the shaft is felid-like. This specimen does not have the more proximally oriented head and neck of *Ursus*, nor does it have the even more rounded head of *Enhydriodon*. The fovea is deep and rounded and differs distinctly from the ursid material in shape. Other than the relatively large size and roundedness of the head and the distinctness of the fovea, it is similar to other large felids.

The base of the greater trochanter suggests that it would have been quite robust. The inferior portion of a robust intertrochanteric crest can be seen (unlike in the ursid material where there is no crest). The lesser trochanter is robust and projects superomedially and posteriorly. Its placement is similar to the West Turkana WT 16826 femur, but differs from the Senèze specimen. The Senèze femur (Ballesio 1963) has a more typical felid placement towards the medial side of the shaft. In this specimen, however, the tuberosity is located just medial to the long axis of the femur. The intertrochanteric fossa is large and extends laterally under the greater trochanter, but does not extend to anywhere near the lesser trochanter.

The shaft of ER 2092 is extremely robust. Along the lateral edge is a sharp ridge running from the base of the greater trochanter down to what might be the midline. This ridge is rugose and gives the shaft the appearance of being pinched and pulled outwards laterally. Although the shaft is much more rounded than in ursids, it is wider mediolaterally relative to anteroposterior than in *Dinofelis* and extant *Panthera*. This increase in relative mediolateral width is also seen in *Ursus*. Interestingly, *H. hadarensis* from Hadar and *Dinobastis* are much like *Panthera*, while the extremely large Omo *Homotherium* specimen F267-1 and the Koobi Fora *Homotherium* ER 3096 are quite narrow anteroposteriorly just like ER 2092. The shaft is massive and larger absolutely than the Hadar and Omo material. The Senèze femora are more like *H. hadarensis* than the Omo and Koobi Fora material.

The left distal femur and shaft, ER 3096 (Fig. 8.7d, e), includes the shaft up to the lesser trochanter. There is considerable erosion of the distal epiphyses. The specimen seems short and stocky. It is from a smaller individual than ER 2092, but the shaft is similar in morphology in that the entire shaft is very flat (i.e., wide mediolaterally relative to the anteroposterior dimension). The lateral edge above the midshaft forms a sharp ridge. The lesser trochanter is missing, but its base is present. It is further lateral than in *Dinofelis* and appears to have been similar to ER 2092. The greater mediolateral shaft width continues into the distal shaft, as also seen in the Tulu Bor *Homotherium*, ER 3750. The margins of the patellar groove are difficult to assess due to weathering. However, the groove appears to be similar in proportions to ER 3750.

An eroded right distal femur, ER 2125 (Fig. 8.7f), was found in sediments dating from Upper Burgi to KBS Members, but will be described here. The shaft just proximal to the condyles is very narrow anteroposteri-
orly. Although this is true of all Koobi Fora Homotherium, it is very pronounced in this specimen. The insertion of the lateral head of gastrocnemius is prominent, but not as large as in some specimens. The mediolateral width of the shaft and its shape as it joins the distal epiphysis looks like that of ER 3096.

The right fibula ER 45540 (Fig. 8.7g-j) is the only relatively complete Homotherium fibula known from Koobi Fora and is the only specimen to include the proximal end. The specimen is broken into the proximal end with a bit of shaft, the shaft, and a distal fragment. The superior proximal tibial articular facet is relatively barbell or figure-8 shaped, but with less of an indentation than in most felids. There is almost no indentation on the lateral side of the facet. On the tibial side of the shaft, the proximal end appears somewhat triangular, with the apex being posterolateral and with the tibial facet sitting superior to the base of the triangle. The shaft is wide anteroposteriorly and the inner surface is grooved. The entire surface, inner and outer, is rugose. The distal end includes the distal tibial facet. The facet is a somewhat pointed oval, similar in shape to that of ER 3093AB. Unfortunately, the posterior portion of the distal end is broken off.

Three Homotherium calcanei have been recovered from Upper Burgi sediments, a right calcaneum ER 4979 and two left calcanei, ER 44650 and ER 44710. ER 4979 is complete and slightly smaller and more gracile than the KBS Homotherium ER 894 described below. The sustentacular facet of ER 4979 (Fig. 8.7k, l) is small and round and relatively flat (with a slight rounding on the dorsalmost surface). It is angled far anteriorly to accommodate the acute angle of the calcaneal facets on the astragalus. The sustentacular facet appears to run anteriorly all the way to the dorsal edge of the navicular facet, as is the case in many carnivorans (Davis 1964). The navicular facet seems a little superior in position in comparison to ER 894. ER 4979 is similar to the Senèze H. latidens except that the immense dorsoventral thickness present in both specimens at the midpoint of both calcanei tapers more dramatically to the calcaneal tuberosity in ER 4979. Thus, ER 4979 has a tuberosity that is shorter dorsoventrally relative to the maximum dorsoventral width of the specimen than in H. latidens.

The calcaneum ER 44650 (Fig. 8.7m, n) is complete, well-preserved and larger than either ER 894 or ER 4979. In morphology it appears to be identical to ER 894 and ER 4979. ER 44710 is similar in size and morphology to ER 44650.

**KBS Member**

Very few Homotherium specimens have been found from the KBS Member. Unassociated right and left distal humeri, ER 696 and ER 704, are quite similar, although ER 704 is much better preserved. ER 704 (Fig. 8.8a-c) is similar to Upper Burgi humerus ER 791A, but is much larger and slightly more robust. From what can be seen in ER 696, the lateral epicondyle is not very projecting, but large, as in ER 704 and all Homotherium. There is a depression for the radial head. The region of the anconeal fossa is not very projecting, but large, as in ER 704 and all Homotherium. There is a depression for the radial head. The region of the anconeal fossa is broken off. In posterior view, the trochlea is flat, but with a large lateral crest for the edge, as in ER 704. In anterior view it is much more curved due to the anterior projection of the capitulum. The articular surface is relatively narrow for the size of the specimen and the trochlea is rather deep, as in all Homotherium. The capitulum is rounded.

In anterior view, the articular surface of ER 704 is narrow and very robust. The portion of the shaft superior to the trochlea is much more robust than in ER 791A. There is
a slight but tall indentation for the anconeal process and a somewhat deeper indentation for the radial head. The indentation for the anconeal process is more medial than in ER 791A. In fact, it lies immediately adjacent to the entepicondylar foramen. The lateral and medial epicondyles are not very projecting, but are massive in diameter.

In distal view, ER 704 appears thicker anteroposteriorly relative to mediolateral width than ER 791A. It is certainly thicker relative to width than the humerus of *D. serus*.

In posterior view, the entepicondylar foramen of ER 704 is almost invisible. It is much further forward than in ER 791A. The olecranon fossa is very deep and has rugose ridges. The most superior point is almost in line with the median plane of the shaft, unlike that of *D. serus*. The lateral edge of the trochlea projects posteriorly and is slightly medially curved. The medial edge is less projecting, but leads to the posterior projection of the medial epicondyle. This portion of the medial epicondyle projects further posteriorly than any other portion. In lateral and medial views, the ER 704 articulations appear to be slightly more under the shaft. In ER 791A, they are slightly more anterior.

Although little can be said about the eroded left proximal tibia ER 3744 (Fig. 8.8d), it is, with a few exceptions, similar to the Senèze *Homotherium*. The tibia does not appear to be relatively as wide anteroposteriorly as the Senèze specimen due in part to the fact that the tibial tuberosity probably did not project as far anteriorly. However, it is diffi-
cult to judge this due to breakage. The shaft narrows quickly, suggesting that the tibia may not be particularly long.

The left calcaneum ER 894 (Fig. 8.8e, f) is relatively well preserved except for the fact that part of the carpal facet is broken off inferolaterally and the sustentaculum tali is broken off dorsally and has a large hole on the remaining dorsal aspect. This specimen articulates fairly well with the much older ER 3093F astragalus, suggesting individuals of the same size. ER 894 is relatively short in length and thick dorsoventrally for a saber-tooth, as are all Homotherium calcanea. The manubrium is particularly short, as in all Homotherium, which is consistent with the short, squat astragalus of the genus. The navicular facet is present on the inferomedial side of the carpal facet, but is difficult to see due to erosion. Its placement is like that figured in Ballesio (1963). The facet on the sustentaculum tali does not connect anteriorly to the edge of the carpal facet. In medial view, the sustentaculum is wide and chunky. There is a deep groove under the sustentaculum for tendons. The carpal facet is almost at right angles to the main axis of the bone. In lateral view, the bone is dorsoventrally deep. In both this specimen and ER 4979, the lateral astragalar facet is somewhat flattened in comparison to the taller, more rounded Senèze specimen. This could correspond to the differences in the lateral facet of the Koobi Fora astragalus ER 3093F and the Senèze astragalus. The tuber calcanei is large and relatively rounded and does not taper as dramatically as in the Upper Burgi calcaneum ER 4979.

**Okote**

Only one individual represented by two elements is known from the Okote Member. Oddly, this includes the right third metatarsal, ER 44013A (Fig. 8.9a, b), and a more rare element, the entocuneiform ER 44013B (Fig. 8.9c, d). The third metatarsal is complete and is robust. The head is very round. Overall, this is consistent with the morphology of other Homotherium specimens. The entocuneiform is much larger than ER 722AL, the Dinofelis piveteaui entocuneiform. The proximal articulation bears the shape of the proximal metatarsal 2 surface. It is very narrow. There is less dorsomedial buttressing of the proximal articulation than in ER 722AL. The distal half is enlarged relative to the proximal half and there is a definite valley between the two on the dorsal surface. The enlarged distal half leads to a very rounded facet on the distal articular surface. This is rounded to a greater degree than in ER 722 AL.

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Fig. 8.9: Homotherium sp. material from the Okote Member. a-b) right third metatarsal ER 44013A in a) dorsal and b) proximal view; c-d) right entocuneiform ER 44013B in c) medial and d) proximal view.
Chapter 8: Family Felidae

REMARKS

The craniodental material of *Homotherium* from Koobi Fora is limited in extent and not particularly informative as to relationships. The most informative metric analysis is the length relationship between p4 and m1, which is shown in Fig. 8.10. Despite the limited data, it suggests that African *Homotherium*, and especially ER 931 from Koobi Fora has a longer m1 relative to p4 than in European or North American Homotheriini. This is a derived character, but clearly the material is not adequate to draw any major conclusions from this. Of considerable interest, however, are the differing allometric patterns of European *H. latidens* and North American *D. serus*. The difference hints at something fundamentally different in the feeding patterns of these taxa. However, this is beyond the scope of the present volume and will be pursued further elsewhere.

Fortunately, the postcranial skeleton of *Homotherium* is better represented at Koobi Fora than the craniodental material, and more informative. Based on the postcranial material, *Homotherium* has among the longest temporal ranges of any carnivorean taxon at Koobi Fora, spanning from the Lonyumun Mb. to the Okote Mb. While not all the material is well preserved, some possible trends can be seen.

While there are relatively large and small individuals in most of the members, there may be a general trend towards an increase in size in the largest individuals through time. However, considering how few specimens are known from the KBS and Okote Mbs, it is possible that this has more to do with taphonomic processes than an actual size trend.

It must also be remembered that the proportions within *Homotherium* are quite different than in other felids. For example, when just comparing radial head measurements, it is clear that largest *Dinofelis aronoki* and smallest *Homotherium* overlap in mediolateral width, but then the head of *Homotherium* is not as wide relative to the overall size of the bone as it is in most other felids. In fact, in *Homotherium* the head is only slightly wider mediolaterally than the shaft, while in *Dinofelis* it is much wider than the shaft. This results in *Homotherium* having a rounder head in contrast to the more oval shape of *Dinofelis* and *Panthera*. The only felid with a similar head morphology is the much smaller *Acinonyx*. The morphology is also quite different from ursids, which also have a head that flares much more medially than in *Homotherium*.

The femur may also change through time. In earlier specimens of *Homotherium* at Koobi Fora, the distal femur is more like other large felids. Later specimens may have a slightly wider and flatter patellar groove, as in the younger *D. serus*. The femoral distal...
shaft becomes wider and flatter relative to the bicondylar width through time, which may be another adaptation in Koobi Fora *Homotherium* to increased weight bearing and stability during the presumably more difficult prey grappling with reduced supinatory abilities.

In addition to decreased rotatory abilities noted in many previous studies (Antón et al. 2005; Ballesio 1963; Lewis 1995, 1997; Lewis and Lague 2010; Rawn-Schatzinger 1992), *Homotherium* differs in significant ways from other large felids. Previous studies have suggested limited claw retraction in *Homotherium* and related taxa, much like that of extant cheetahs (Antón et al. 2005; Rawn-Schatzinger 1992), but with the retention of grasping ability (Antón et al. 2005). Most felids have middle phalanges with asymmetrical shafts and a lateral extension to the head that permits retraction of the terminal digit (Bryant et al. 1996; Gonyea, 1976; Gonyea and Ashworth 1975), although cheetahs have reduced the asymmetry and lateral shelf (Russell and Bryant 2001). The morphology of the Koobi Fora middle phalanx ER 3093M accords very well with the morphology of the Incarcal *H. latidens* (Antón et al. 2005) and the abilities reconstructed for that specimen.

However, there are some differences from *H. latidens*, particularly within the hindlimb. If the os coxae ER 1665B truly belongs to *Homotherium*, it suggests that either *H. latidens* had a longer iliac blade than reconstructed by Ballesio (1963) in his diagrams or that the Koobi Fora material differs in locomotor capabilities from *H. latidens*. As discussed above, the blade may be longer (or at least long relative to its breadth) and more like extant cheetahs than lions or tigers. This may indicate a slightly longer lever arm for some of the muscles originating here, such as hip extensors (e.g., gluteus medius) and flexors (e.g., iliacus), as well as muscles dealing with trunk movements (e.g., iliocostalis).

The placement of the fovea capitis posterior to the middle of the head in medial view in Koobi Fora *Homotherium* (e.g., ER 2092) indicates a somewhat abducted femur in normal stance, in contrast to the more centrally placed foveae of cheetahs, pumas, and wolves (Hunt 2009). On the other hand, *H. latidens* appears to have a more centrally placed fovea (Ballesio 1963, fig. 45d), which may be a derived character within this lineage.

The lesser trochanter of the femur in ER 2092 and other *Homotherium* specimens mentioned above is not placed as far medially as in *Panthera*, ursids, or *Enhydriodon* (see Lewis 2008). It is not as far superolateral as in cheetahs, but it is more like cheetahs in its placement than any other extant carnivoran. Ballesio (1963, p. 90) states that the Senèze femur has a lesser trochanter that is “plus interne” than in lions. From fig. 45 in that publication, it is clear that by internal, he means that it is closer to the midline of the femur and not medial. However, the lesser trochanter of ER 2092 is even closer to the midline than in the Senèze femur and much more like extant cheetahs. This is the insertion point of the iliopsoas muscle, which flexes the hip joint, among other actions. This placement allows the iliopsoas to play a greater role in hip stability.

The only Koobi Fora astragalus, ER 3093F, also differs from *H. latidens* (Ballesio 1963, fig. 50) in its wider, flatter head and possibly in the orientation of the calcaneal facets. The difference in facets may be a problem of figuring. The wider, flatter head provides better weight-bearing ability and would provide a more stable ankle.

Finally, in comparison to *Homotherium* from other eastern African localities, the Koo-
bi Fora material shares affinities with material from the Omo and West Turkana. Previous studies (Lewis and Lague 2010) have demonstrated that the Hadar material, *H. hadarensis*, differs from the Koobi Fora and Omo material. *H. hadarensis* also tends to be within the smaller range of *Homotherium* body size. This genus is clearly in need of revision.

**Genus Megantereon**

* Croizet and Jobert, 1828

*Type species*: *Ursus cultridens* Cuvier, 1824 (partim)

*Generic diagnosis*: Upper canines elongate, compressed and recurved; permanent teeth not serrated; upper and lower incisors somewhat enlarged; P2 lost; long postcanine diastema; p3 reduced; P4 protocone reduced; m1 not elongated, metaconid and talonid lost; extensive mandibular flange; coronoid process strongly reduced; lower canines strongly reduced; limbs and feet short and stocky.

*Stratigraphic range in Africa*: Early Pliocene (ca 3.5 Ma) – ?Middle Pleistocene. Based on first occurrence at South Turkwel, Kenya, last occurrence at Elandsfontein, South Africa. We do not here recognize the late Miocene Bone Valley, Florida material (Berta and Galiano 1983), the Baode specimen (Sardella 1998; Zdansky 1924), or the Lukeino specimen (Morales et al. 2005) as belonging to *Megantereon* (Lewis and Werdelin 2010). The Bone Valley material, or at least part of it, was recently described as a new species of Smilodontini, *Rhizosmilodon fiteae*, by Wallace and Hulbert (2013). In addition, Sotnikova (pers. comm.) has stated that material from the Odessa Catacombs previously referred to *Megantereon* in faunal lists is more likely to belong to *Dinofelis*. This could make the South Turkwel record, along with approximately coeval sites in Italy, the oldest record of *Megantereon* worldwide. The Elandsfontein material is of uncertain age, but is currently (Klein et al. 2007) considered to date between 1-0.6 Ma.

*Stratigraphic range at Koobi Fora*: Early Pleistocene. Based on definitely referable specimens from the KBS (≤1.87 Ma) and Okote (≥1.38Ma) Mbs. Many specimens definitely or probably referable to *Megantereon* from Koobi Fora are poorly located stratigraphically. Thus, it is possible that the genus’ stratigraphic range extends from the late Pliocene (Tulu Bor Member) to the Middle Pleistocene (Chari Member).

**REMARKS**

There has been a long string of papers in recent years discussing the morphology and taxonomy of *Megantereon* spp. (Berta and Galiano 1983; Christiansen and Adolfsson 2007; Lewis and Werdelin 2010; Liu 2005; Martínez Navarro and Palmqvist 1995, 1996; Palmqvist et al. 2007; Qiu et al. 2003; Sardella 1998; Turner 1987; Werdelin and Lewis 2000, 2002). In particular, the important paper of Turner (1987), synonymizing all species of *Megantereon* under the nomen *M. cultridens* generated a number of responses, especially from the group of Palmqvist and Martinez-Navarro, who have defended the views that 1) *Megantereon whitei* from Africa is a species separate from *M. cultridens* and 2) certain European early Pleistocene specimens of *Megantereon* belong to this species, which migrated out of Africa to replace *M. cultridens*. The latest paper of this group (Palmqvist et al. 2007 – including Turner as a coauthor)
may be said to successfully resolve point 1),
while assuming that if 1) is resolved, 2) is also
dealt with. However, this is far from clear, as
should be evident from a perusal of Werdelin and Lewis (2002) and Lewis and Werdelin
(2010).

**Megantereon whitei** (Broom, 1937)

*Fig. 8.11 – 8.12*

**Synonyms:** Megantereon gracilis Broom in Broom and Schepers, 1946; Megantereon euryodon Ewer, 1955.

**Diagnosis:** A Megantereon with entire cheek dentition reduced compared to other species. Anterior dentition especially reduced. Mandibular symphysis more vertically oriented than in other Megantereon.

**Holotype:** TM 856, left mandibular ramus fragment with p4-m1. Housed in the Ditsong National Museum of Natural History, Pretoria, South Africa.

**Type locality:** Schurveberg, South Africa.

**Stratigraphic range in Africa:** Late Pliocene – ?Middle Pleistocene. Based on a first occurrence at Sterkfontein, Member 4 and a last occurrence at Elandsfontein. Material older than Sterkfontein Mb. 4 has not been positively identified as *M. whitei* rather than some other species, e.g., *Megantereon ekidoit* Werdelin and Lewis, 2000.

**Stratigraphic range at Koobi Fora:** Early Pleistocene. Based on FAD and LAD in the Okote Mb. (1.56 – 1.38 Ma). Older material is too incomplete to be positively identified as *M. whitei*.

KOBI FORA RESEARCH PROJECT VOLUME 7: THE CARNIVORA

KOBI FORA MATERIAL

**CRANIODENTAL**

The horizontal ramus of ER 701A (Fig. 8.11d-f) is relatively mediolaterally thick for the size of the individual. The masseteric fossa reaches to just mesial to the distal end of m1. In dorsal view the ramus is strongly convex with its lateralmost point around the middle of the m1. It is not clear to what extent this convexity is exaggerated by damage to the ramus. The m1 is short with a tall and short paraconid and still taller and longer protoconid. There is no trace of a metaconid/talonid complex. The tooth appears fully erupted, but is unworn and unserrated. ER 701B is the distal end of a left p4 with a large distal accessory cusp. The specimen is heavily damaged and fragmented. ER 701C represents the mesial? end of the right? p4. This specimen has a long mesial? root. ER 701D is a left lower canine. The crown is mediolaterally compressed and distally recurved. The tip is broken so the degree of wear is not apparent. There are no serrations in evidence. Only the proximal part of the root remains. Immediately distal to the crown it bends at about 20 degrees towards medial and is subsequently straight throughout the preserved part. ER 701E is a broken left i3. It has a well-developed lateral accessory cusp and a robust main cusp, but is otherwise too damaged to interpret with confidence. ER 701F is a left i1 that is small, incisiform and has two cusps, a larger medial one and a smaller lateral one. The crown is recurved in mediolateral view. ER 701G is a fragment with the right i2 and root of i1. The i2 is somewhat more caniniform than i1 and I1, the main cusp is larger and more pointed and the lateral accessory cusp is lower and set distinctly apart from the main cusp. ER 701H is a right I1. It is similar
Fig. 8.11: Mandibular material of *Megantereon whitei* from Koobi Fora. a-c) ER 793B in a) buccal, b) lingual, and c) occlusal view; d-f) ER 701A in d) buccal, e) lingual, and f) occlusal view.
to the I2 but smaller and with a less individuated lateral accessory cusp. ER 701I is a right P4. This tooth is long and slender, and retains a low but well developed protoconid that is set well distal to the mesial end of the parastyle. The parastyle is large and trenchant and well set off from the paracone. The latter is tall and triangular, while the metastyle is lower and quite short. ER 701J is a long and slender but mediolaterally crushed right upper canine and ER 701K is a mediolaterally crushed left upper canine crown. ER 701L, finally, is a fragment incorporating the left I2 and I3.

The mandibular ramus of 793B (Fig. 8.11a-c), has previously been figured by Turner (1987, fig. 2.1), Martínez Navarro and Palmqvist (1995, fig. 6.12; 1996, fig. 1 – incorrectly labeled Elandsfontein), and Palmqvist et al. (2007, fig. 1E). The mandibular corpus is transversely thickened beneath p4-m1. Mesially, there is a large ventral mandibular flange and the postcanine diastema is angled from dorsal (anterior) to ventral (posterior), resulting in the incisors being set well above the level of the cheek tooth row. There is a single, large mental foramen beneath the anterior part of the diastema. It is set very low on the ramus, nearly at the level of the horizontal extension of the ventral border of the ramus, excluding the mandibular flange. The masseteric fossa is shallow and reaches to the posterior end of m1. The mandibular condyle is set beneath the level of the occlusal surfaces of the cheek teeth. The coronoid process is very low, only just rising above the level of the tips of the trigonid cusps of m1. The angular process, though broken, must have been very small. It is set nearly vertically. The symphysis is tall, slender, and very short. It is nearly vertical in orientation. The masseteric foramen is very large. The incisors all have diastemas between them, and there is an additional one between i3 and c. All incisors are tall and pointed. The lower canine is small and slender, nearly incisiform in shape. The postcanine diastema is longer than the cheek tooth row. The cheek teeth are nearly unworn. The p3 is minute and single-rooted. The p4 is larger and slender, with small but well developed anterior and distal accessory cusps. The m1 is short and robust, with a short paraconid and taller and longer protoconid.

The skull ER 793A (Fig. 8.12a-d) is missing most of the braincase and frontals, as well as a large part of the basicranium and palate. It is quite robust, with wide zygomatic arches. The incisors are set in a regular arch, and increase in size from I1 to I3. They protrude well anterior to the canines. Judging from the roots, the latter would have been moderately to strongly compressed. The diastema is long and the P3 small and single-rooted. The P4 is short, with a very small protocone, a large parastyle well set off from the paracone, a tall paracone, and a lower, short metastyle. The M1 is very small.

cf. Megantereon sp.
Fig. 8.13

KOOBI FORA MATERIAL

POSTCRANIAL

ER 966 is relatively fragmentary and contains mainly hand and foot bones. However, there are some extremely fragmentary long bones including a fragment of a distal tibia (ER 966L), and a femoral condyle (ER 966M).

ER 706 (Fig. 8.13a-c) is the distal half of a humerus that is smaller than those of Dinofelis, even D. piveteaui. The distal articualr morphology is also different. This
Fig. 8.12: Megantereon whitei, ER 793A, cranium. a) dorsal view; b) ventral view; c) anterior view; d) right lateral view.
Fig. 8.13: Material referred to cf. *Megantereon* sp. a-c) distal right humerus ER 706 in a) anterior, b) posterior, and c) distal view; d-e) distal left humerus ER 6111 in d) anterior and e) posterior view; f-h) proximal radius ER 698 in f) anterior, g) posterior, and h) proximal view; i-j) metacarpal 4 ER 1662A in i) dorsal and j) proximal view; k-l) metacarpal 5 ER 1662B in k) dorsal and l) proximal view; m-n) right metacarpal 2 ER 4413 in m) dorsal and n) proximal view; o-p) right metacarpal 4 ER 363 in o) dorsal and p) proximal view; q) distal view of magnum ER 966B; r) lateral view of unciform ER 966C; s) proximal view of trapezoid ER 966J; t) dorsal view of first metacarpal ER 966D; u) Dorsal view of first proximal phalanx ER 966G; v-w) astragal trochea ER 966A in v) dorsal and w) medial view.
specimen has an anteroposteriorly narrower trochlea than *D. aronoki* or *Homotherium* in distal view. The shaft is relatively gracile.

In posterior view, the deep olecranon fossa is oval with only a slightly rounded point superiorly. The lateral lip of the trochlea is sharp and aids the impression of a deep fossa. The trochlea seems narrow in this view. There is slight age-related arthritic lipping of the trochlea. The lateral epicondyle is relatively smooth and does not project as far as expected. The medial epicondyle is large and projects far medially. The entepicondylar foramen is tucked posteromedially behind the shaft but is still visible in anterior view. On the anterior surface, the anconeal fossa is distinct and deep. The medial border of the fossa lips anteromedially such that it obscures the entepicondylar foramen slightly from view.

The left distal humerus ER 6111 (Fig. 8.13d-e) is that of a moderately large felid similar in size to extant jaguars *Panthera onca* and slightly larger than ER 706. As such, it is larger and more robust than both extant leopards and the Koobi Fora *P. cf. P. pardus* material. However, in comparison to *Dinofelis*, it is more gracile. The olecranon fossa is skewed in a manner similar to that of ER 4419. There is a slight excavation anteriorly for the olecranon.

The right radius ER 698 (Fig. 8.13f-h) is relatively gracile in comparison to KNM *Dinofelis*. What is preserved of the shaft suggests that it curves more medially from the proximal end than in *Dinofelis*, indicating greater supinatory abilities. The articular surface is kidney bean-shaped with the medial portion being much larger than the lateral. The head arises relatively smoothly from the neck with some lateral lipping. The neck is angled obliquely from the shaft due to the mediolateral curvature of the shaft.

The carpals of ER 966 includes the magnum (ER 966B), unciform (ER 966C), scapholunar (ER 966F), and trapezoid (ER 966J). The magnum of *Homotherium* has a distal articular surface that is different from the roughly rectangular one in *Dinofelis*. On the other hand, ER 966B (Fig. 8.13q) has a large medial indentation and is slightly more compressed mediolaterally. Other than this major difference, they are relatively similar. The proximal and distal articular surfaces of the unciform (ER 966C; Fig. 8.13r) are flatter than in *Dinofelis*. The distal articular surface is taller dorsoventrally. The scapholunar ER 966F is fragmentary, while the trapezoid ER 966J (Fig. 8.13s) is typical for a felid.

The rest of the ER 966 manus includes the left and right first metacarpal (ER 966D, E; Fig. 8.13l), the first proximal phalanx (ER 966G; Fig. 8.13u), a partial fifth proximal phalanx, and various metapodial fragments (ER 966H, K). The first metacarpals are missing their proximal ends, although the left one is relatively complete. The heads are larger relative to the shaft than in *D. piveleurii*. The nearly complete proximal phalanx I, ER 966G, is missing its proximal end. It is larger than in *D. piveleurii* and a little more robust, but similar in morphology.

Several associated elements of the manus of another individual (ER 1662) have been found, including three metacarpals (ER 1662A, B, E; Fig. 8.13i-l), a proximal phalanx (ER 1662D), and various fragments. The metacarpals all belong to the right manus. The proximal end of the second metacarpal (ER 1662E) is very fragmentary. The proximal end can be seen to be laterally offset from the shaft, as in large felids. Much of the lateral shelf for articulation with the third metacarpal has been broken off. The fourth
metacarpal (ER 1662A) is missing the ventral half of the proximal articulation and is weathered. The head is robust and large relative to the shaft. The two dorsal tubercles are large and projecting. The portion of the proximal articulation that is present is robust and wide mediolaterally. This specimen is a slightly larger version of ER 363. Although similar in length, the robust fifth metacarpal (ER 1662B) is quite different from the Koobi Fora Dinofelis specimens. The head slopes laterally to a greater extreme than in any of these, although part of the sloping region is broken off. The proximal end is very robust and has a larger medial projection than in any KNM Dinofelis specimen. The shaft is robust and very thick. The proximal half of the shaft is particularly thick dorsoventrally. This specimen is shorter and more robust than the Megantereon from Kromdraai B (KB 5333). The fragmentary phalanx, ER 1662D, associated with this material is large and robust. There is a slight dorsoventral curvature to the shaft.

ER 4413 (Fig. 8.13m, n), a right second metacarpal, is similar to ER 1662E, but smaller. This specimen is quite different from KNM Dinofelis although similar in length. The proximal end is mediolaterally narrower in dorsal view. The proximal articular surface is flatter, in part due to less curvature at the medial and lateral edges. The head also differs from Dinofelis in that it slopes at a greater angle on the medial side. The articular surface is quite rounded in comparison to Homotherium. The shaft is straight with slight dorsoventral curvature at the distal end.

The complete right fourth metacarpal, ER 363 (Fig. 8.13o, p), is similar to Megantereon specimen ER 1662A, but a little smaller and from an individual similar in size to ER 4413. This specimen is much larger than the Megantereon material from Kromdraai B, South Africa and is stockier and larger than modern Panthera pardus. However, ER 363 is unlike any Dinofelis housed at the KNM. The proximal end is more robust relative to the shaft than in Dinofelis. The carpal surface is very rectangular in appearance (not including the medial projection) due to the extremely parallel edges of the articular surface. The medial projection is more prominent than in Dinofelis. In overall size, this specimen is relatively smaller than Dinofelis.

The only portion preserved of the ER 966A astragalus is the trochlea (Fig. 8.13v, w). It is slightly smaller than known specimens of Dinofelis. Not enough remains to distinguish differences between this specimen and Dinofelis astragali.

**REMARKS**

We have discussed African and other Megantereon extensively elsewhere (Lewis and Werdelin 2010) and need not belabor this issue further here. The Koobi Fora material is limited, but the skull and mandibular ramus ER 793 are among the most important material of Megantereon in its relative completeness, allowing for a firm assessment of relative tooth size.

Postcranial material tentatively assigned to Megantereon is very poorly preserved. However, what can be seen confirms that Megantereon had great supinatory abilities. This machairodont was more gracile than larger taxa such as Homotherium and D. aronoki.

The metacarpals are similar in length to Dinofelis but are more robust. The articular surfaces differ in morphology from Dinofelis and are relatively more robust. The material is within the size range or slightly larger than the Kromdraai Megantereon partial skeleton KB 5333 (Vrba 1981).
**Genus Dinofelis Zdansky, 1924**

**Synonyms:** Therailurus Piveteau, 1948

**Type species:** Dinofelis abeli Zdansky, 1924 (=D. cristata [Falconer and Cautley, 1836])

*Generic diagnosis:* Machairodontinae of moderate to large size. Sexual dimorphism distinct but not great. Cranium rounded, with large to very large sagittal crest. Lower jaw stout. Coronoid process large compared to most other Machairodontinae. No mesial mandibular flange present, but mesial margin of ramus strong and flat. Upper canine short and only moderately or not at all compressed relative to Felinae. No longitudinal grooves. Distal crest well developed but no serrations present. P2 lost except in *D. cristata*. P3 not or only slightly reduced and slender, but less so than in other Machairodontinae. P4 with somewhat reduced protocone. Lower canine reduced but not incisiform. p3-p4 slender, m1 elongated, but less so than in other Machairodontinae (emended from Werdelin and Lewis, 2001).

**Stratigraphic range in Africa:** Late Miocene - Middle Pleistocene based on an FAD in the Lower Member, Nawata Formation (≤7.9 Ma), Lothagam and an LAD at Kanam East (≥0.99 Ma).

**Stratigraphic range at Koobi Fora:** Late Pliocene - Early Pleistocene based on FAD in the Tulu Bor Mb. (≤3.44 Ma) and LAD in the Okote Mb. (≥1.38 Ma).

**REMARKS**

The genus was recently revised by Werdelin and Lewis (2001) and the present discussion of the Koobi Fora material closely follows that paper. However, some significant material has been recovered subsequent to 1999, when the revision of *Dinofelis* was completed, and this material is emphasized herein.

*Dinofelis petteri* Werdelin and Lewis, 2001

Fig. 8.14

**Synonyms:** Dinofelis sp. (Howell and Petter 1976, p. 323); Dinofelis sp. (Howell and Petter 1979, p. 291); Dinofelis sp. (Petter and Howell 1985, p. 144); Dinofelis sp. (Barry 1987, p. 248); Dinofelis cf. *D. barlowi* (Harris et al. 1988, p. 37).

**Holotype.** KNM-ER 2612, damaged cranium with lt and rt canine roots and nearly complete lt P3-P4, partial rt P3-P4. Housed in the National Museums of Kenya, Nairobi, Kenya.

**Type locality:** Koobi Fora, Il Naibar Lowlands, Area 117.

**Nomenclatural note.** When we named *D. petteri* after Dr. Germaine Petter, we neglected to provide it with the appropriate feminine declension. Thus, by rights, it should have been *D. petterae*. However, the most recent edition of the Code of Zoological Nomenclature (ICZN 1999) no longer requires that such errors be corrected in revision. Hence, we are free to leave the name unchanged, which is our preference as it promotes nomenclatural stability.

**Specific diagnosis:** A *Dinofelis* of moderate size. Postcanine diastema much shorter than in older forms. Cranium low, rounded, with moderately large sagittal crest. Lower border of horizontal ramus of mandible straight
Fig. 8.14: *Dinofelis petteri*, ER 2612, type specimen. a) right lateral view; b) ventral view; c) dorsal view.

and transversely thickened. P3 somewhat reduced, P4 protocone not reduced, relative to Felinae. Lower canine much reduced, lower premolars less so.

*Stratigraphic range in Africa:* Early Pliocene – Late Pliocene (c. 4.2 – 2.62 Ma) based on an FAD at Kanapoi and an LAD in the Tulu Bor Mb., Koobi Fora Fm. (see below).

*Stratigraphic range at Koobi Fora:* Late Pliocene. Based on FAD and LAD in the Tulu Bor
KOOBI FORA MATERIAL

The Tulu Bor Member has yielded a partial cranium lacking the premaxillae, zygomatic arches, part of the basisphenoid and the distal part of the basicranium and occiput, KNM-ER 2612 (Fig. 8.14a-c). This specimen is the holotype of *Dinofelis petteri* and the only specimen of the species identified at Koobi Fora.

CRANIODENTAL

The cranium is small, with a relatively vertical snout. The nasals are broad and end just anterior to the caudalmost extent of the frontomaxillary suture, which is about at the middle of the orbit. The anterior end of the cranium is, as far as can be determined, relatively squared off. The infraorbital foramen was very large and nearly round. The frontals are convex, with a median valley and only a shallow anterior naso-frontal depression. The postorbital processes are short and wide and the postorbital constriction moderately narrow.

Of the teeth, the left and right C roots, nearly complete left P3-P4 and partial right P3-P4 are preserved. The canine is moderately transversely flattened. The P3 is long and very slender, with a low mesial accessory cusp, a small main cusp and a long, wide distal shelf. The carnassial has a large parastyle and very reduced protocone. The relative sizes of the paracone and metastyle cannot be determined because of damage to the tooth crown.

REMARKS

*Dinofelis petteri* is a small species of *Dinofelis* and the earliest that is known from more than a single site. While older specimens of *Dinofelis* are known from African sites like Lothagam and Langebaanweg, in addition to sites in Eurasia (Werdelin and Lewis 2001), all of these apparently record the presence of a unique species (or non-diagnostic material) at each site. *D. petteri*, on the other hand, is known from a number of sites in Africa, including Kanapoi, Allia Bay, Koobi Fora Fm., Tulu Bor Mb. and West Turkana, Lomekwi Mb., LO10, all in Kenya, Laetoli in Tanzania, and sites in the Shungura Fm. and Hadar in Ethiopia.

This species is distinguished from earlier members of the genus by a strongly reduced postcanine diastema in the lower jaw and from later *Dinofelis* by its moderate sagittal crest and its less reduced premolars. In addition, *D. petteri* is uniquely identified by the thickened horizontal ramus of the mandible.

Although *D. petteri* has been identified at nearly all known localities that lie within its stratigraphic and geographic range, it appears not to have been common at any of them. This is true at Koobi Fora as well, where this species is known from only the single specimen described above, as compared to the several specimens and partial skeletons of the succeeding species, *D. aronoki* and *D. piveteaui*. Whether this represents a true difference in abundance, pure chance, or a habitat shift between *D. petteri* and *D. aronoki* that led the latter to be more abundantly preserved in the fossil record is a matter for conjecture. Some combination of these three causes may come closest to the truth. The Koobi Fora record of *D. petteri* may be one of the youngest of this species, but the exact stratigraphic position of the specimen within the Tulu Bor Fm. is unknown.
**Dinofelis aronoki**  
**Werdelin and Lewis, 2001**  
Fig. 8.15 – 8.16

*Synonyms*: *Dinofelis barlowi* (Leakey 1976).


*Type locality*: Koobi Fora, Karari Ridge, Area 129.

*Stratigraphic range in Africa*: Late Pliocene – early Pleistocene (3.18 Ma – 1.56 Ma) based on an FAD in the Kada Hadar Mb., Hadar Fm. and an LAD in the KBS Mb., Koobi Fora Fm.

*Stratigraphic range at Koobi Fora*: Early Pleistocene, based on FAD in the Upper Burgi Mb (≤ca 2.0 Ma) and LAD in the KBS Mb. (≥1.56 Ma). One specimen (KNM-ER 3747a-c) is recorded as coming from “Tulu Bor – Upper Burgi”. We consider it unlikely that this specimen would be from the Tulu Bor Member.

**KOObI FORA MATERIAL**

**CRANIODENTAL**

The mandibular ramus KNM-ER 3880R (Fig. 8.15g-i) is dorsoventrally slender but mesiodistally thickened, especially distally. There is a single mental foramen set beneath the middle of p3. The masseteric fossa reaches the distal end of m1. The lower incisors are small and have small lateral cusps. The canine is moderately flattened. The postcanine diastema is >1 cm in length. The p3 is small and two-rooted. There is no mesial accessory cusp, but a small distal one is present directly behind the triangular main cusp. The p4 is slender, with large, almost cheetah-like mesial and distal accessory cusps. The m1 is long and robust. The protoconid is broken on both sides.

The upper dentition is associated with several cranial fragments (Fig. 8.15a-f). The I3 is somewhat caniniform, with a posterior medial crest. The upper canine is moderately flattened and has strong mesial and distal crests. The postcanine diastema is short. There is no P2. The P3 is slender and short, with a very low mesial accessory cusp and larger distal one. There is a small cingulum on P3 distal to the distal accessory cusp. The P4 is long and slender with a very reduced protocone. The paracone is large, the paracone tall and the metastyle long and low. It is clear that the specimen had a very large sagittal crest, similar to that seen in *Dinofelis cristata* from the Siwaliks (Hemmer 1973; Lydekker 1884).

KNM-ER 4419 includes some fragments of the dentition, including the crown of the right lower canine and the distal parts of the left and right p4. The lower canine was robust and not very tall, but has a prominent distal crest. The distal part of p4 is very similar to that of the p4 of ER 3880.

ER 1549 has a slender but thick corpus, with a flat mesial portion and very small chin. There is a single, large mental foramen beneath the mesial part of p3. The masseteric fossa reaches to the distal end of m1. The i1 is strongly asymmetric, with a large medial cusp and smaller lateral one. There is no buccal cingulum. The i2 is similar to i1, but the medial cusp is broader and the lateral one smaller. The i3 is somewhat caniniform, but has a small lateral cusp that touches the erupting canine on its medial side. The lower canines appear to be moderately flattened. The postcanine diastema is greater than 1 cm in length and would probably have increased further.
Fig. 8.15: *Dinofelis aronoki*, ER 3880, type specimen, selected elements. a-c) ER 3880A, left premaxilla/maxilla fragment with C-P3 in a) lateral, b) medial, and c) anterior view; d-f) ER 3880A, left maxilla fragment with P4 in d) buccal, e) lingual, and f) occlusal view; g-i) right mandibular ramus ER 3880R in g) buccal, h) lingual, and i) occlusal view.
with age. The p3 is small, but two-rooted. There is a small mesial accessory cusp and slightly larger distal one. The latter is bounded distally by a cingulum. The p4 is long and slender, with large, almost cheetah-like mesial and distal accessory cusps. The distal shelf widens lingually. The m1 is long and robust with a tall paraconid and longer and slightly lower protoconid. There is a minute talonid cusp appressed to the protoconid.

The erupting m1 of KNM-ER 365 matches the lower carnassial of KNM-ER 1549 in size. The specimen shows no other particularly distinguishing morphological characteristics.

In KNM-ER 3739 the masseteric fossa ends just distal to the m1. The p4 is long and slender, with prominent, nearly cheetah-like mesial and distal accessory cusps. The m1 is long and robust but otherwise too damaged to allow for a more complete description.

The p4, ER 44607 has a broken anterior accessory cusp, but it is clear that it was large and set free of the main cusp. The main cusp is tall and slender, with somewhat of a fleur-de-lis shape to it. The apex of this cusp is worn. The posterior cusp is tall and somewhat appressed to the main cusp. It also has a fleur-de-lis shape and is unworn. Distally, the tooth ends in a low but well developed cingulum cusp.

**POSTCRANIAL**

Most of the material assigned to *D. aronoki* has been described previously (Werdelin and Lewis 2001). Updates and corrections to that monograph will be made before describing the new material.

Werdelin and Lewis (2001, p. 168) state that there are four middle manual phalanges for partial skeleton ER 4419 (X, Y, Z, AB), but only describe and figure three (digits 2, 3, 4). In fact, ER 4419AB is a craniodental specimen. Thus, there are only three middle phalanges associated with this skeleton.

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![Distal femur ER 44718, assigned to *Dinofelis aronoki*.](image)

Fig. 8.16: Distal femur ER 44718, assigned to *Dinofelis aronoki*. a) anterior view; b) distal view.
Since the initial description of ER 4419, the caudal vertebra listed as having no suffix (Werdelin and Lewis 2001, p. 169) has been assigned the number ER 4419BS. The unnumbered pubic ramus (Werdelin and Lewis 2001, p. 173) has been given the number ER 4419BU. Several fragments have also been identified since the publication of the Werdelin and Lewis (2001) monograph, including a number of small rib fragments (ER 4419BQ), a fragment of the pedicle of the fifth lumbar vertebra (ER 4419BT), and a fragment of the neck of the right femur (ER 4419BV).

One new specimen of *D. aronoki* has been discovered since the initial description of the species. This specimen, ER 44718 (Fig. 8.16) is a cracked distal left femur missing the medial condyle. It is the size of *D. aronoki* specimen ER 987. The shape of the lateral condyles in the two specimens differs somewhat, with ER 44718 having a relatively wider condyle. However, the lateral epicondylar region appears identical. The shape of the patellar groove and overall femoral morphology is similar to *D. piveteaui* specimen KA 547 from Kromdraai A, South Africa.

**REMARKS**

What we now recognize as *D. aronoki* at Koobi Fora was originally identified as *D. barlowi*, a South African species, in Leakey (1976). However, the latter species is more primitive in having relatively less reduced premolars and a longer postcanine diastema. *D. aronoki* is a considerably larger species than *D. petteri*, its putative ancestor, and has more reduced premolars and a longer postcanine diastema (Fig. 8.17). Together with the Asian *D. cristata*, *D. aronoki* is the largest species of *Dinofelis*. Despite this, it is in most respects a transitional form between older species like *D. petteri* and *D. barlowi* and the terminal African species, *D. piveteaui*. Although both are present at Koobi Fora, *D. petteri* is known from a broad range of localities, while *D. aronoki* is only known from Koobi Fora, Hadar (Kada Hadar Mb), Lothagam (the Kaiyumung Mb.), and the undescribed site of Nakoret (West Turkana). By far the best material of the species is that from Koobi Fora.

Fig. 8.17: a) bivariate diagram showing relationship between lengths of P3 and P4 for Koobi Fora *Dinofelis* and other, selected, large felids. Despite the small sample, the trend at Koobi Fora is clear: as P4 becomes longer, P3 becomes shorter; b) bivariate diagram showing relationship between lengths of P4 and M1 for Koobi Fora *Dinofelis* and other, selected large felids. Note that in this relationship *D. aronoki* and *D. piveteaui* are more similar than in the P3/P4 length relationship.
**Dinofelis piveteaui (Ewer, 1955)**

Fig. 8.18 – 8.20

*Synonyms:* *Therailurus piveteaui* Ewer, 1955; *Dinofelis piveteaui* (Hemmer 1965); *Dinofelis cf. piveteaui* (Leakey 1976); *Dinofelis piveteaui* (Cooke 1991); *Dinofelis sp. aff. piveteaui* (Asfaw et al. 1992); *Dinofelis piveteaui* (Ditchfield et al. 1999); *Dinofelis cf. piveteaui* (Suwa et al. 2003).


*Type locality:* Kroomdraai A, South Africa.

*Stratigraphic range in Africa:* Early Pleistocene - Middle Pleistocene. Based on an FAD in the Okote Mb., Koobi Fora (≤1.56 Ma) and an LAD at Kanam East (possibly Jaramillo Subchron [1.070 – 0.990 Ma]).

*Stratigraphic range at Koobi Fora:* Early Pleistocene. Based on FAD and LAD in the Okote Mb. (≤1.56 – ≥1.38 Ma).

**KOBOI FORA MATERIAL**

**CRANIODENTAL**

The corpus of specimen KNM-ER 666 is slender. The mesial symphyseal face is flat but there is no distinct ventral chin or flange. There are two mental foramina, the mesial of which is placed just mesial to p3 and the distal posteroventral to the first, beneath the distal end of p3. The postcanine diastema is <1 cm in length. The p3 is very small, though apparently still two-rooted. Not enough remains of the other teeth to characterize them properly.

ER 40482 includes the following craniodental elements. A) Left maxilla fragment with P3-M1. The P3 is slender and relatively small compared with P4. The mesial accessory cusp is small but sharp. The main cusp is tall, conical and short. The distal accessory cusp is strong and is followed by a prominent distal cingulum cusp. The P4 is a long, slender tooth. There is no preparastyle. The parastyle is strong and robust. The protocone is reduced to a small bump on the dorsolinguval side of the tooth. The paracone is tall and sharp, while the metastyle is long and slender. There is a buccal wear facet from the distal half of the paracone and distally. The M1 is a small, oval tooth with its long axis set transversely to the tooth row as in other felids. B) Right maxilla with P3-P4 (Fig. 8.18d-f). Morphologically it matches the left side in all respects. C) Left mandibular ramus with c-m1 (Fig. 8.19a-c). The ramus is very damaged on the buccal face, with large pieces of bone flaked off. The distal part, from the middle of the massteric fossa and distally, is broken off. No mental foramen can be identified. The ventral face of the ramus is only very slightly convex. The massteric fossa reaches to the distalmost point of m1. The canine includes part of the root and the mesiolateral part of the crown. Its proportions in life are difficult to determine from the remaining parts. The postcanine diastema is about 8 mm from the distal part of the canine root to the mesial end of the mesial p3 root. The p3 retains only its mesial root and distal two-thirds. The main cusp is tall and sharp, while the distal accessory cusp is small and appressed to the main cusp. The p4 is slender and sharp. The mesial accessory cusp is tall and set free of the main cusp. The main cusp is tall and sharp. The distal accessory cusp is large and somewhat crest-like and set entirely
Fig. 8.18: D. piveteaui, ER 40482, upper dentition material. a-c) ER 40482F, premaxilla with left and right I1-I3 in a) anterior, b) ventral, and c) left lateral view; d-f) ER 40482B, right maxilla fragment with P3-P4 in d) buccal, e) lingual, and f) occlusal view; g-j) ER 40482G, right upper canine in g) medial, h) anterior, i) lateral, and j) posterior view.

free of the main cusp in a fleur-de-lis form. There is a marked cingulum cusp at the distal end of the tooth. The m1 is long and low. The paraconid and protoconid are subequal in height. The paraconid is broader but the protoconid longer. There is a wear facet on the buccal face of both cusps. D) Right mandibular ramus, very damaged and retaining only c, distal part of p4 and mesial part of m1, the latter glued in the wrong place. The angular process is preserved on this side, and is small and straight. E) Piece of frontal with lyriform crests back to nearly the point where they meet to form the sagittal crest. The frontals are strongly inflated. F) Premaxilla with all incisors complete except for the tip of the left
I3 being broken (Fig. 8.18a-c). The incisors are set in a curving arch. The I1 is small, with a sharp main cusp and two small distal accessory cusps. The I2 is similar in morphology but larger. The distal accessory cusps on I2 are smaller and set farther apart, forming a V-shaped crest at the back of the tooth. The I3 is caniniform and considerably larger than the other incisors. There is a prominent medial accessory cusp on I3, but no lateral cusp. G) Right upper canine (Fig. 8.18g-j). The crown is short, with sharp mesial and distal crests. It is moderately laterally flattened. The root is robust, bulging out a few mm below the enamel/dentine juncture.

POSTCRANIAL

Most of the material assigned to *Dinofelis piveteaui* has been described previously (Werdelin and Lewis 2001). A new partial skeleton, ER 40482, was recovered in 2000 and will be described here together with the proximal right ulna ER 703 that was inadvertently left out of the monograph.

Two elements of the partial skeleton ER 722 were not mentioned by Werdelin and Lewis (2001). This includes a sesamoid, ER
722AC, and the distal half of a left metacarpal 4, ER 722V. The distal metacarpal is well preserved and the morphology of the head is consistent with a fourth metacarpal. The size and morphology are consistent with the other metacarpals from this individual. While the overall length is unknown, it is clear that the fourth metacarpal is robust, as is to be expected.

**Axial Skeleton**

One of the most important aspects of the ER 40482 skeleton is that it expands our knowledge of the vertebral column of *D. piveteauii*. Elements include cervical, thoracic, and lumbar vertebrae, as well as ribs.

The axis, ER 40482AO (Fig. 8.20a, b), is missing the caudal half of the centrum and the cranial and caudal ends of the spinous process. The tip of the left caudal zygapophyseal facet is broken off. Although the centrum is not complete, the nearly complete spinous process indicates that this specimen, like all axes of *Dinofelis*, is relatively short craniocaudally. The preserved morphology is consistent with other specimens of *Dinofelis*, such as ER 4419AN.

Four vertebral specimens have been cataloged as ER 40482AU: four cervical centra and one thoracic centra. The four cervical centra include primarily the ventral surface. The most complete specimen may be C7 and includes the pedicles. These specimens are consistent in size and morphology with axis ER 40482AO. A fragment of a cervical vertebra, ER 40482X, is also present.

Lumbar vertebrae include the well preserved ER 40482AP from the mid-lumbar region (Fig. 8.20c). The cranial and caudal zygapophyses are typically lumbar in shape and the centrum is not sacralized, indicating that this is not too close to either thoracic or sacral vertebrae. The transverse processes are broken off. The cranial zygapophyses are large and the cranial articular facets are deep. The caudal zygapophyses are narrow, but robust. The centrum is oval, as expected, but is relatively rounder than in larger felids. The rounded, heart-shaped cranial articulation of the centrum is angled such that the dorsal and ventral edges project further cranially than the mid-section. The ventral keel appears to taper out before reaching the cranial end of the centrum. The spinous process is short and in the shape of a blunt-end triangle, as expected.

Two eroded vertebrae, ER 40482AT, may also represent lumbar vertebrae. These specimens are both smaller than ER 40482AP and are very eroded. The smallest specimen may be a thoracic vertebra close to the lumbar, but the surface is too eroded to see facets.

Other axial elements include a fairly complete mid-caudal vertebra, ER 40482Q. There are also twelve eroded rib fragments (ER 40482AE-AG).

**Thoracic Limb**

Most of the elements of the thoracic limb of ER 40482 are fragmentary and eroded. The left distal humerus ER 40482AM is poorly preserved, with most of the external surface worn away from the articular surfaces (Fig. 8.20d). From what can be seen, the overall morphology is consistent with other specimens of *Dinofelis*.

The distal third of the left radius, ER 40482L is eroded, leaving primarily cancellous bone showing. Little can be said about its morphology. However, its general size is as expected given what is known about other specimens of *Dinofelis*.

The ulna of ER 40482 is represented by two fragments of the shaft of the right ulna. One fragment is just below midshaft (AK)
and the other is the distal portion of the shaft (AJ). Both are similar to the ulnae of Koobi Fora *D. piveteaui* partial skeleton ER 722.

In contrast, the proximal right ulna ER 703 (Fig. 8.20e, f) includes only the proximal end of the ulna down to the middle of the semilunar notch, but that portion is well preserved. Part of the medial edge of the olecranon process is eroded away, but appears to have been prominent. The scar superomedial to the semilunar notch is present, indicating that the specimen belongs to a machairodont. The anconal process is short and wide. The tubercles forming the triceps groove are prominent. The medial tubercle is broken so the relative heights cannot be compared. This specimen is almost identical to the ER 722 ulnae. The only differences are that ER 703 has a slightly shorter and stouter anconal process and is slightly more robust overall.

The only carpal preserved from the ER 40482 individual is the pisiform ER 40482AA...
(Fig. 8.20p). This is the only machairodont pisiform from Koobi Fora. It is only slightly larger than the *Panthera* cf. *P. pardus* pisiform ER 44523F, although it is not as well preserved. While it appears that the distal end is smaller relative to overall bone size than in the *Panthera* specimen, erosion makes this difficult to assess. It is consistent with the morphology expected of a large felid.

Two metacarpals of ER 40482 have been recovered. The fourth metacarpal (ER 40482O) includes only the distal third. It is similar to ER 722V, but is slightly smaller. However, this impression may be due to the more broken nature of ER 40482O. The fifth metacarpal (ER 40482N; Fig. 8.20g) is very similar to ER 722P, but is slightly smaller and more gracile, perhaps indicating a female. The articular surfaces are robust as in all *Dinofelis*, but not to the degree seen in *Megantereon*.

Several phalanges of ER 40482 are known. Proximal phalanx 1, ER 40482P is large, robust and stocky as expected (Fig. 8.20j). Of the two middle phalanges, only one, ER 40482R (Fig. 8.20i) is complete. It is robust, as one would expect from examining other *Dinofelis* phalanges. A fragment of terminal phalanx, ER 40482AD, and two sesamoids, ER 40482AC and AH, have been recovered.

**Pelvic Limb**

A fragment of right os coxae, ER 40482AN includes the entire acetabulum, the ilium up to the middle of the auricular surface and a little of the ischium below the acetabulum (Fig. 8.20h). The acetabulum is round and deep. The morphology of the specimen overall is similar to an enlarged, robust leopard.

While none of the long bones of the pelvic limb were preserved (with the excep-
cent stops in the midline. The tuber calcanei is well preserved. As in ER 722Q, the groove for the triceps surae tendon is deep. The excellent preservation indicates that the medial portion of the tuber calcanei extends even further proximally than could be judged from the more eroded ER 722 Q.

The astragalus, ER 40482K, is extremely fragmentary. The head is missing and the trochlea is eroded. Very little can be said about it. The neck is set at an oblique angle. It appears similar to ER 3742 (the small *D. aronoki*), but smaller. However, it is so fragmentary that distinguishing features cannot be seen.

Four metatarsals have been recovered (Fig. 8.20k-m): the second (ER 40482AR) and third (ER 40482AQ) right metatarsals and the left and right fifth metatarsals (ER 40482M, Y). The right second metatarsal is complete. Like all *Dinofelis* metatarsals the proximal and distal ends are robust, but to a lesser degree than in the metacarpals. The carpal articulation is a triangular wedge with a rounded top. There is a slight lateral indentation for the base of the third metatarsal. The joint between the two bones is not tightly interwoven. The right third metatarsal is identical in morphology to ER 722T, but is complete and better preserved. The left fifth metatarsal is longer overall than the fifth metacarpal, although the shaft is only slightly longer. The distal end is quite gracile, as expected. The morphology of the tuberosity on the proximal end is like other specimens of *Dinofelis*. There is a slight dorsoventral curvature to the shaft. The right fifth metatarsal (Y) is represented only by the head.

Two pedal phalanges have been recovered (Fig. 8.20q, r). ER 40482T is a second proximal phalanx, while ER 40482S is a third. Both show the greater waisting seen in pedal phalanges.

**REMARKS**

*Dinofelis piveteaui* is the last species of the African *Dinofelis* lineage to evolve, and also the one that shows the most typical machairodont characteristics: the most reduced premolars (Fig. 8.17), the most flattened upper canines, etc. *D. piveteaui* was first identified at Kromdraai A in South Africa (Ewer 1955), but probably evolved in eastern Africa, where it was first recognized by Leakey (1976) (Werdelin and Lewis 2001; but see Kuhn et al. 2011; O’Regan and Menter 2009). *Dinofelis piveteaui* may also be the last surviving species of the genus *Dinofelis*, if the date suggested for the Kanam East deposit where a partial skeleton of *D. piveteaui* was found (Ditchfield et al. 1999) is upheld. All known material of this species at Koobi Fora is from the Okote Member. It is more gracile than the Upper Burgi *D. aronoki* or than the South African *D. barlowi* from Bolt’s Farm.

Ballesio (1963) noted navicular facets on the calcanei of *Homotherium* and *Smilodon*. Rawn-Schatzinger (1992) infers that this is a machairodont character as it is not present in *Panthera*. Werdelin and Lewis (2001) questioned the presence of this facet in *D. piveteaui*. The facet is small in other species of *Dinofelis* (e.g., *D. aronoki*) and it was not clear whether this facet existed in *D. piveteaui* due to the poor preservation of the material at that time. The discovery of ER 40482 confirms the presence of a small facet in this species, much like in *D. aronoki*.

*Dinofelis* sp.

In the monograph by Werdelin and Lewis (2001, table 3), material here listed as *Dinofelis* sp. (Appendix 1) and material from Lothagam were incorrectly listed as *Dinofelis* sp.
indet. A. However, later in the text, the name “Dinofelis sp. indet. A” is given to material from Venta del Moro, Spain. The Lothagam material is placed in a separate indeterminate species. Thus, the inclusion of this material and the Lothagam material together in *Dinofelis* sp. indet. A was incorrect. The Lothagam and Venta del Moro material most likely represent two different species. The Koobi Fora material is highly unlikely to belong to either of those species due not only to age, but to morphological differences from the Lothagam material noted by Werdelin and Lewis (2001).

ER 359 is of unknown age, while ER 5475 and ER 364 are from the KBS Mb. ER 359 and ER 364 are more similar to *D. piveteaui* (Werdelin and Lewis, 2001). The affinities of the larger ER 5475 are less clear.

**GENERAL DISCUSSION OF DINOFELIS**

The genus *Dinofelis* is a genus of machairodont felids with characters, such as the limited mediolateral compression of the canines, that argue for an adaptive convergence with modern day pantherines such as lions and leopards. The genus was recently revised by Werdelin and Lewis (2001) and only a brief summary will be provided here. *Dinofelis* evolved in the Late Miocene. Material of that age thought to belong to the genus has been recorded from Europe, Asia, and Africa, so the center of origin of the genus is at present not certain. It reached North America considerably later, appearing there in the uppermost Blancan (Early Pleistocene). The genus appears to have had its main center of diversity in Africa, where it is known from a series of species from the Late Miocene to the earliest Middle Pleistocene. It is a less common and less diverse element in Plio-Pleistocene fauna of Eurasia. The adaptations of the various species of *Dinofelis* varied from very similar to extant pantherine cats (e.g., *D. cristata* from Asia) to more machairodont-like (e.g., *D. piveteaui* from Africa). There is no definite overall trend in the evolution of the genus is one or the other direction.

At Koobi Fora, however, there is a clear local evolutionary trend from more...
pantherine-like forms (D. petteri) over an intermediate form (D. aronoki) to a machairodont-like form (D. piveteaui). Figure 8.17a shows the relationship between the length of P3 and length of P4. Though based only on three specimens, this diagram matches what is seen from larger samples; the early species D. petteri has a relatively long P3, D. aronoki a somewhat shorter one, and D. piveteaui a still shorter one. The reduction of the anterior premolars and relative lengthening of the carnassial are typical machairodont features. No lower dentition of D. petteri is available from Koobi Fora. However, Fig. 8.17b, plotting out the relationship between p4 and m1 length, shows that both D. aronoki and D. piveteaui had relatively short p4 compared to pantherines as well as other Dinofelis. In this way, the Koobi Fora material encapsulates an important aspect of Dinofelis evolution in the movement towards the more machairodont D. piveteaui.

**Subfamily** Felinae Fischer, 1817

**Genus** Panthera Oken, 1816

*Synonyms:* Leo Frisch, 1775 (For additional synonyms, see Wozencraft 2005).

*Type species:* Felis pardus Linnaeus, 1758

*Generic diagnosis:* Large-sized Felidae; dental formula I 3/3, C 1/1, P 3/2, M 1/1; hyoid ossified; premolar accessory cusps, especially the posterior, generally large; small talonid present on m1; canines short and robust.

*Stratigraphic range in Africa:* Early Pliocene – Recent based on FAD in the Upper Laetolil Beds, Laetoli (≤3.85 Ma).

*Stratigraphic range at Koobi Fora:* Early Pleistocene based on FAD in the Upper Burgi Mb. (≤c. 2.0 Ma) and LAD in the KBS Mb. (≥1.56 Ma).
REMARKS

The evolution of the genus *Panthera* represents one of the most interesting aspects of the study of fossil Felidae (Werdelin et al. 2010). Despite being apparently readily distinguishable from other Felidae on the basis of osteological features, they have a ghost lineage that is twice the length of the documented part of their lineage. Several reasons for this discrepancy are possible. It may, of course, be due to chance, although this is unlikely given the fossil record of other Felidae (especially Machairodontinae) in the Late Miocene – Early Pliocene. Second, it may be due to early *Panthera* being strongly tied to tropical forests, possibly in southeastern Asia, thus limiting their fossilization potential. Thirdly, it may be that the increase in size and attendant changes in morphology on which we base our identification of fossil *Panthera* did not evolve until the later part of the Early Pliocene and that, therefore, we have already recovered remains of early *Panthera* but have not recognized them as such.

The geologically oldest *Panthera* known are from Africa and the oldest of these are remains from the Upper Laetolil Beds at Laetoli, Tanzania (dated 3.85 – 3.63 Ma; Deino 2011). Despite some claims to the contrary (e.g., Turner 1990), these fossils show significant differences from extant lions and leopards (Werdelin and Dehghani 2011). This is in line with molecular dates (Johnson et al. 2006) that indicate that the split between lions and leopards is younger than 3 Ma. It is of considerable interest that the Laetoli material includes material of one lion-sized and one leopard-sized species, suggesting that there is something fundamental about these sizes and size differences that may be explained by the biology of two large, hypercarnivorous ecological (habitat) generalists. The Laetoli material is not of sufficient quality or quantity to determine whether there is a direct relationship between the larger species and extant lions, or the smaller species and extant leopards.

Subsequent to these finds at Laetoli, the fossil record of *Panthera* in Africa is limited. Material of a leopard-sized *Panthera* has been recovered from Members B, C, and G of the Shungura Fm. of the northern Turkana Basin, dated between ca. 3.36 and 1.88 Ma (Brown 1994). Material of lion-sized *Panthera* is known from the Shungura Fm. Mbs. B, C, G, and L. However, with the exception of a maxilla from Member L (1.39 – 1.12 Ma) none of this material is definitely diagnostic at the species level. Elsewhere, material referable to modern lion is present at Olduvai, Bed I. Finally, material of lion- and leopard-sized *Panthera* is known from several sites in South Africa dated to ca. 2 ma or younger.

*Panthera pardus* (Linnaeus, 1758)

Diagnosis: Medium-sized *Panthera*; pelage with rosettes lacking central spots; body lithe, low; dentition relatively robust within genus; premolar accessory cusps low, blunt; m1 generally with slightly concave distal face of trigonid; development of talonid variable.

Type locality: “Egypt”, see Pocock (1930)

Stratigraphic range in Africa: Late Pliocene – Recent based on FAD at Sterkfontein Mb. 2 (≤2.8 Ma).

Stratigraphic range at Koobi Fora: Early Pleistocene based on FAD in the Buri Mb. (≤ca 2.0 Ma) and LAD in the KBS Mb. (≥1.56 Ma).
KOOGI FORA MATERIAL

CRANIODENTAL

ER 3848 (Fig. 8.22a-c) is a right mandibular ramus with i3, c, p3-m1. The ramus is long but fairly robust with its deepest part beneath m1, where the ventral side is produced into a noticeable bulge. The symphysis is long, reaching posteriorly to the shallowest part of the postcanine diastema, just anterior to p3. The masticatory fossa reaches nearly to the posterior end of m1. It takes the form of a blunt V with a somewhat drawn out apex. The coronoid process is tall and anteroposteriorly broad, with a slight posterior inclination. The i3 is small. The lower canine is large and moderately compressed, with marked grooves on the medial and lateral sides. The p3 is slender, with small mesial and distal accessory cusps bounding a conical main cusp. The p4 is robust, with a large, pyramidal main cusp surrounded by large mesial and distal cusps (the latter of which is damaged, but complete), as well as a distal cingulum cusp. The m1 is short and tall. The protoconid is taller than the paraconid. The
distal part of the tooth is slightly damaged, but the talonid appears to have been almost completely reduced. This specimen does not differ either metrically or morphologically from extant *P. pardus* and can therefore confidently be assigned to that species.

The isolated P4, ER 44496 is damaged distally and is strongly abraded. The parastyle is well developed and somewhat crest-like. The protocone is large but low. The paracone is tall and conical. The metastyle is broken but was not long. This tooth matches extant *P. pardus* in morphology and metrics. However, its state of preservation means that we only tentatively assign it to the extant species.

**POSTCRANIAL**

ER 44523 (Fig. 8.23h-n) is the partial skeleton of a leopard-sized felid. Although the skeleton is very fragmentary, key portions are preserved (e.g., proximal tibia, astragalus, calcaneum). There are vertebral fragments (ER 44523G) including caudal vertebra, suggest-
ing a long tail, as in felids. A series of bone fragments including distal femoral condyle, proximal tibia, and carpal fragments are also known from this specimen.

The left radial head ER 47 (Fig. 8.23a-b) is the size of a small leopard radius. The angle of the head is unlike the much smaller serval in that the fossil head is oriented more obliquely. However, the fossil head and neck are oriented more medially than in extant leopards. The bicipital tuberosity is large and leopard-like in shape and is relatively the same distance from the head. In extant caracals, which are much smaller than this specimen, the distance between the bicipital tuberosity and head is shorter relative to the overall size of the bone.

The distal left radius ER 3102 (Fig. 8.23c-d) is clearly that of a felid and is the size of a small leopard. It is from an individual similar in size to the previously described specimen. Both this specimen and extant *P. pardus* have flat posterior surfaces. *Acinonyx* and hyenids, the only other taxa within a similar size range, have rounded surfaces. The medial flange is slightly eroded, which gives the specimen a more mediolaterally compressed appearance than it probably had in life. The anterior projections to guide the extensor tendons are large, but not to the degree seen in *Dinofelis*. The styloid process is thick but pointed. When viewed anteriorly, the styloid process begins just medial to the main axis of the specimen.

From the partial skeleton, very few elements of the thoracic limb are reasonably well-preserved. The right pisiform (ER 44523F; Fig. 8.23k) is clearly felid. The only distal metapodial (ER 44523E; Fig. 8.23j) is broken through the epiphysis of the head and has been reattached, which may account for its more flattened, mustelid-like appearance.

However, the ridge marking the epiphyseal area suggests that it was not very well fused to begin with. The shaft next to the head is wide mediolaterally and flat anteroposteriorly.

The os coxae of the partial skeleton (ER 44523B) includes a small bit of acetabulum and the ilium going up to most of the sacral articulation. The specimen cannot be a hyenid based on the fact that there is no sloping of the ilium above the acetabulum. The ilium seems to flare a little at the end of the neck as in felids, but does not curve.

The femur ER 6016 (Fig. 8.23e-g) is in the middle size range of extant leopards. The shaft is less robust in comparison to that of extant leopards. The greater trochanter is flatter on the lateral surface than is typical in *Panthera*, but this may be individual variation. The head is slightly rounder and more cranially oriented. The greater trochanter arches less over the intertrochanteric fossa. The lesser trochanter is slightly more distal and projects more posteriorly, while in most leopards it is more posteromedial. It is smaller and less gracile than the femur of *Megantereon* from Kromdraai, South Africa.

The tibia (ER 44523A; Fig. 8.23h-i) includes only the proximal portion. The patellar tendon inserts distally, such that the maximum projection of the tibial tuberosity is more distal in this specimen than in other similarly sized carnivorans such as hyenids. It is also angled more in parallel with the shaft, as one would expect in a leopard-sized felid. In posterior view, there is a sharp ridge running inferiorly from the posterior edge of the medial condyle. The posterior surface is deeply concave between this ridge and the normal buttressing of the lateral condyle. In medial view, the shaft is more rounded and buttressed distal to the medial condyle such that there is little concavity on the medial side of the shaft.
CHAPTER 8: FAMILY FELIDAE

leading to the tibial tuberosity.

The astragalus (ER 44523C; Fig. 8.23m-n) has a thin neck and is more like a leopard than any other felid. The medial and lateral lips of the trochlea are sub-equal in size and the trochlea seems a little narrow overall in comparison to larger felids. The trochlear surface ends and bone continues stepped down from the articular surface. The head is oval with the largest portion being lateral.

The calcaneum (ER 44523D; Fig. 8.23l) has a projecting fibular tubercle on the lateral side of the manubrium, as in felids. The cuboidal facet is offset laterally from the main axis of the tuber calcanei. The sustentaculum tali is eroded. The medial end of the tuber calcanei projects only slightly and slopes relatively gently towards the lateral side. There appears to be a slight flare in the tuber on the lateral side distal to the actual tuber surface.

REMARKS

Leopard-sized pantherines are not well represented at Koobi Fora and are not found there until the Upper Burgi Mb. (≤2.0 Ma). Even taking the depositional hiatus at Koobi Fora (ca 2.5 – 2 Ma) into account, this is much later than in the northern Turkana Basin, where leopards, or at least leopard-sized Panthera, are present already in Member B of the Shungura Fm. (≤3.36 Ma). Whether this represents differences in habitat between the different parts of the basin or whether it is simply due to sampling effects of always rare taxa is not possible to say at present.

Panthera leo (Linnaeus, 1758)

Fig. 8.24 – 8.26

Diagnosis: Second largest species of Feli- dae, slightly smaller than the tiger, Panthera tigris. Skull similar in appearance to that of the leopard (Panthera pardus) but nearly twice the size. Digitigrade with sharp retractile claws; broad face, rounded ears, relatively short neck. Well-proportioned, muscular body more drawn in at belly compared with the tiger. (After Haas et al. 2005).

Type locality: Constantine, Algeria (Allen 1924).

Stratigraphic range: Early Pleistocene – Recent. Based on FAD in Olduvai Bed I (≤1.92 Ma) and the Upper Burgi Mb., Koobi Fora (≤ca 2.0 Ma).

Stratigraphic range at Koobi Fora: Early Pleistocene. Based on FAD in the Upper Burgi Mb. (≤ca 2.0 Ma) and LAD in the Okote Mb. (≥1.38 Ma).

Fig. 8.24: P. leo, ER 874, right p4. a) buccal view; b) lingual view; C) occlusal view.
KOOLI FORA MATERIAL

CRANIODENTAL

The mesial accessory cusp of the right p4 ER 874 (Fig. 8.24) is small and low and set well anterior on the tooth. The main cusp is tall and conical. The distal accessory cusp is considerably larger than the mesial one. It is situated some way up on the distal face of the main cusp. The distal cingulum is strong, with a small distal cusp and distolinguinal crest.

ER44535 has a single alveolus for a P2. The P3 is broken mesiolingually and is abraded and flaked along the entire lingual face. There is a small mesial shelf but no distinct accessory cusp. The main cusp is conical but broken apically. The distal shelf is damaged but had a small accessory cusp and a general widening of the posterior end of the tooth.

The ramus ER 44267 (Fig. 8.25), is damaged, broken ventrally and worn and abraded throughout. It is broken mesial to the p4 mesial root and distal to the m1. The p4 has a large mesial accessory cusp that is distinctly separate from the main cusp. The main cusp is tall and conical. The distal accessory cusp is smaller than the mesial one, set higher up on the distal face of the main cusp, and appressed to it. The distal shelf is short but relatively

Fig. 8.25: *P. leo*, ER 44267, right ramus fragment. a) lingual view; b) buccal view; c) occlusal view.
wide. There is a ca 1 mm diastema between p4 and m1, which may be due to a break and subsequent widening of the ramus between these two teeth. The m1 has a paraconid that is shorter and lower, but wider than the protoconid. The metaconid is absent and the talonid minute. The isolated lower canine is broken midway up the crown. The tooth bulges out at the crown/root juncture. The root is long and straight, tapering to a distinct point. The isolated m1 (left) is identical in all preserved aspects to the right.

ER 44652 is a damaged right m1. Due to mesial and distal breakage length can only be approximated, but even so, the proportions of this specimen place it squarely within the range of variation of modern *P. leo*.

**POSTCRANIAL**

No partial skeletons have been found of *P. leo*. Instead, elements representing individuals varying in size from the smallest to the largest extant lions have been found.

ER 44656 (Fig. 8.26a, b) is comprised of a right shaft and distal humerus that do not conjoin due to a missing piece of shaft. The shaft includes everything from the deltoid tuberosity down to the expansion leading to the distal end. The distal end is eroded. This large specimen is similar to *P. leo* and differs from *Homotherium* in a series of features. First, it has a mediolaterally relatively wide trochlea/capitulum complex relative to the minimum anteroposterior width of the trochlea. Although the capitulum is damaged, what remains of the trochlea suggests that it was not as deeply grooved as in *Homotherium*. Finally, the medial epicondyle is much larger and more projecting than in *Homotherium*.

The distal portion of a left humerus, ER 4456 (Fig. 8.26c-e), belonged to a very old individual with abundant signs of arthritis. There is distinct osteoarthritic lipping around the articular surface, particularly anterosuperiorly. Some of the bone between the medial epicondyle and the posteromedial edge of the trochlea appears to have been resorbed. The specimen is, overall, extremely robust and most similar to extant lion, but with greater relief to the medial lip of the trochlea.

The ER 4456 humerus is similar in size to *Homotherium, D. aronoki, and P. leo*. It differs from *Homotherium* in having an obliquely oriented olecranon fossa and trochlea, reflecting the angle at which the elbow was held. In distal view, the trochlea is extremely narrow, as opposed to the anteroposteriorly thick trochlea of *Homotherium*. In anterior view, there is a deep excavation for the radial head with a deep indentation in the superior edge of the capitulum. The medial edge of the trochlea is taller and flatter than in *Homotherium* and its medial edge curves as it sweeps superiorly towards the medial epicondyle. *Homotherium*, in contrast, actually bulges medially from the medial trochlear lip to the medial epicondyle.

The medial and lateral epicondyles of ER 4456 are large and the medial epicondyle is especially large. These are much bigger than in *Homotherium* and more in line with the robust condition seen in *Panthera*. Although the ER 4419 (*D. aronoki*) specimen is missing its medial epicondyle, its lateral epicondyle is absolutely smaller than that of ER 4456 despite the overall slightly larger size of ER 4419. Thus, ER 4456 is consistent in both size and morphology with *P. leo*.

ER 795, a right ulnar shaft, is in the size range of *Homotherium* or *Panthera leo*. The shaft includes some of the proximal end, such as the distal half of the semilunar notch. Unfortunately, both coronoid processes are bro-
ken off and the surface of the radial notch is completely eroded. The large muscle insertion is partially preserved on the lateral side. The shaft is very flat on the medial side. On the lateral side, the shaft below the radial notch extending to the muscle insertion seems a little excavated. What remains of the semilunar notch suggests that the medial coronoid process would not have been as wide as in *Homotherium*. The semilunar notch also appears not to have been as tall given its curvature, suggesting a narrower distal humerus than in *Homotherium*. The shaft behind the notch is also not particularly wide anteroposteriorly,
but the whole bone is robust. This specimen appears to be from a larger individual than *Panthera leo* specimens ER 1815 or ER 2013.

The ER 41507 left second metacarpal is the size of *Homotherium*, but the head seems too rounded to be that of *Homotherium* or any machairodont. In comparison to metacarpal and metatarsal specimens of *Lokotunjailurus*, *Homotherium*, and *Dinofelis* it is quite distinct in the roundness of the head and more like *Panthera leo*. The sagittal crest is relatively short and blunt. The dorsum of the head is very globular, but not perfectly symmetrical. The shaft is oval; not as flat as in *Homotherium*.

The distal third metacarpal, ER 700 (Fig. 8.26i), is very lion-like. The carpal articulation is extremely wide and robust and its surface is greatly curved. There is a great lateral shelf for articulation with the metacarpal 4. The medial articulation also projects somewhat medially. The shaft is robust, but not flattened. Like ER 795, this specimen appears to be from a larger individual than ER 1815 or ER 2013.

ER 44532 (Fig. 8.26m) is the proximal phalanx of a very robust, large felid. It is in the size range of lions and of *Homotherium*. However, the morphology of this specimen seems different from *Homotherium* due to its elongated and slightly curved shaft. The manual phalanges of *Homotherium* are chunky with a huge head and base that are deep anteroposteriorly. Although most of the head is broken off in the specimen, it does not seem to have had that type of morphology. In the pedal specimen of *Homotherium* (ER 3112J), the head and base are not as deep anteroposteriorly, but the base maintains the squared off articular surface seen in the ER 791 manual phalanx of *Homotherium*. ER 44532 has the more rounded triangular base of *Panthera*. In this specimen the overall appearance is more gracile with features associated with greater grasping capabilities than either the manual or pedal phalanges of *Homotherium*.

The proximal left femur ER 402 (Fig. 8.26f-h) is very similar in size and morphology to the other probable *P. leo* femur, ER 3756, and quite different from both *Homotherium* and *Dinofelis*. Even though the greater trochanter is not preserved in most Koobi Fora *Dinofelis* femora, it is clear that their greater trochanter would not have flared laterally to the same degree. That flaring is seen in *P. leo*. The intertrochanteric fossa is extremely deep and the intertrochanteric crest extends medially over it. The crest remains a little more distinct as it ends at the lesser trochanter, reflecting the greater robusticity overall of this specimen. The lesser trochanter is oriented slightly more inferiorly and is more robust in ER 402. The insertion for the capsular ligament on the posterior side of the shaft inferolateral to the head is much larger and more distinct from the lateral edge of the head than in *Dinofelis*. Overall, this specimen is more robust than any of the *Dinofelis* specimens and looks most like extant *Panthera leo*.

The proximal left femur and shaft ER 3756 is too eroded and weathered to measure. It is a little larger than the *D. aronoki* material, however. The morphology is quite similar to ER 402 described above. As the greater trochanter is reasonably well preserved, one can see just how large and projecting this portion is. The greater trochanter flares out laterally from the shaft and then angles back medially at the level of the inferior edge of the head. The lesser trochanter is large and protrudes inferomedially. It is slightly visible in anterior view. The shaft is relatively narrow below the proximal end, but widens mediolaterally past the midpoint. These proportions are quite different from the
uniformly wide shaft of *Homotherium*.

The ER 2013 left astragalus (Fig. 8.26k, l) is extremely well preserved. The head and neck are oriented much like the morphology of modern *Panthera*. It is similar to the other possible lion astragalus, ER 1815, but has a slightly thicker neck ventrally. ER 2013 articulates well with ER 693. The trochlea is extremely deep and is more mediolaterally compressed than in *Dinofelis* and even more so in comparison to *Homotherium*. The trochlea is relatively rectangular in overall shape, with only a small posterior narrowing as the lateral lip moves medially. The medial edge of the neck of ER 2013 comes from the anteromedial inferior surface of the medial side. As such it is directly anterior to the medial malleolus. The neck has some twisting to accommodate the fact that the lateral facet rides high on the calcaneum relative to the medial facet and is longer than in *Homotherium*.

On the lateral side, the anterior portion projects slightly laterally for the distal fibula. In ventral view, the lateral facet is very rectangular until it ends at the posterior edge of the trochlea. It is slightly rounded anteriorly. Its ventral surface is quite curved anteroposteriorly and is highly angled to accommodate the calcaneum. The medial facet is slightly wider anteriorly, but peters out to almost nothing by the time it ends at the posterior end of the trochlea. It makes an almost 90 degree turn as it runs along the ventral surface of the trochlea. The anterior portion of the medial facet is relatively flat. The head extends quite a way from the anterior end of the medial facet. In other words, the medial facet does not extend onto the neck. A large buttress runs from the lateral edge of the medial facet down the neck to the head. Medial to this buttress is a fossa.

The right astragalus, ER 1815, is missing the lateral half of the trochlea. The medial side and head and neck are well-preserved. This specimen is nearly identical to ER 2013. The ventral end of the medial trochlea is crushed flat, giving it a different appearance, but this is taphonomic in origin.

The left calcaneum ER 693 (Fig. 8.26j) is missing the tuber calcanei and much of the lever arm. The rest is well preserved. The manubrium is not particularly wide and rather short. There is a slight fibular tubercle that does not quite run all the way to the cuboidal articulation. The lateral astragalar articulation is curved at the top and slopes rather quickly to the floor of the manubrium. The sustentaculum tali of ER 693 has a very round articular surface. It is not as parallel to the ground as in *Homotherium*, but is angled more anteriorly. It does not appear to have any portion that continues anteriorly to the cuboidal facet. In medial view, it is not particularly thick. There is a groove under the sustentaculum for tendons, as expected. The cuboidal facet is almost a rounded triangle that is skewed laterally. This appearance is enhanced by the presence of the lateral shelf.

ER 45523 (Fig. 8.26n) is the pedal proximal phalanx of a large felid that is more like *Panthera* than *Homotherium*. The shaft shows some waisting, hence the suggestion of pedal. The right side of the head is damaged, but seems quite round, unlike in *Homotherium*. Only the right side of the proximal articulation is present. The specimen would have been longer than 44 mm, but not by much.

A second proximal phalanx, ER 40450 (Fig. 8.26o), is similar in size to the ER 44532 phalanx. It is larger than *D. aronoki* but probably within that general size range. However, its length and the slightly smaller proportions of the proximal and distal ends relative to the shaft, suggest that this is likely to be a lion-sized *Panthera*. 
Fig. 8.27: Bivariate diagrams of dentition of *P. pardus* and *P. leo*. a) length versus width of p4; b) length versus width of m1; c) length versus width of P3; d) anterior versus blade width of P4. Note that all specimens except ER 44535 lie within the 95% confidence ellipses of the respective taxa, and even that specimen is not far away.

**REMARKS**

Despite some minor morphological differences, such as the relative sizes of the accessory cusps on p4, the craniodental specimens described above can confidently be assigned to a single taxon. This is true also when metric differences are taken into account. As can be seen from Fig. 8.27, all the specimens discussed lie within the range of variation of modern lions, except the P3, ER 44535, which is just outside it. However, that specimen is damaged and the measurements may not be accurate.

It is of interest that the two better specimens, ER 874 and ER 44267, both are smaller than any specimens in the comparative sample of lion specimens available to us (which includes lions from Asia, as well as eastern and southern Africa), although they lie within the confidence limits. This suggests, although it does not prove, that the lions of at least the time of the Okote Mb., from which all cranio-
dental Koobi Fora lion specimens come (ER 44267 is of unknown provenance but likely to be from the Okote as well) were on average very small. This suggestion is supported by the Okote postcranial material, which falls within the lower size range of modern lions. In contrast, a similarly aged large Panthera mandible (specimen 1273, 1957) from Olduvai, Bed II (Ewer 1965) is of the size of a large modern lion, as is a damaged P4 (P998-1b) from Mb. L of the Shungura Fm. (1.39 – 1.12 Ma). A large felid specimen from Olduvai, Bed IV (ca 0.8 – ca 0.6 Ma) is similar in size to the Okote specimens, on the other hand. In contrast, the Upper Burgi postcrania is at the upper size limit of extant lions. Although the available material is limited, the data suggest that there was considerable temporal and/or geographic variation in the size of lions in the eastern African Pleistocene. This variation may be climate-related, as suggested for several carnivoran taxa in southern Africa (Klein 1986).

In any case, by the Upper Burgi there were two species of Panthera that look very much like modern lions and leopards. Their postcranial morphology suggests that they did not behave in a manner that was significantly different from their modern relatives. What is interesting is their disappearance in the KBS and the sole reappearance of lions in the Okote, even though leopards and lions clearly survive to the present day. It is reasonable to speculate that the greater diversity of large felids meant that lions and leopards were not found in the great numbers that they are today. As generalists, they also had the ability to utilize a great diversity of habitats, leading to their persistence today (Lewis and Werdelin 2007; Werdelin and Lewis 2005, 2013). This ecological flexibility may have allowed them to utilize habitats less frequented by machairodont felids, including habitats not sampled at Koobi Fora.

**Genus Acinonyx Brookes, 1828**

*Synonyms: Cynailurus Wagler, 1830; Guepardus Duvernoy, 1835; Cynofelis Lesson, 1842; Paracinonyx Kretzoi, 1929a*

*Type species: Acinonyx venator Brookes, 1828 (=Felis jubata Schreber, 1776)*

*Generic diagnosis: Skull vaulted and raised high above muzzle. Short and broad with enlarged nasal openings. Relatively small auditory bullae with strong paroccipital process. Premolars with notably enlarged mesial and distal accessory cusps. Lower carnassial with larger talonid than in Panthera. Slender body with elongated, slender limbs.*

*Stratigraphic range in Africa: Early Pliocene – Recent based on FAD in the Upper Laetolil Beds (≤3.85 Ma).*

*Stratigraphic range at Koobi Fora: Early Pleistocene based on FAD in the Upper Burgi Mb. (≤ca 2.0 Ma) and LAD in the Okote Mb. (≥1.38 Ma).*

**REMARKS**

The evolution of cheetahs has recently been the subject of discussion with the publication of *Acinonyx kurteni* from the earliest Pleistocene of the Linxia Basin, Gansu Province, China (Christiansen and Mazak 2009). The type and only specimen of this taxon purported to show a surprisingly modern cranial architecture, thereby pushing back the evolution of modern cheetah ecology into the Pliocene (the lineage itself is likely to be consid-
erably older, cf. Johnson et al. 2006; Werdelin
et al. 2010). However, it has been convinc-
ingly shown that *A. kurteni* is based on a com-
posite and substantially restored skull (Deng
2011) and the original paper has since been
retracted.

The oldest cheetah material known
is from the Upper Laetolil Beds, dated 3.85
– 3.63 Ma (Deino 2011; Werdelin and Deh-
ghani 2011). This is very fragmentary, how-
ever. More representative material is avail-
able from the earliest Pleistocene in the form
of *A. pardinensis* from Europe (Hemmer et
al. 2011; Viret 1954), *A. aicha* from Africa
(Geraads 1997), and *Sivapanthera linxiaensis*
from Asia (Qiu et al. 2003). None of these is
fully modern in morphology and presumably
ecology.

**Acinonyx sp. nov.**
Fig. 8.28 – 8.29

KOOBI FORA MATERIAL

POSTCRANIAL

The specimen ER 2037 includes portions of
both the thoracic and pelvic limbs, as well as
the axial skeleton. While one fragment may
have come from the mandible (ER 2037Y),
no definitive craniodental material is associ-
ated with this skeleton.

Fragments of the ER 2037 vertebral
column are present with some representation
in each region. Unfortunately, only two frag-
ments of the axis are preserved: the cranial
portion including the dens and left articular
surface (ER 2037AL) and a fragment of the
spinous process (ER 2037AD). The dens is
very triangular and straight and seems rela-
tively gracile and short. The articular condi-
lar surface seems to slope more than in *Pan-
thera* and machairodont felids. The fragment
of spinous process includes the right side of
the caudal portion. The right and left caudal
articul ar facets for C3 on the ventrum of the
spinous process are both preserved due to the
preservation of part of the neural arch. This
does not conjoin with ER 2037AL. Three ad-
ditional cervical fragments are known: the
caudal half of a cervical vertebral centrum in-
cluding the ventral keel (ER 2037AK), a C5
or C6 centrum fragment with ventral keel (ER
2037AM), and a fragment of caudal articular
process (ER 2037AT).

Five thoracic vertebral centra are vari-
ably preserved (ER 2037AC, AE, AF, AH,
AI). ER 2037AE preserves the cranial costal
facets, while AF includes the caudal costal
demifacets. ER 2037AC is rather wide medi-
laterally relative to its dorsoventral dimen-
sions. There is a clear costal facet on the cra-
nial end of the left side. There do not seem to
be any demifacets on the caudal end.

Three fragmentary lumbar vertebral
centra are preserved: ER 2037AB, AG, and
AJ. In addition, a fragment (ER 2037AS) of
the caudal articular process is present. ER
2037AG is missing the caudal half, but the
cranial articular surface is very wide medio-
laterally and very narrow dorsoventrally. It is
much more narrow than ER 2037AB. The lat-
er is an extremely large lower lumbar centrum
that may be an L4. ER 2037AJ includes just
the caudal half of a lumbar vertebra centrum.
The caudal surface is not well preserved, but
a little of the dorsal keel can be seen.

A portion of the scapula (ER 2037E) is
preserved. The glenoid is an elongated lima bean shape with the superior extension for the supraglenoid tubercle (Fig. 8.28i). The medial edge of the tubercle is in the midline, while the lateral edge comes from the lateral edge of the glenoid fossa. The infraglenoid tubercle is not apparent, but there may be some erosion. The glenoid fossa is relatively deep. The glenoid is ovoid in overall shape, as in most felids, in contrast the slightly rounder glenoid of modern cheetahs (i.e., cheetahs have increased the transverse width of their glenoid relative to its height). The posterior edge of the neck is somewhat flattened where the long head of triceps brachii originates. The spine is broken off.

Portions of both the right and left humerus of ER 2037 are preserved, although neither is complete. The left humeral head fragment (ER 2037K) is missing everything but the articular surface. A little of the base of the greater tuberosity is visible, indicating that it projected at least 9 mm lateral to the head.

The head appears very round and com-
pressed mediolaterally (Fig. 8.28a). In comparison to extant cheetahs, the head is tall relative to its transverse width. In this respect, it is more like other extant felids. In proximal view the head is a rounded triangular shape as in felids, as opposed to the more rounded head with less anterior mediolateral expansion of canids. In lateral view, the head is less projecting relative to the beginning of the greater tuberosity than in leopards, but both this specimen and leopards are quite rounded. In cheetahs, the head is offset from the greater tuberosity, such that the tuberosity begins towards the edge of the articular surface and the heads juts more from the shaft. This specimen is more leopard-like than cheetah-like in this feature.

The base of the greater tuberosity is present in lateral view. The greater tuberosity projects in a straighter fashion than in modern leopards and cheetahs. The greater tuberosity of leopards forms a low rounded arc. In cheetahs it runs at an oblique angle before forming an arc. The shape of the groove between the lesser tuberosity and the head is the same as in all felids, which are less grooved than canids. With their anteroposteriorly shortened heads, felids have a less extensive and more rounded groove. In Hyaena, the groove is deep and the head extends further. This is the area of subscapularis attachment.

The shaft is known from the right midshaft (ER 2037J) and the left distal shaft (ER 2037F). The midshaft is relatively gracile and includes what appears to be the end of the deltoid tuberosity. There is little angulation in the shaft from this point. The distal shaft (ER 2037F) includes the lateral side of the shaft and the very top of the olecranon fossa. The lateral side flares out from the shaft to form a ridge leading the lateral side of the fossa. The shaft leading to the top of the fossa is extremely flat. The region of attachment for the extensor carpi radialis is similar in size and robusticity to that of a leopard. This region has the large, bulging area seen in felids in contrast to the flared area seen in dogs. The distal humerus does not appear to have been particularly wide. It conjoins with ER 2037H indicating that the olecranon fossa is tall and narrow. A fragment of the lateral shaft of the right humerus is also preserved (ER 2037Z) and is identical to ER 2037F.

The distal humerus (ER 2037G, H) is represented by two portions that are broken apart in the midline and conjoin posteriorly, but not anteriorly. The medial specimen (G; Fig. 8.28b) includes the medial side of the trochlea and the medial epicondyle. The lateral specimen (H; Fig. 8.28c) includes the capitulum and the lateral epicondyle. Not enough of the shaft is preserved to see the entepicondylar foramen. In posterior view, it is clear that the olecranon fossa is relatively narrow. The medial epicondyle has a great posterior projection. The capitulum is quite rounded and narrow mediolaterally (21.2 mm), while the trochlea is even narrower (13.8 mm). The entire distal end is mediolaterally compact. The lateral epicondyle is almost negligible. The compactness of the distal end is consistent with the much larger and more robust Dmanisi A. pardinensis described by Hemmer et al. (2011), as well as with extant cheetahs.

The distal humerus is wider anteroposteriorly than in cheetahs or leopards and the inferior surface of the trochlea is flatter. It is cheetah-like in the blending of epicondyle with trochlear lip. However, it is leopard- and hyena-like in having a low epicondyle. In anterior view, the slope of the trochlea is straighter and less rounded than in cheetahs and appears more leopard-like. In lateral view, the capitu-
lum is more rounded and shortened anteroposteriorly than in leopards. This short, round morphology is cheetah-like. In inferior view, the specimen is cheetah-like due to the flat medial epicondyle. The connection between the condyle and the posterior extension of the medial lip of the olecranon fossa is greater in the fossil, as well as leopards and hyenas, than in cheetahs, but the shape of the extension is cheetah-like. The distance from the deepest part of the trochlea to the medial lip is longer than in cheetahs and the curvature of the edge of the lip is like a leopard.

ER 705 (Fig. 8.28d, e) is a relatively well-preserved proximal left ulna, but is missing roughly the distal third. The morphology is halfway between an extant cheetah and a leopard. The olecranon is somewhat rectangular in lateral view and long and narrow. It is not as rectangular as a canid, but slopes to a point. In posterior view, the olecranon remains in line with the shaft on the lateral side, but flares medially. Unfortunately, this region is broken off. The olecranon is not very deep anteroposteriorly. In anterior view, the lateral guide to the triceps groove is apparent, but not large. The medial side slopes posteriorly to the olecranon process and does not include as much of a wall. The anconeal process is directly above the radius rather than the medial coronoid process. In the superior portion of the semilunar notch, the capitular side is much wider than the trochlear side. There is a clear delineation between the two in a ridge where they meet. The medial coronoid process is relatively narrow for a felid and is reminiscent of Hyaena. The lateral coronoid process is small but laterally projecting.

Immediately inferior to the medial coronoid process is a deep groove that runs about 15 mm straight down the shaft. This is approximately where the brachialis attaches. There is a nutrient foramen a few mm distal to the end of the groove. The groove seems a little pathological, as there is some remodeling lateral to it below the base of the anterormost point of the medial coronoid process. This results in a rounded bony projection below the base of the medial coronoid process when viewed medially. Like the proximal end, the shaft is also relatively gracile. For its mediolateral width, it is not particularly widened anteroposteriorly as in other felids. The muscle scar is about 29 mm below the radial notch and seems rather close.

While portions of both the left and right ulna of ER 2037 have been recovered, neither is well preserved. The left ulna (ER 2037A) includes two fragments: one including the olecranon and anconeal processes and another including much of the semilunar notch and below. The connection between the two specimens is eroded or missing so that they cannot be conjoined. The radial notch is very eroded and the lateral coronoid process is missing. The medial coronoid process is eroded and the shaft is very fragmentary. The right ulnar fragment (ER 2037B) includes the medial coronoid process with much of the radial notch being broken and eroded. These specimens are not as large as modern cheetah comparative material housed at the KNM (e.g., OM 4193). In comparison to other Koobi Fora taxa, the coronoid process is wider mediolaterally and more square than the similarly-sized Hyaena cf. H. makapani (ER 1548G). Overall, ER 2037 looks very similar to the better preserved ER 705 described above, with only a few differences. ER 2037 is slightly larger and a little more robust. There is also no groove below the medial coronoid process in ER 2037 and thus no resulting bony projection, reinforcing the pathological nature of this feature in ER 705. The medial side of the triceps groove
projects further proximally in ER 2037, but is still sloped posteriorly relative to the lateral guide.

Proximal portions of both right and left radii of ER 2037 are also preserved, although the right radial head (ER 2037D) is fragmentary. The radial head of the proximal left radius (ER 2037C, Fig. 8.28f, g) is eroded in part. However, one can still see that the head is relatively oval, although much rounder than in Dinofelis or Megantereon, and angles medially from the neck, as in most felids. The shaft is gracile and its posterior surface has a ridge extending distally and medially from the bicipital tuberosity. The shaft is oval in cross-section. The bicipital tuberosity seems relatively far down the shaft in comparison to extant cheetahs, but this is difficult to assess given the incomplete nature of the material.

Very little of the ER 2037 manus is preserved. The left scapholunar (ER 2037U; Fig. 8.28h) is quite different from Panthera. The rectangular portion is quite short mediolaterally. The radial surface is highly curved and also compressed mediolaterally. The distal surface is extremely eroded, but appears to have been relatively deep in its relief.

The left second metacarpal ER 3764 (Fig. 8.28j) is missing the head and part of the distal shaft. The size and morphology of the specimen are most similar to extant Acinonyx. It is too elongated and narrow to be P. pardus.

![Fig. 8.29: Koobi Fora material referred to Acinonyx sp. nov. a-b) distal femur ER 2037L in a) anterior and b) distal view; c-d) distal femur 18914 in c) anterior and d) lateral view; e) proximal view of tibia ER 2037O; f) anterior view of patella ER 2037W; g) dorsal view of calcaneum ER 2037S; h) dorsal view of astragalar trochlea ER 2037T.](image-url)
and the shaft is quite gracile. The proximal end is slightly larger relative to the size of the shaft than in extant cheetahs. The groove on the dorsal surface of the distal end seen in machairodonts and some larger felines is flat and wide and barely discernible. The proximal articulation is rounded on top, such that in lateral view, the articular surface is crescent-shaped. The overall morphology is quite similar to the larger *A. pardinensis* material from Dmanisi (Hemmer et al. 2011).

As with the thoracic limb, the pelvic limb of ER 2037 does not include any complete long bones. The right femur is represented by a proximal fragment (ER 2037N) and the distal end (ER 2037L). A third specimen, the distal left femur (ER 2037M), is an extremely fragmentary and eroded version of ER 2037L. A femoral shaft fragment (ER 2037CE) is relatively round, as in cheetahs, but is much smaller than that of ER 3740, the other partial *Acinonyx* skeleton.

The proximal portion (ER 2037N) includes only part of the greater trochanter and intertrochanteric fossa. The greater trochanter is triangular and points primarily proximally. The anterior projection does not extend far beyond the shaft. The intertrochanteric fossa extends below the greater tuberosity. This is the only part that is preserved. However, its relatively rounded shape suggests that it does not extend down towards the lesser trochanter.

The distal femur (ER 2037L; Fig. 8.29a-b) is extremely cheetah-like, with the medially laterally narrow, compact articular region. The patellar groove is deep, mediolaterally narrow, and long anteroposteriorly. It projects anteriorly from the shaft, as in cheetahs. The knee is quite valgus due to the projection of the medial condyle. The shaft is gracile. The lateral and medial epicondyles are not very large. A fabellar pit can be seen on the medial side infero-medial to the epicondyle. In posterior view, the condyles are not very tall proximodistally.

The ER 18914 distal right femur (Fig. 8.29c-d) is quite similar to ER 2037, but better preserved. The more inferiorly projecting medial condyle means that the shaft angles more than in extant *Acinonyx*. The attachment for the lateral gastrocnemius is more distally placed in comparison to the relatively high placement in extant cheetahs, suggesting less leverage in the fossil species. The lateral condyle is eroded laterally but appears more narrow and less projecting. The attachment of the anterior cruciate ligament is just visible as an indentation on the lateral condyle. In extant cheetahs, this attachment is relatively larger. The attachment for the meniscofemoral ligament seems more superior than in extant cheetahs.

The shaft of cheetahs has a posterior ridge that is not found in the fossil. In this specimen, there is a larger attachment for popliteus on the lateral condyle and a large groove for the fabella. The lateral condyle extends less posteriorly and is slightly more round. The medial condyle also extends less posteriorly. When viewed distally, the patellar groove is not as deep as in cheetahs and the distal end does not project to the same degree as extant cheetahs. Like in the cheetah, the patellar groove projects more anteriorly than in leopards.

The patella (ER 2037W; Fig. 8.29f) is well preserved and projects greatly anteroposteriorly, as in extant cheetahs. The most proximal part is slightly narrowed and projects slightly to the specimen’s left and posteriorly. The facets are a little eroded, but the right and left portions appear smooth with no ridge. Overall, the bone is narrow mediolaterally in comparison to its overall length as in extant cheetahs, but not leopards or other *Panthera*.

The tibia is represented by the proximal
and distal ends of the left tibia (ER 2037O, P) and the shaft and distal end of the right tibia (ER 2037R, Q). The shaft fragment (ER 2037R) preserves some of the lower end of the tibial crest allowing it to be sized. Not much else can be said. The distal left tibia (ER 2037P) is extremely eroded, but is the same general size and shape as the right side (ER 2037Q).

The proximal left tibia (ER 2037O; Fig. 8.29e) is too eroded around the edges for most measurements. The tibia seems relatively narrow anteroposteriorly, although this is enhanced by the erosion of the tibial tuberosity. The lateral condyle is larger than the medial condyle in both mediolateral and anteroposterior width. While the medial shaft flares only slightly to accommodate the medial condyle, the lateral shaft must flare a great deal laterally to accommodate the lateral condyle. The small fibular facet appears to be on the posterolateral edge almost beyond the shaft. This is hard to assess due to erosion. The posterior surface of the shaft continues straight down from the medial condyle. There is a wide groove on the posterior surface of the shaft however, from the level of the intercondylar groove to the most projecting point of the posterior end of the lateral condyle where this is some buttressing that causes a posterior projection. The intercondylar eminence is eroded and cannot be assessed.

The distal tibia (ER 2037Q) is not particularly wide anteroposteriorly. The anterior process projects distally such that there is a lot of curvature to the articular surface from anterior to posterior. The posterior shaft is rather flat. Unfortunately, the medial malleolus is broken off.

Among the tarsals, only the right calcaneum and astragalus are known, along with a sesamoid (ER 2037CD). The calcaneum (ER 2037S; Fig. 8.29g) is well preserved. The entire specimen is relatively narrow mediolaterally, as in extant cheetahs. The cuboidal surface is rotated and a rounded rectangle. The most lateral point of its long axis runs at about 50 degrees to a horizontal axis through the bone. Both astragalar facets are round and very distally (i.e., anteriorly) directed. They are also a little closer together than in the average felid and more like canids. The lateral facet is very humped, reflecting the great curvature in the astragalar trochlea. The lever arm is about the same length as the manubrium. The medial end projects far beyond the lateral end of the calcaneal tuberosity. A shallow groove runs under the sustentaculum. The ventral surface has a slight proximodistal curvature.

The right astragalus (ER 2037T; Fig. 8.29h) is missing the head and neck, but is otherwise reasonably well preserved. The trochlea is extremely short and curved anteroposteriorly, suggesting a wide range of dorsiflexion and plantarflexion. It is also narrow mediolaterally, with a high lateral lip. The posterior end of the trochlea is very interesting. The articular area seems to end, posterior to which is a fossa. The posteriormost end is slightly lipped. This fossa and lip suggest a forceful limit to plantarflexion of the pes. In ventral view, most of the medial facet is broken off. The lateral facet is sharply angled mediolaterally reflecting the high lateral lip of the trochlea. Both facets appear to extend to the very end of the specimen despite the dorsal morphology.

**REMARKS**

Although previously published as “KF Panthera A” (Lewis 1997), ER 2037 is clearly more closely aligned with Acinonyx than Panthera. As noted above, it shares many features with extant Acinonyx, but has not
evolved the complete set of features associated with hypercursoriality in extant cheetahs. In essence, this is a medium-sized felid in transition to a more cursorial lifestyle, while retaining some flexibility, particularly within the forelimb. This mosaic change makes sense, as losing flexibility in the forelimb signifies the need for a significant change in prey capture techniques. Thus, this specimen represents the transitional period in the evolutionary trade-off that cheetahs made for increased speed at the expense of the intensive prey grappling/capturing abilities of most felids.

*cf. Acinonyx sp.*

Fig. 8.30

KOOGI FORA MATERIAL

CRANIODENTAL

ER 3740C is a right maxilla fragment with a mesiolingually broken P3. The tooth is long and slender, with a small distolingual bulge and well developed distal accessory cusp. The distal cingulum forms a prominent bump but not quite a cusp.

Although the slenderness of the tooth

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Fig. 8.30: Material referred to *cf. Acinonyx sp.* a-c) distal humerus ER 2009A in a) posterior, b) anterior, and c) distal view; d) dorsal view of right metatarsal 4 ER 3740E-F.
and the development of its distal part are both indicative of referral to *Acinonyx*, they are not by themselves sufficient to definitively place the specimen in that genus. However, the association with the postcranial elements described below makes this identification more likely.

**POSTCRANIAL**

The left humerus, ER 2009A (Fig. 8.30a-c), is missing the proximal end, but is the most complete of the potential *Acinonyx* humeri and similar in size to the ER 2037 humerus described above. The medial epicondyle of ER 2009A appears to project further medially than in the fragmentary ER 2037 humerus, but the two specimens are otherwise similar (as far as can be seen from the fragments of ER 2037).

Although the distal end of ER 2009A is within the size range of a small extant *P. pardus*, the shaft looks like it would be relatively long for a leopard (e.g., it is about 99 mm from the inferior end of the deltoid tuberosity to the distal end of the medial lip of the trochlea). The shaft is also relatively straight. There is a slight posterior curvature after the level of the deltoid tuberosity, but the shaft does not thicken appreciably in the anteroposterior dimension. However, the distal end is not as mediolaterally compressed as in extant *Acinonyx jubatus*. All of these characteristics fit with that of a primitive cheetah that had not fully evolved hypercursoriality.

The partial skeleton ER 3740 is much more fragmentary than the younger ER 2037 *Acinonyx* skeleton. The fragments of femur include a portion of the head (ER 3740B) and distal shaft (ER 3740A). The head is so fragmentary that little can be said except that it is quite small and rounded. The fovea capitis is somewhat diffuse and not particularly deep. The other fragment includes the distal half of the shaft down to the point where it begins to widen to join the distal epiphysis. The shaft is extremely round, as in extant *Acinonyx*. The cortical bone seems a little thick (~ 5 mm on average) and the specimen seems rather large relative to extant *Acinonyx*. The distal tibia (ER 3740D) is extremely fragmentary.

ER 44653 is the distal half of a distal left second metatarsal within the size range of cheetahs. While the complete length is unknown, judging by the shaft shape this would probably have been a relatively elongated specimen for a felid and most like *Acinonyx*. The shaft is relatively rounded and the head is mediolaterally compressed for a felid, as in *Acinonyx*. However, this specimen is smaller than extant *Acinonyx* and the shaft is more robust relative to its size. In comparison to other Koobi Fora felids, it is much larger than the felid third metatarsal ER 45539. The size of this specimen is proportional to the ER 3740 E, F fourth metatarsal described below.

The only well-preserved portion of ER 3740 is the right metatarsal 4 (ER 3740E, F; Fig. 8.30d), although the head is slightly eroded. It is somewhat elongated and different from larger felids. It is much smaller and more gracile than a lion or the machairodont *Homotherium*. While the proximal end is similar in size to that of *Dinofelis*, the specimen is much longer overall and the head is much more gracile. In addition, the shaft is curved slightly dorsoventrally, which is not seen in *Dinofelis*. In proximal view, the lateral portion of the articulation is on a bar of bone that projects more proximally relative to the medial portion. It is very similar to a cheetah specimen from West Turkana, WT 14993, but much smaller. Despite being longer than metatarsals of much larger taxa, this
specimen is shorter and wider than metatarsal 4 in modern *Acinonyx*. Other fragments of ER 3740 include a possible vertebral fragment (G), shaft fragment (H), fibula fragment (I), and four rib fragments (J-M), including rib 1 (L).

The distal right fifth metatarsal (ER 2009B) is quite slender and the head is broken. The shaft is gracile and relatively round, with some flattening on the ventral and medial surfaces. Although the articular surface of the head is quite eroded, it does not seem to have been particularly wide.

**REMARKS**

If these specimens are indeed attributable to *Acinonyx*, it suggests that during the Upper Burgi, the elongated, hypercursorial limbs of modern cheetahs had begun to evolve, but had not yet become as elongated, and the ability to supinate (as judged by the size of the medial epicondyle of ER 2009) was not as reduced as in extant cheetahs (Andersson 2004). While cheetahs today are relatively gracile for their size as part of their adaptation to great speed, possible cheetahs in the Upper Burgi were not as gracile. Thus, specimens from this time period indicate the beginnings of hypercursoriality and match what is seen in the younger specimens more definitely attributable to *Acinonyx*. These Upper Burgi specimens are an appropriate ancestor for the younger KBS *Acinonyx*. It is unfortunate that no diagnostic craniodental material of Upper Burgi *Acinonyx* is available, as this might indicate whether it is conspecific with the slightly older *A. aicha* from Ahl al Oughlam in Morocco, the available postcranial material of which is limited to a tibia, a tarsal, and some incomplete metapodials (Geraads 1997).

**Caracal sp. or Leptailurus sp.**

Fig. 8.31

**Stratigraphic range in Africa:** Early Pliocene (ca. 4 Ma) – Recent based on FAD in the Usno Fm., Ethiopia.

**Stratigraphic range at Koobi Fora:** Late Pliocene – Early Pleistocene based on FAD in the Tulu Bor Mb. (≤3.44 Ma) and LAD in the Upper Burgi Mb. (≥1.87 Ma).

**REMARKS**

The genera *Caracal* and *Leptailurus* are medium-sized felids with wide geographic distributions. The former includes two species, *C. caracal* (the caracal) and *C. aurata* (the African golden cat, previously placed in the genus *Profelis*), while the latter includes the single species *L. serval* (the serval). These genera are very difficult to distinguish from each other on the basis of morphological characters of the skull and dentition. This is in contrast to the living animals, which are readily distinguishable on the basis of, e.g., pelage characteristics, and despite the fact that the lineages have been separate for some 5.5 million years (Johnson et al. 2006). The single metric difference between the genera in the lower dentition (nearly all the eastern African fossils are from the lower dentition) lies in the longer p3 relative to the other cheek teeth of *Leptailurus*. One or two of these species (most likely *C. caracal* and *L. serval*, as *C. aurata* is restricted to forested habitats and less likely to have been fossilized than the open habitat-adapted caracal and serval) are present at a number of eastern African sites, including the Usno Fm., Shungura Fm., Hadar, and Laetoli. The relative lengths of p3 and m1 support placing the
Laetoli specimen LAET 75-991 in *Caracal* (Werdelin and Dehghani 2011), but none of the other specimens retain the relevant dentition. Distinctions based on the postcranial skeleton are discussed below.

KOOBI FORA MATERIAL

POSTCRANIAL

The well-preserved distal right humerus, ER 44654 in a) posterior, b) anterior, and c) distal view; d-e) right metatarsal 3 ER 45539 in d) dorsal and e) proximal view; f-g) left calcaneum ER 44719 in f) dorsal and g) medial view; h-i) right astragalus ER 3094 in h) dorsal and i) ventral view.
44654 (Fig. 8.31a-c), is that of a medium-sized felid. The entepicondylar foramen is present. On the anterior surface there are well-marked anconeal and radial fossae. In most respects, this is a typical felid. In size and proportions, this specimen is most similar to extant forms of *Lynx*, extant servals and extant African golden cats (Fig. 8.32). While it is only slightly larger than modern caracals, it has a slightly wider biepicondylar width relative to the overall anteroposterior width of the distal end.

The left tibial shaft, ER 62, of a medium-sized felid is missing both the proximal and distal ends. The shaft curvature and the shape of the proximal half of the shaft are most similar to modern servals.

While the humerus varies in size in extant members of this lineage, the astragalus varies less in size. The right astragalus ER 3094 (Fig. 8.31h, i) is in the size range of astragali of extant caracals, servals and golden cats. The neck is more gracile than in caracals or servals. The lateral lip of the trochlea projects further anteriorly than in caracals, servals or leopards. The posterior portion of the trochlea is wider than in caracals or servals and is similar to a leopard. The medial arch of the trochlea is caracal-like.

The head of ER 3094 is similar in shape to extant members of the genus *Caracal*. It is more compact anteroposteriorly than caracals and slightly more compact than servals. The head is quite unlike that of leopards. The head is also much more rounded than caracals, servals or leopards. The calcaneal facets of ER 3094 are more narrow than in extant species of *Caracal*, but are more like them than like leopards. The medial facet is oriented more obliquely. The medial edge is more superior than in caracals or servals. The medial facet does not extend as far anteriorly as in caracals and servals. The lateral facet does not project as far anterolaterally.

In all, ER 3094 is more like caracals than leopards or servals. However, caracals and servals are more similar to each other than the fossil is to either. This specimen is too small for the calcaneum ER 44719.

The ER 44719 calcaneum (Fig. 8.31f, g) falls within the size range of extant species of *Caracal*, although it is closest in size to servals. It fits well with other *Caracal* sp. specimens. As in all felids, the fibular trochlea on the lateral side of the bone is flaring. The groove for the fibularis longus tendon on the dorsal surface of the fibular trochlea at its origin from the body is quite clear and is offset posteriorly from the cuboidal facet.

Although the specimen is a little wide mediolaterally relative to its overall length, it is not outside the range of variation of *Caracal* spp. and servals in particular. In comparison to similarly sized hyenids, the overall
length is shorter relative to the dorsoventral width of the body and the robusticity and size of the sustentaculum. This shorter length is reflected in both the proximal and distal portions and suggests, not surprisingly, an animal that is less cursorial than hyenids.

The nearly complete right third metatarsal, ER 45539 (Fig. 8.31d, e), has an eroded and broken distal end. It is clearly a felid, with the characteristic T-shaped carpal articular surface. The shaft is curved, with the majority of curvature in the distal third. The shaft is not particularly elongate nor is the specimen particularly robust. The proximal end is more mediolaterally compressed than in machairodonts, but that is not surprising for a medium-sized felid. The head is not preserved well enough to comment on.

REMARKS

Caracals, servals, and African golden cats are closely related species that branched off from other felids roughly 8.5 Ma (Johnson et al. 2006; Werdelin et al. 2010). While each species has a unique combination of morphological features, identification of individual bone fragments can be difficult, even among the modern taxa. *Leptailurus* may have split off from *Caracal* roughly 5.5 Ma (Werdelin et al. 2010). All of the Koobi Fora material from this lineage comes from the Tulu Bor and Upper Burgi Members and is therefore younger than this split. Even though the distinctions between the three extant taxa had probably not fully evolved at this point, servals had split from caracals/golden cats while the latter were in the process of splitting during that time (Werdelin et al. 2010).

With the exception of the astragalus ER 3094, all of the above specimens fall within the size ranges of servals and golden cats and are larger elements than are possessed by most extant caracals. Given that there is no evidence of African golden cats having occurred east of the rainforest belt in Africa, it is more likely that this material belongs to a primitive serval. However, it is possible that the larger, serval/golden cat morphology is primitive for the *Caracal* lineage and that this is an ancestor of extant caracals recently split from African golden cats. Although the astragalus ER 3094 came from a smaller individual than the other specimens, all of the above specimens could fit comfortably within the range of a single species.

The similarity of the humeral specimen ER 44654 to species of *Lynx* is not surprising. Previous research has demonstrated that most extant felids, regardless of size, are similar in humeral morphology (Lewis and Lague 2010). However, there are several exceptions to this, including, but not limited to, extant servals and cheetahs, with their elongated limbs relative to the overall size of the bone (Lewis and Lague 2010). While *Lynx* is not as elongated as cheetahs or caracals, it is still relatively long-limbed. The length of the fossil, however, is unknown. And, while Lewis and Lague (2010) did not include African golden cats in their study, golden cats do not appear to have the particularly elongated legs of servals or cheetahs or even *Lynx*. Thus, it is more likely, given the fairly conservative nature of felid humeral morphology, that the relationship to *Lynx*, servals, and golden cats has to do with overall size in combination with the slightly greater biepicondylar width as noted above.

Felinae indet.

Fig. 8.33

The ramus ER 3758 (Fig. 8.33a-c) is slender but thick for its size. There are two mental
foramina. The anterior of these lies beneath the middle of the postcanine diastema, while the posterior lies at about the same height beneath the middle of p3. The masseteric fossa reaches mesially to nearly half the length of the m1 protoconid. The m1 is long and slender. The paraconid is wide. The protoconid is broken apically. The carnassial notch is wide. The metaconid/talonid complex is prominent.

REMARKS

The m1 of this specimen is of about the size of an average C. caracal carnassial. However, it is considerably more slender (Fig. 8.34) and well outside the 95% confidence ellipse for C. caracal. It is also more slender than any of the other comparative specimens in this general size range, including Felis chaus, the largest African species of Felis. That said, we do have a single very large extant caracal specimen in our sample that is also very slender and outside the normal distribution of the species in m1 proportions. Therefore, it is not impossible that ER 3758 represents an aberrant Caracal specimen. However, the proportions, as well as the unusually well developed metaconid/talonid complex of ER 3758 creates considerable uncertainty regarding its taxonomic identity, and we here prefer to place it in Felinae indet. rather than in the caracal/serval species complex.

Felidae indet.

REMARKS

This heading includes specimens that in most cases could belong to either Machairodontinae or Felinae. As such, they merely record the presence of the family in their respective members and areas.

KOOBI FORA MATERIAL

CRANIODENTAL

ER 5676 includes three isolated teeth: A is a probable left P1, B an I2, and C a probable i2. Although they were found in close proximity,
the specimens need not belong to the same individual or species. The crown of ER 5676A is relatively featureless and has a slight lingual bulge near its middle. The main cusp is low and crest-like. There is a low distal accessory cusp that reaches about one third of the height of the main cusp. The main cusp of ER 5676B is broad. There are two well developed lingual accessory cusps that reach about half the height of the main cusp. The tooth is very symmetric and it is difficult to state whether it belongs on the right or left side. The third specimen, ER 5676C is probably a right i2, but could be an i1. The crown consists of two distinct cuspules, with the medial cusp the larger, but with a prominent lateral accessory cusp.

The mesial end of the ramus ER 3746 is broken at the distal end of the canine root, whereas distally it is broken along an oblique line from the base of the coronoid process mesioventrally to the mesial root of m1. The ramus is low but broad. There are two mental foramina. The larger of the two is situated

![Fig. 8.35: Material referred to Felidae indet. a-d) right humerus ER 1538 in a) medial, b) lateral, c) posterior, and d) proximal view; e-f) fourth metatarsal ER 38522 in e) dorsal and f) proximal view.](image)
beneath the postcanine diastema somewhat nearer the ventral border of the ramus than the dorsal border. The second, smaller mental foramen is situated beneath the middle of p3 on the same dorsoventral level as the larger one. The p3 is small and two-rooted. The p4 is larger, with a larger distal than mesial root. The m1 is short, with a very small distal root.

POSTCRANIAL

The ER 1538 (Fig. 8.35a-d) humerus is an enigmatic specimen due in part to its morphology and in part to being somewhat incomplete. Some pieces of shaft are missing and the head is a little eroded on the medial edge. The greater tuberosity is broken off and the lateral edge is chipped.

ER 1538 is distinct from *Dinofelis* in numerous features, such as the lack of anteroposterior thickening and the proportions of the articular surfaces. The distal end seems quite small for a machairodont, even for *Megantereon*. The distal end is most similar to *Panthera*, but the proximal portion of the specimen is unusual.

The head is rather small relative to the length of the shaft in comparison to machairodonts. This feature is more like *Panthera*. Although a portion is missing, the head is quite rounded. The greater tuberosity is broken anteriorly, but did not rise very far above the superior surface of the head. The greater and lesser tuberosities extend about the same distance outwards from the shaft. The lesser tuberosity does not extend as far superiorly as in extant lions or tigers.

The deltopectoral crest is not as robust as in extant lions or tigers, but this is a smaller species. It is barely raised from the shaft on the pectoral (medial) side. The distal end of the pectoral side flares slightly medially before ending at the level of the deltid tuberosity. The deltid side (lateral) forms a sharp ridge leading to the large, rugose deltid tuberosity. Posterior to this ridge is an unusual, smooth, lateral bulge that, along with the medial expansion of the pectoral portion gives the shaft an unusually wide (for a felid) appearance in this region when viewed anteriorly or posteriorly. The shaft then narrows to more typical pantherine proportions distal to the tuberosity. This mediolateral swelling is different from machairodontines, as well.

This enlargement of the shaft gives the proximal portion a mediolateral width that is roughly equivalent to that of the head. In posterior view, the proximal half of the shaft has parallel sides. Perhaps, given the extreme rugosity of the deltid side of the crest and the deltid tuberosity, there was a deltid injury or partial separation from the shaft that caused such extensive remodeling. However, the bulge itself is quite smooth and does not appear to be a pathology.

The deltid tuberosity extends almost to the midshaft. The distal half of the shaft is quite gracile in comparison. Overall, the shaft has a rather tubular aspect similar to *Acinonyx*, although it is not as elongated and gracile. The shaft is relatively straight in lateral view, but in anterior view has more mediolateral curvature than is typical for felids. This curvature and the great transverse thickness of the proximal shaft make this look a little mustelid-like. Larger, more cursorial mustelids such as the extinct *Ekorus* (Werdelein 2003) or extant *Gulo* lack this curvature.

The entepicondylar foramen and medial epicondyle are about what one would predict in size for this size of *Panthera*. The lateral epicondyle and supinator crest are broken. The sharp ridge of the supinator crest extends superiorly almost to midshaft where it has
moved to a more posterior position that is almost in the midline of the shaft.

Despite the small size of the distal end, the trochlea is rather wide and flat relative to the size of the end, but not as much as one would see in larger Panthera. The lateral lip of the trochlea is not tall (although it is broken in places) and the capitulum is only moderately rounded and rather small. The lateral epicondyle is much smaller than the medial epicondyle. The entire distal end seems quite narrow anteroposteriorly. Anteriorly, there are two excavated portions in the region of the coronoid fossa where the medial coronoid process of the ulna and the radial head contacted the humeral shaft during extreme flexion of the elbow. This sort of excavation is seen to a much greater degree in Megantereon than in this specimen.

Two specimens that may be associated with each other, a femoral head fragment (ER 38522A) and proximal right metatarsal 4 (ER 38522B), are too fragmentary to assign to a specific genus. Both specimens are roughly the size of an extant leopard. The femoral head is too fragmentary to observe any morphology. The proximal end of the metatarsal is missing the lateral portion of the articular surface (Fig. 8.35e, f). The medial tubercle for articulation with the third metatarsal is prominent. The articular surface is relatively flat. The lateral shelf for articulation with metatarsal 5 is broken off. Thus, proportions are difficult to assess in this specimen. Given the size, these specimens could belong to Panthera pardus or Megantereon whitei.

ER 44715 includes one distal metapodial (possibly metatarsal 3 or 4) and 12 other fragments of vertebrae, ribs, etc. Little can be said about these specimens except that the metapodial morphology suggests that it is a large felid.

**REMARKS**

None of these specimens can be definitively placed in either Machairodontinae or Felinae. Incisors of Dinofelis and Megantereon (but not Homotherium, which has distinctive and highly specialized incisors) are very similar to those of Felinae. Specimen ER 3746 is most similar to Dinofelis in the shape and thickness of the ramus, but more like Panthera in the proportions of the teeth. The specimen is unlikely to have been fully grown, which makes taxonomic assignment still more difficult.

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Werdelin, L., and Lewis, M. E. (2002). Spe-


The carnivoran fossil record at Koobi Fora provides an intriguing glimpse into the ever changing faunal diversity of eastern Africa. While carnivorans are far less common in the fossil record than are their prey taxa, they are sufficiently well represented at Koobi Fora that it is possible to examine both patterns of overall species richness through time, and patterns within smaller taxonomic groups such as families.

While examining changes in species richness, it is important to consider the role that sampling plays. In addition, when drawing conclusions from patterns of change in richness, it is important to remember that richness is only one of many measures of biodiversity and is not a proxy for measures such as abundance, evenness and others. The following sections present a quick look at issues of sampling and species richness, with some final comments on overall changes in carnivoran diversity and turnover through time.

GENERAL COMMENTS AND SAMPLING

The stratigraphic distribution of the carnivoran taxa identified from Koobi Fora and described in Chapters 3-8 is shown in Table 9.1. No specimens in our sample came from the Moiti or Lower Burgi Mbs, and these have therefore been deleted from the table. The Chari Mb. has yielded only three carnivoran specimens and has therefore also been deleted. In Table 9.1, ‘X’ marks the definite presence of a taxon in that member, while ‘?’ denotes probable or possible presence.

In order to provide data for analysis, Table 9.1 has to be consolidated and transformed into quantitative estimates of number of taxa per member. To do this we have eliminated possible or probable duplications. For example, it is probable that Crocuta dietrichi and C. cf. C. dietrichi are the same taxon, so when both are present in a member as given in Table 9.1 (Upper Burgi Mb.), they should only count as one taxon. Most probable or possible presences record at least the presence of some taxon, and thus have been retained. In a few cases, ‘?’ records uncertainty in the stratigraphic position of a specimen, such as Vulpes sp. In these few cases, both or all stratigraphic attributions have been recorded. This will somewhat inflate species numbers, but this is counterbalanced by not counting range-through taxa. In many cases absence of a taxon from a member despite its presence in the bracketing members (‘range-through taxa’) is simply an error of sampling. However, it is also possible that, due to changing environmental regimes in the region, the taxon was genuinely absent from the time period, and we have opted to accept the latter possibility and consider such absences genuine. This will likely reduce taxon numbers somewhat from what they should be. Most importantly, we have tried to maintain consistency throughout this process, so that even if the numbers of taxa are not directly comparable to a modern list, at least the data are internally consistent. Thus, comparisons between members should not be strongly af-
Table 9.1: Stratigraphic representation of carnivoran taxa in the different Members at Koobi Fora. Members not shown here have yielded no or very few Carnivora. For details see this Chapter and Chapters 3-8.
fected by biases in taxon counts. The final taxon counts per member are given in Table 9.2.

Before discussing patterns of change through time generally, and specifically for each family, we must consider issues of sampling and other biases. Table 9.2 gives the total number of specimens (counted as catalog numbers) per member and Fig. 9.1 plots out the number of taxa and the number of specimens per member. The numbers presented show that samples are generally small, but it is not entirely clear how adequate they are. However, the three oldest members represented, Lonyumun, Lokochot, and Tulu Bor, are clearly under-sampled. The fossiliferous sediments of the Tulu Bor Mb. extend over 720 Ka, and within this time period only 23 carnivoran specimens have been collected, which is clearly inadequate. Even more inadequate are the Lonyumun and Lokochot Mbs, with seven and five specimens, respectively. Overall, Fig. 9.1 shows that the number of taxa found is closely correlated with number of specimens ($r = 0.94$). Despite this, some interesting patterns emerge from the consideration of the number of specimens per taxon (Table 9.2, Fig. 9.2). Not unexpectedly, the poorly sampled older members have few specimens per taxon identified, while in the better sampled members this number has risen considerably. However, among the latter, the KBS Mb. stands out as having more taxa recorded relative to the number of specimens found than would be expected. The following Okote Mb. has many fewer taxa despite a closely similar number of specimens collected, suggesting that the loss of species richness in the latter member is real rather than a reflection of sampling. Further supporting this decrease as a true event is the fact that the Okote Mb. with 14 species has nearly the same richness as the Tulu Bor Mb. despite having more than twice the number of specimens compared to the latter, in a much shorter period of time.

So, despite the generally poor and uneven sampling of the Koobi Fora carnivorans, some possible facts can be established. The most important of these is that species richness in the Okote Mb. ($\leq 1.56$ Ma) is lower than in the Upper Burgi and KBS Mbs. This difference is in line with conclusions we have drawn earlier based on data from the entire eastern African fossil record of carnivorans (Lewis and Werdelin 2007; Werdelin and Lewis 2005). We shall return in this chapter to a consideration of when the reduction in richness actually occurred, since 1.56 Ma is just a minimum date.

RICHNESS PATTERNS IN DETAIL

In this section we will consider the richness patterns of each family, with some comments on the underlying taxa and a consideration of changes through time. This will be followed by a discussion of the richness pattern of the Carnivora as a whole.

Canidae

The most striking aspect of canid representa-

<table>
<thead>
<tr>
<th>Member</th>
<th>Lonyumun</th>
<th>Lokochot</th>
<th>Tulu Bor</th>
<th>Upper Burgi</th>
<th>KBS</th>
<th>Okote</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of taxa</td>
<td>4</td>
<td>4</td>
<td>12</td>
<td>22</td>
<td>21</td>
<td>14</td>
</tr>
<tr>
<td>Number of specimens</td>
<td>7</td>
<td>5</td>
<td>23</td>
<td>99</td>
<td>63</td>
<td>56</td>
</tr>
<tr>
<td>Specimens per taxon</td>
<td>1.8</td>
<td>1.3</td>
<td>1.9</td>
<td>4.5</td>
<td>3.0</td>
<td>4.0</td>
</tr>
</tbody>
</table>

Table 9.2: Table showing the number of taxa and specimens in each member. See text for details and discussion.
tion at Koobi Fora is how few there are, both specimens (11) and species (2), even by comparison with contemporaneous eastern African sites (see Chapter 10). Figure 9.3 shows canid species richness through time. This figure is somewhat misleading, since there is only one specimen of *Vulpes* sp., but its stratigraphic origin is either Upper Burgi or KBS Mb. In the figure, both are included, so that actual richness was only one, rather than two, in one of those two members, not both. Nevertheless, although significant in terms of percentage for Canidae, this difference is minor when viewing the Koobi Fora carnivoran fauna as a whole.

**Mustelidae**

Taxon richness in Mustelidae rises gradually from the Lonyumun Mb. to the Upper Burgi Mb. and then tapers off equally gradually (Fig. 9.4). However, specimen numbers show a very large peak in the Upper Burgi, which is probably related to the presence of the lacustrine facies of the Lorenyang Lake in the lower part of the Upper Burgi Mb., starting ca 2 Ma (Gathogo and Brown 2006; Gathogo 2003; Leakey et al. 2008). Most of these specimens have here been referred to *Torolutra* sp. or cf. *Torolutra* sp., clearly the most common lutrine genus during Upper Burgi time. Overall, given that there are only three extant lutrine taxa present in Africa today (common clawless otter, *Aonyx capensis*, Congo clawless otter, *Aonyx congicus*, and spotted-necked otter, *Hydrictis maculicollis*) one of which is very rare (*A. congicus*), the taxon richness and apparent abundance of otters in the past is both surprising and a topic for further study on a regional and continental basis. It is interesting that there are more specimens of Mustelidae in the Upper Burgi Mb. sample than of any other carnivoran family except Felidae.

**Ursidae**

The most noteworthy aspect of ursid taxon richness and specimen numbers at Koobi Fora (Fig. 9.5) is that they are there at all. Ursids are very rare in the Plio-Pleistocene of Africa in general and sub-Saharan Africa in particu-
larr. The Koobi Fora ursid specimens have been referred to cf. *Agriotherium* sp. herein, and if this is correct, the Tulu Bor specimen is the youngest representative of this genus in Africa, and the youngest ursid known from sub-Saharan Africa.

Fig. 9.4: Diagram showing the number of taxa (solid line) and specimens (dashed line) among Koobi Fora Mustelidae.

**Viverridae**

Only a single viverrid specimen comes from pre-Upper Burgi Mb. deposits. Apart from this the richness curve for Viverridae is similar to that for Mustelidae, with a gradual decline from the Upper Burgi Mb. to the Okote Mb. (Fig. 9.6). The specimen representation curve has a very sharp peak in the Upper Burgi Mb., though not as precipitously steep as that of the Mustelidae. Since we have many Viverridae indet., both taxa and specimens, it is difficult to enumerate possible causes of this peak. We note, however, that if micro-mammals were better represented at Koobi Fora, species richness of Viverridae would probably be greater, though the difference would not be as marked as for the Herpestidae, which are not known with certainty in our Koobi Fora material.

**Hyaenidae**

The richness curve for Hyaenidae differs from the preceding ones in showing a steady increase until the KBS Mb., and then a slight
decrease in the Okote Mb. (Fig. 9.7; note that the scales of the left and right Y-axes are different in this figure and Fig. 9.8, while in Figs. 9.3-9.6 they are the same). This family is also unique among the families represented at Koobi Fora by having its peak specimen number in the KBS Mb. The reasons for this are unknown, but may, of course, be due simply to a random fluctuation in sampling. It is noteworthy that species richness of Hyaenidae exceeds current richness in the region (three species) from the Upper Burgi Mb. onwards, despite the absence of material of Proteles, one of the hyenid genera currently living in eastern Africa.

**Felidae**

Taxon richness in Felidae is again different, in that the peak in diversity is equal in the Upper Burgi and KBS Mbs (Fig. 9.8). In addition, richness in the Tulu Bor and Okote Mbs is only slightly less. This is the only family to have a significant taxon representation in the Tulu Bor Mb., though this is due to a pattern where each individual specimen represents a different taxon. Specimen representation of Felidae peaks in the Upper Burgi Mb., and dips to the KBS Mb., with a slight increase again in the Okote Mb., which is a pattern unique to this family. It is of interest to contrast the specimen representation of all Felidae with that of *Homotherium* sp., which is one of the few genera that is known from a sufficient number of specimens to make such a comparison feasible. Figure 9.8 shows that the specimen representation curves for Felidae and *Homotherium* follow each other from the Lonyumun Mb. to the KBS Mb. (though *Homotherium* sp. naturally forms a subset of the whole). In the Okote Mb., however, there is a marked difference in that the specimen number for Felidae shows a slight increase while that of *Homotherium* shows a precipitous drop to only a single specimen. This is strong indication that, although the genus is still present, the abundance of *Homotherium* is strongly reduced in the Okote Mb. In addition, it is not known in Africa from deposits younger than the Okote Mb.
**Turnover**

Due to the small sample sizes, we can only make a few general statements regarding carnivoran turnover at Koobi Fora, i.e., the eastern part of the Turkana Basin. After more detailed work on the western and northern parts, a more coherent picture may emerge of turnover in the Turkana Basin as a whole. Previous discussions of turnover in the basin have largely ignored the Carnivora (e.g., Behrensmeyer et al. 1997).

We shall not discuss origination and extinction patterns here as the data for Koobi Fora are inadequate on their own for such an analysis and we have discussed them previously within a larger study of the eastern African carnivoran record (Werdelin and Lewis 2005). We will, however, consider one aspect of turnover, and that is simply how large a percentage of the species in one member are still present in the next member. This will provide a rough estimate of turnover that, although biased by the strong possibility of conflating real extinctions and pseudo-extinctions, will at least allow us to suggest where faunas show the most change. The Lonyumun and Lokochot Mbs have so few taxa that they are not included in this analysis, the results of which are shown in Table 9.3.

In reading this table it should be kept in mind that there is a ca 500 Ka hiatus in sedimentation between the Tulu Bor and Upper Burgi Mbs as discussed herein. Therefore, it is not unexpected to see a relatively low percentage of holdovers between these members, nor that the number of holdovers should increase between the Upper Burgi and KBS Mbs, which are generally viewed as fairly similar in faunal content. The more unexpected aspect of this is that only 38% of the taxa in the KBS Mb. are also present in the Okote Mb. This suggests considerable faunal change between these members, similar to that posited by us for eastern Africa as a whole (Lewis and Werdelin 2007).

The base of the Okote Mb. is dated at ca 1.56 Ma (McDougall and Brown 2006), which is later than our previous estimates for post-2 Ma carnivoran turnover in the region (Lewis and Werdelin 2007). There is no reason to believe that this turnover began at the boundary between the KBS and Okote Mbs, however, but can we find support for an earlier date in our material? In fact, by looking at the pattern of number of specimens per taxon (Table 9.2), we believe that we can. The number of specimens per species takes a sharp dip in the KBS Mb. compared to the Upper Burgi and Okote Mbs, indicating that the number of taxa in that member is greater than the number of collected specimens would suggest. One plausible reason for this is that turnover began within this member, so that the fauna was substantially different at the end of the KBS Mb. than it was at its beginning. This would inflate the number of taxa relative to the number of specimens in a way analogous to the reason...
for the low number of specimens per taxon in the poorly sampled older members, i.e., during initial sampling the number of taxa will rise rapidly, and then the increase tapers off as sampling improves. Viewed this way, the KBS Mb. sample is really two samples, each of which is less well sampled than the whole would indicate. This perspective can be tested in the future by more precise stratigraphic delimitation of the specimens, but this information is not yet available to us.

This pattern may be specific to Carnivora. A very preliminary survey of ungulates from the KBS and Okote Mbs as recorded in the Turkana Basin database compiled by Dr. René Bobe suggests that about 75% of ungulate species in the KBS Mb. are also found in the Okote Mb.

CONCLUSIONS

The patterns observable in the Koobi Fora carnivoran record are striking, even if the causation is not always clear. Richness curves vary among carnivoran families, presumably due to general differences in behavior, ecology, and overall life history strategies among families and the resulting differing responses to ecological/environmental shifts. To some degree, an aspect of ecology that differs between families is the proportion of different levels of ecological specialization (e.g., relatively generalist vs. relatively specialist species). As we have noted elsewhere (Lewis and Werdelin 2007, 2013), the depauperate extant carnivoran fauna is comprised mainly of generalists as a result of the extinction of most specialist species. Koobi Fora records this period of change, particularly as read from the felid record, where the more generalist Panthera species and more specialist machairodont felids coexist in the region for some time. The subtle changes in the Okote Mb., in contrast to those of earlier members, are significant in part because we know the end of the story: the specialist machairodonts are extinct and the generalist lion and leopard remain with us to this day.

The case of the Okote felids reminds us that richness does not equal abundance. Rare taxa may appear in well-sampled members and be hidden in poorly sampled ones. Analysis of the machairodont Homotherium, in particular, provides clues to changes in abundance from member to member. Thus, the eventual extinction of machairodonts, at least as seen in the record of Homotherium, followed a period of decline in abundance. The same may or may not be true of other specialist genera, such as the machairodont Dinofelis, due to the less extreme nature of their specialization (Werdelin and Lewis 2001). Based on numbers of individuals and species at Koobi Fora, Dinofelis was not only more speciose than Homotheri-
um”, but possibly more numerous as well, while *Megantereon*, the third machairodont genus, was neither speciose nor (presumably) numerous.

A final note on the faunal assemblages recorded here in Table 9.1. A recent study (Du et al. 2012) suggested that sampling only craniodental material as opposed to craniodental and postcranial material has only slight effects on taxon richness estimates for ungulates. This does not hold for Carnivora, where even fragmentary postcranial material can be identified to low taxonomic levels. In our case the number of taxa identified from postcranial material alone varies between members from ca 50% (Tulu Bor Mb.) to ca 10% (Upper Burgi and KBS Mbs), and overall, there are at least nine species-level taxa and one family that are known on the basis only of postcranial material. Thus, it is essential that all carnivoran material is collected.

REFERENCES


Placing the Koobi Fora carnivoran fauna in a broader African context is made difficult by the small samples of carnivorans not just at Koobi Fora, but generally across Africa. There are often a large numbers of species-level taxa in the carnivoran samples, but the numbers of specimens are usually quite small. These low numbers make it difficult to demonstrate that any differences between Koobi Fora and other sites are due to real ecological differences and not just random sampling effects. The fact that those eastern African sites with sufficient carnivoran material to be most useful for comparison come from pre-2.5 Ma time intervals, which, in turn, are those that are most poorly sampled at Koobi Fora, further complicates matters. Unfortunately, there are few sites for comparison with the better sampled post-2.0 Ma Koobi Fora Fm. Members.

Despite these general problems we shall in this chapter try to place the Koobi Fora carnivorans in a broader context, starting with the poorly sampled early members and working upwards through the stratigraphic sequence. Our main comparisons will be with sites from Kenya, Ethiopia, and Tanzania, but we will also include some brief comparisons with northern and southern Africa. The comparative faunal lists are given in Table 10.1. Only a few of the faunal lists have been published, e.g., Kanapoi (Werdelin 2003; Werdelin and Manthi 2012) and Laetoli (Werdelin and Dehghani 2011). Most of the rest are original to this volume and represent work in progress, so that changes may still occur. Faunal lists that are based on the work of others are indicated as such.

**LONYUMUN AND LOKOCHOT MEMBERS**

These are the least well sampled Koobi Fora Fm. Members, with seven and five specimens, respectively (Table 9.2). Since the age range of these members is ca 4-3.4 Ma, the appropriate comparative samples available to us come from Kanapoi (4.23-4.07 Ma; Leakey et al. 1998), Allia Bay (ca 3.9-3.7 Ma; Leakey et al. 1998), and the Upper Laetolil beds (3.85-3.63 Ma; Deino 2011).

Of the few species-level taxa present in the Lonyumun and Lokochot Mbs., *Enhydridon* spp. is shared with Kanapoi and Allia Bay, but not the Upper Laetolil Beds, which lacks aquatic carnivorans entirely. Interestingly, Kanapoi has two species of *Enhydridon* (Werdelin and Manthi 2012), neither of which appears to be conspecific with *E. afman* from Koobi Fora. Further, *Homotherium* sp. is nearly ubiquitous in these early faunas. This may in part be because it was truly abundant, but this ubiquitousness may also be due to the relative ease with which even partial postcranial elements, let alone craniodental material, of *Homotherium* can be identified. Among all of the samples, the Lokochot Mb. is unique in lacking *Homotherium*, or any Felidae at all, but we assume that this is a sampling artifact.
<table>
<thead>
<tr>
<th>Location</th>
<th>Age Range</th>
<th>Faunal List</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kanapoi</td>
<td>4.23-4.07 Ma</td>
<td><em>Enhydriodon ekecaman</em> Enhydriodon cf. <em>E. dikikae</em> <em>Torolutra</em> sp. <em>Genetta</em> sp. <em>Helogale</em> sp. <em>Parahyaena howelli</em> <em>Homotherium</em> sp. <em>Dinofelis petteri</em> <em>Felis</em> sp.</td>
</tr>
<tr>
<td>Allia Bay</td>
<td>3.9-?3.7 Ma</td>
<td><em>Enhydriodon</em> sp. <em>Viverridae</em> sp. A (large) <em>Viverridae</em> sp. B (small) <em>Viverridae</em> sp. C (small) <em>Parahyaena howelli</em> <em>Chasmaphrothetes</em> sp. <em>Homotherium</em> sp. <em>Dinofelis petteri</em></td>
</tr>
<tr>
<td>Upper Laetolil Beds</td>
<td>3.85-3.63 Ma</td>
<td><em>?Nyctereutes barryi</em> cf. <em>Canis</em> sp. A <em>Lutrinae</em> indet. <em>Viverridae</em> or <em>Herpestidae</em> <em>Crocuta</em> cf. <em>C. dietrichi</em> <em>Mellivora</em> sp. <em>Viverra leakeyi</em> <em>Genetta</em> sp.</td>
</tr>
<tr>
<td>South Turkwel</td>
<td>3.5-3.2 Ma</td>
<td><em>Canis</em> n. sp. A <em>Lutrinae</em> indet. <em>Viverridae</em> or <em>Herpestidae</em> <em>Crocuta</em> cf. <em>C. dietrichi</em> <em>Mellivora</em> sp. <em>Viverra leakeyi</em> <em>Genetta</em> sp.</td>
</tr>
<tr>
<td>Sidi Hakoma</td>
<td>3.40-3.28 Ma</td>
<td><em>Canis</em> sp. A <em>Enhydriodon</em> sp. A <em>Enhydriodon</em> cf. <em>E. dikikae</em> <em>Helogale</em> sp. <em>Parahyaena howelli</em> <em>Chasmaphrothetes</em> sp. <em>Homotherium</em> sp. <em>Dinofelis petteri</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Felinidae</em> sp. <em>Civettictis</em> sp. <em>Enhydriodon</em> sp. B <em>Poecilogale</em> sp. <em>Helogale</em> sp. <em>Herpestes</em> sp. <em>Crocuta dietrichi</em> <em>Ikelohyaena abronia</em> <em>Chasmaphrothetes</em> cf. <em>C. nitidula</em> <em>Homotherium</em> sp. <em>Megantereon</em> sp. <em>Dinofelis petteri</em> <em>Panthera</em> sp. <em>Caracal</em> or <em>Leptailurus</em></td>
</tr>
<tr>
<td>Location</td>
<td>Time Range</td>
<td>Genus/Species</td>
</tr>
<tr>
<td>----------------</td>
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<td>-----------------------------------</td>
</tr>
<tr>
<td>Shungura B</td>
<td>3.36-2.85 Ma</td>
<td><em>Enhydriodon</em> sp. E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lutrinae indet.</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Genetta</em> sp.</td>
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<tr>
<td></td>
<td></td>
<td><em>Helogale kitafe</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Hyaena</em> cf. <em>H. makapani</em></td>
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<tr>
<td></td>
<td></td>
<td>* Megantereon* sp.</td>
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<tr>
<td></td>
<td></td>
<td><em>Dinofelis petteri</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>cf. <em>Panthera pardus</em></td>
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<tr>
<td></td>
<td></td>
<td>cf. <em>Panthera</em> sp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Felidae indet. (small)</td>
</tr>
<tr>
<td></td>
<td>3.36-2.52 Ma</td>
<td><em>Canidae</em> indet.</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Enhydriodon</em> sp. B</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Torolutra</em> cf. <em>T. ougandensis</em></td>
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<td></td>
<td></td>
<td>cf. <em>Ursidae</em></td>
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<tr>
<td></td>
<td></td>
<td><em>cf. Viverridae</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Crocuta dietrichi</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Pachycrocuta brevirostris</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Dinofelis petteri</em></td>
</tr>
<tr>
<td></td>
<td>3.36-2.52 Ma</td>
<td><em>Mungos dietrichi</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Crocuta ulra</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Pachycrocuta brevirostris</em></td>
</tr>
<tr>
<td></td>
<td>3.36-2.52 Ma</td>
<td><em>Homotherium</em> sp.</td>
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<td></td>
<td></td>
<td><em>cf. Ursidae</em></td>
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<td></td>
<td></td>
<td><em>cf. Viverridae</em></td>
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<td></td>
<td></td>
<td><em>Crocuta</em> sp.</td>
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<td></td>
<td></td>
<td><em>Mellivora</em> sp.</td>
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<tr>
<td></td>
<td>3.22-3.18 Ma</td>
<td><em>Canis</em> sp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Enhydriodon</em> sp. B</td>
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<tr>
<td></td>
<td></td>
<td><em>Enhydriodon</em> sp. C</td>
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<tr>
<td></td>
<td></td>
<td><em>Mellivora</em> sp.</td>
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<tr>
<td></td>
<td></td>
<td><em>Mustelidae</em> indet.</td>
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<tr>
<td></td>
<td></td>
<td><em>Viverridae</em> indet.</td>
</tr>
<tr>
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<td>3.18-2.92 Ma</td>
<td><em>Nyctereutes lockwoodi</em></td>
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<tr>
<td></td>
<td></td>
<td><em>Canis</em> sp.</td>
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<tr>
<td></td>
<td></td>
<td>cf. <em>Mellivora</em> sp.</td>
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<tr>
<td>Denen Dora</td>
<td>3.22-3.18 Ma</td>
<td><em>Viverridae</em> indet.</td>
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<tr>
<td></td>
<td></td>
<td><em>Dinofelis</em> sp.</td>
</tr>
<tr>
<td></td>
<td>3.22-3.18 Ma</td>
<td><em>Helogale</em> sp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Crocuta dietrichi</em></td>
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<td></td>
<td></td>
<td><em>Crocuta</em> sp.</td>
</tr>
<tr>
<td></td>
<td>3.18-2.92 Ma</td>
<td><em>Dinofelis petteri</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Homotherium</em> sp.</td>
</tr>
<tr>
<td>Kada Hadar</td>
<td>3.18-2.92 Ma</td>
<td><em>cf. Ursidae</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>cf. Viverridae</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Crocuta</em> sp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Dinofelis</em> sp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Panthera</em> sp.</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Felis</em> sp.</td>
</tr>
<tr>
<td>Location</td>
<td>Member</td>
<td>Faunal List</td>
</tr>
<tr>
<td>------------</td>
<td>----------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Shungura G</td>
<td>2.34-1.88 Ma</td>
<td><em>Shungura G</em></td>
</tr>
<tr>
<td>Kalochoro</td>
<td>2.35-1.88 Ma</td>
<td><em>Enhydriodon</em> sp. E Mustelidae indet. <em>Canis</em> sp. <em>Pseudocivetta ingens</em> <em>Viverridae</em> indet. <em>Prototocyon recki</em> <em>Aonyx</em> sp. <em>T. ougandensis</em> <em>Mustelidae</em> indet. <em>Viverridae</em> indet. (large) <em>Helogale hirtula</em> <em>Hyaena sp.</em> <em>Crocuta ultra</em> <em>Viverridae</em> indet. <em>Pseudocivetta ingens</em></td>
</tr>
<tr>
<td>Bed I</td>
<td>1.92-1.8 Ma</td>
<td><em>Enhydriodon</em> sp. E Mustelidae indet. <em>Canis</em> sp. <em>Pseudocivetta ingens</em> <em>Viverridae</em> indet. <em>Prototocyon recki</em> <em>Aonyx</em> sp. <em>T. ougandensis</em> <em>Mustelidae</em> indet. <em>Viverridae</em> indet. <em>Crocuta ultra</em> <em>Viverridae</em> indet. <em>Pseudocivetta ingens</em></td>
</tr>
<tr>
<td>Bed II</td>
<td>1.8-1.2 Ma</td>
<td><em>Enhydriodon</em> sp. E Mustelidae indet. <em>Canis</em> sp. <em>Pseudocivetta ingens</em> <em>Viverridae</em> indet. <em>Prototocyon recki</em> <em>Aonyx</em> sp. <em>T. ougandensis</em> <em>Mustelidae</em> indet. <em>Viverridae</em> indet. <em>Crocuta ultra</em> <em>Viverridae</em> indet. <em>Pseudocivetta ingens</em></td>
</tr>
</tbody>
</table>

Table 10.1 (above and preceding pages): Faunal lists for sites suitable for comparison with Koobi Fora Members. The majority of these lists are drawn from our work in progress or published. Shungura Fm. lists partly after Howell and Petter (1976), Olduvai lists partly after Petter (1973). For dating sources, see text.
Both the Lonyumun and Lokochot Mbs. have material we have here referred to *Hyaena* cf. *H. hyaena*. These identifications are mainly based on these specimens larger size than those referred to *H. cf. H. makapani*. They are unlikely to actually represent *H. hyaena* and are much more likely to pertain to the early hyenid *Ikelohyaena abronia* (Werdelin and Solounias 1991). This species is present in the Upper Laetolil Beds, as well as some other Pliocene sites in Africa, such as Langebaanweg (Werdelin 2006; Werdelin et al. 1994) and Hadar (herein). It is not present at Kanapoi or Allia Bay, where the common hyenid is the early brown hyena *Parahyaena howelli* (also present at Laetoli), which is not present at Koobi Fora. On the other hand, *Crocuta* is present in the Lokochot Mb., as well as the Upper Laetolil Beds. These differences in representation of hyenids at the different sites may be due to sampling, but may also hold biogeographic and ecological significance (Werdelin and Lewis 2008).

The only taxon that at this point is unique to either the Lonyumun and Lokochot Mbs is the bear, cf. *Agriotherium* sp., which is not present elsewhere, and at Koobi Fora only in the Lonyumun and Tulu Bor Mbs. However Ursidae are so rare in the African fossil record that no specific conclusions can be drawn from the presence of this taxon.

Overall, the data suggest a more or less uniform carnivoran fauna across eastern Africa in the early Pliocene, with *Enhydriodon* and *Homotherium* present, as well as one or two species of hyenid, including first *Parahyaena* and then *Crocuta*, but with an increase in the number of taxa to a maximum in the latest early Pliocene and earliest late Pliocene, which represents the time of greatest species richness of carnivorans in eastern Africa (Werdelin and Lewis 2005). The small samples from Koobi Fora do not alter this picture.

**TULU BOR MEMBER**

As previously noted, the Tulu Bor Mb. is also not well sampled, although the sampling is better than in the Lonyumun and Lokochot Mbs. It spans a large time range (ca 720 kyr), so that considerable amounts of faunal change could have occurred during the time interval of the Tulu Bor Mb. Suitable comparative faunas in this time range include South Turkwel (ca 3.5 – 3.2 Ma; Ward et al. 1999; Werdelin and Lewis 2000), the Sidi Hakoma, Denen Dora, and Kada Hadar Mbs. at Hadar (3.40 – 2.92 Ma; Walter 1994; Walter and Aronson 1993), the Lomekwi Mb. of the Nachukui Fm., West Turkana (ca 3.5 – 2.52 Ma; Brown 1994), the Usno Fm. (ca 3 Ma; Brown 1994), and the Shungura Fm., Mbs. B and C (3.36 – 2.52 Ma; Brown 1994).

Canidae are not known from the Tulu Bor Mb., and in the Turkana Basin as a whole are only known from South Turkwel and the lower part of the Lomekwi Mb., both in West Turkana and approximately coeval. Their absence from the Turkana Basin in the later part of the Tulu Bor time interval may be important. In contrast, Canidae are present and diverse in the Hadar Fm., where they occur in all members at Hadar itself, as well as at Dikika (Geraads et al. 2010). The environmental significance of this difference, if any, is not clear at present.

There is a potentially significant difference between the Tulu Bor Mb. and other sites in eastern Africa regarding the representation of Hyaenidae. In the Tulu Bor Mb., the Hyaenidae are *C. eturono* and *H. cf. H. hyaena* (possibly *Ikelohyaena*). At other sites, the dominant hyenid is *Crocuta dietrichi*, which does not occur at Koobi Fora until the Upper Burgi Mb. (unless the right distal tibia ER
3103 from the Lokochot Mb., here referred to C. cf. *C. dietrichi* in fact does belong in this species). *Crocuta dietrichi* is almost ubiquitous at sites of this age (Werdelin and Lewis 2008), making the Tulu Bor Mb. unusual. *Ikelohyaena* has also been tentatively identified from the Sidi Hakoma Mb. at Hadar, but elsewhere the second hyena is a small *Hyaena* similar to and probably identical with the *H. cf. H. makapani* identified at Koobi Fora from the Upper Burgi and KBS Mbs.

The presence of Lutrinae is strongly dependent on local environmental conditions, specifically the presence of at least moderately large, permanent bodies of water. In the case of *Enhydriodon* spp. one would expect that these water bodies would be quite large, although Geraads et al. (2011) have suggested that at least *E. dikikae* was mostly terrestrial based on the weak humeral medial epicondyle, an element not represented at Koobi Fora. Interestingly, *Enhydriodon* is present at nearly all sites, although there may be differences at the species level. The only sites where the genus is not present are South Turkwel, the Middle and Upper parts of the Lomekwi Mb., and the Kada Hadar Mb. Of these, only the Kada Hadar is reasonably well sampled. This is a strong demonstration of the importance of *Enhydriodon* in the faunas of this time, but also that sites near large bodies of standing water are selectively sampled in the fossil record. There are no specimens from other sites comparable to the poorly understood Tulu Bor Mb. mustelids aff. *Plesiogulo* sp. and aff. *Ictonyx* sp.

The representation of Felidae is almost identical at all sites, taking into account the small samples from some of them. The only interesting aspect worth mentioning is the absence of *Dinofelis* from the Kada Hadar Mb. *Dinofelis* is common in eastern Africa from ca 4 – 1.5 Ma (Werdelin and Lewis 2001), so this is an unusual absence.

In summary, during the time interval represented by the Tulu Bor Mb. there are some important inter- and intra-basinal differences in the carnivoran communities of eastern Africa. These differences are particularly clear in the Canidae and Hyaenidae. Among the former, differences are mainly between the Turkana and lower Awash basins, while among the latter, differences are between Koobi Fora and other sites. Only increased sampling and further analysis can say what these differences might mean in terms of local environmental or other conditions.

**UPPER BURGI MEMBER**

From the time interval represented by the Upper Burgi Mb. onwards, the number of comparative faunas drops off precipitously. Shungura Fm., Members D and E+F are well-sampled, but fall within the Burgi hiatus at Koobi Fora, while Members H, K, and L are very poorly sampled, including only one or two carnivoran species. In West Turkana, the Lokalalei Mb. lies in the Burgi hiatus, while the Kaitio, Natoo, and Nariokotome Mbs include only one or two carnivoran species. For comparison with the Upper Burgi Mb., only Shungura Fm. Mb. G, Nachukui Fm. Kalochoro Mb., and Olduvai Bed I (recently redated by Deino 2012) remain. And even this is optimistic, in that they only partially overlap in time with the Upper Burgi Mb. In addition, the Kalochoro Mb. includes only four carnivoran species.

The limited comparisons available show considerable differences between Mb. G, Olduvai Bed I, and the Upper Burgi Mb., while all taxa present in the Kalochoro Mb. are also present in the Upper Burgi Mb. Among
Mustelidae, Lutrinae dominate in the Upper Burgi Mb., while they are absent or nearly so from Mb. G and Bed I. Vierriidae are quite diverse in the Upper Burgi Mb., but much less so in Mb. G and Bed I. The only viverrid these faunas have in common is the aberrant Pseudocivetta ingens. The Hyaenidae representation is more similar, though with some differences. The Upper Burgi Mb. has Crocuta dietrichi and C. ultra, as well as Hyaena cf. H. makapani, while Mb. G and Bed I have C. ultra only, and H. hyaena. Member G lacks Dinofelis, which is present in both the Upper Burgi Mb. and Bed I (though different species are present), while Bed I lacks the otherwise nearly ubiquitous Homotherium.

Overall, differences between the eastern and northern parts of the Turkana Basin are more distinct in the Upper Burgi time interval than in the Pliocene intervals. This is surprising considering the close geographic proximity of these sub-basins. However, the varying distribution of Lutrinae can be explained by local proximity to large bodies of water and at least some of the other differences can be explained by sampling effects. Nevertheless, these differences need to be explored further in the future, as the faunas are analyzed in greater detail.

**KBS AND OKOTE MEMBERS**

When we reach the time of the KBS and Okote Mbs comparative faunas become even fewer. In fact, only Olduvai Bed II is sufficiently well sampled and studied to serve in this capacity. Bed II overlaps in time with both the KBS and Okote Mbs, and they are therefore treated together.

Detailed comparison shows that the KBS Mb. includes a jackal-sized canid, Lupulella sp., whereas Bed II includes a hunting dog-sized canid, Canis (or Xenocyon) falconeri. The KBS Mb. and Bed II share the presence of cf. Aonyx sp. (unlikely to represent the same taxon but probably related), but the Koobi Fora Mbs also include other Lutrinae, not present at Olduvai. The KBS Mb. and Bed II further share the presence of Pseudocivetta ingens (possibly also present in the Okote Mb). All three faunas include Crocuta ultra, but differ in which Hyaena species are present (H. cf. H. makapani and H. cf. H. hyaena at Koobi Fora, H. hyaena at Olduvai). Finally, the only shared Felidae are Dinofelis (though different species at Koobi Fora and Olduvai), Panthera leo, and P. pardus (the latter not present in the Okote Mb., possibly due to sampling). Olduvai Bed II lacks the derived sabertooth genera Megantereon and Homotherium, as well as Acinonyx sp.

In summary, faunas of this late time period show considerable differences between Koobi Fora and Olduvai. Unfortunately, the lack of other well-sampled carnivoran faunas from this time period makes it impossible to say which of these regions is the ‘odd one out,’ or if both are. Description of coeval carnivoran faunas from other parts of eastern Africa is eagerly awaited.

**SUMMARY**

To the extent that any pattern can be discerned from these admittedly rather meager data, it is one of increasing inter-basinal differentiation through time. This is in contrast to a previous pan-African analysis indicating reduced inter-regional differentiation through time (Werdelin 2008). The combination of these patterns suggests the preliminary hypothesis that the increased inter-basinal differentiation overrides regional differences. Much more work on carnivrans is required to confirm
or falsify this hypothesis. In addition, comparison with other taxonomic or ecological groups needs to be made to determine whether this pattern is specific to carnivorans or part of a larger biogeographic pattern.

REFERENCES


# APPENDIX I

## SPECIMEN ALLOCATION TABLES

### Specimen list for *Lupulella* sp.

<table>
<thead>
<tr>
<th>MEMBER AREA</th>
<th>SPECIMEN №</th>
<th>SPECIMEN DESCRIPTION</th>
<th>FIGURE №</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Burgi</td>
<td>KNM-ER 3741</td>
<td>A: lt radius; B: lt metacarpal 4; C: lt metacarpal 5; D: lt pisiform; E: rt horizontal mandibular ramus with damaged m1, roots of m2; F: rt horizontal mandibular ramus with roots of p1-p3; G: lt ulna lacking distal end</td>
<td>3.3a-b; 3.4a-b; 3.5; 3.6a-b</td>
</tr>
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<td>105</td>
<td>KNM-ER 3767</td>
<td>cranium with lt C root, P1-P2, root of P3, rt C root, P1-M2</td>
<td>3.1a-c</td>
</tr>
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<td>116</td>
<td>KNM-ER 3755</td>
<td>rt horizontal mandibular ramus with roots of m2-m3</td>
<td></td>
</tr>
<tr>
<td>123</td>
<td>KNM-ER 44951</td>
<td>cranium with lt I2-P2, rt I2.I3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>KNM-ER 45536</td>
<td>lt metacarpal 5</td>
<td>3.6c</td>
</tr>
<tr>
<td></td>
<td>KNM-ER 45538</td>
<td>rt horizontal mandibular ramus with roots of p1-p3</td>
<td></td>
</tr>
<tr>
<td>KBS</td>
<td>KNM-ER 895</td>
<td>rt horizontal mandibular ramus with p4-m2</td>
<td>3.2d-f</td>
</tr>
<tr>
<td>104</td>
<td>KNM-ER 895</td>
<td>rt horizontal mandibular ramus with c and p3</td>
<td></td>
</tr>
<tr>
<td>105</td>
<td>KNM-ER 668</td>
<td>rt horizontal mandibular ramus with c, broken p2, p3, p4, m1 roots, m2, root of m3</td>
<td>3.2a-c</td>
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<td>Unknown</td>
<td>KNM-ER 332</td>
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### Specimen list for *Vulpes* sp.

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<th>FIGURE №</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Burgi/KBS</td>
<td>KNM ER 3121</td>
<td>rt horizontal mandibular ramus with p2 roots, p3</td>
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### Specimen list for cf. Canidae

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</tr>
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<tbody>
<tr>
<td>KBS</td>
<td>KNM-ER 44131</td>
<td>rt mandibular ramus fragment with roots of p3-m1</td>
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Specimen list for *Enhydridodon afman*

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<th>SPECIMEN DESCRIPTION</th>
<th>FIGURE №</th>
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</thead>
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<tr>
<td>Lokochot 117</td>
<td>KNM-ER 3110</td>
<td>lt horizontal mandibular ramus with p4 root and m1</td>
<td>4.1a-c</td>
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Specimen list for *Enhydridodon cf. E. afman*

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</tr>
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<tbody>
<tr>
<td>Lonyumun 204</td>
<td>KNM-ER 3107</td>
<td>rt astragalus</td>
<td>4.2a-b</td>
<td></td>
</tr>
<tr>
<td>Tulu Bor 117</td>
<td>KNM-ER 3108</td>
<td>lt m2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KNM-ER 3871</td>
<td>lt i3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper Burgi 123</td>
<td>KNM-ER 44722</td>
<td>rt damaged M1</td>
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Specimen list for cf. *Enhydridodon sp.*

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<td>A: rt metacarpal 2; B: distal metacarpal 3?; C: distal metacarpal 2/4?; E: caudal vertebra 1/2; F: thoracic vertebra middle? transverse process; G: lumbar vertebra spinous process fragment; H: cervical vertebra centrum</td>
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### Specimen list for *Torolutra* cf. *T. ougandensis*

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</thead>
<tbody>
<tr>
<td>Upper Burgi 106</td>
<td>KNM-ER 4568</td>
<td>rt horizontal mandibular ramus with broken p3, p4-m1</td>
<td>4.4a-c</td>
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<tr>
<td>KNM-ER 5895</td>
<td>A: cranium fragment with lt I3, C, P4, M1, alveoli for I1-I2, roots of rt C, P2-P3, alveoli for I1, I3, P1; B: mandible with lt p2-m1, rt ramus broken; C: mandible fragments; D: maxilla with dentition in matrix; E: rt horizontal mandibular fragment with p4-m1; F: cervical vertebra 7; G: cervical vertebra 3; H: cervical vertebra 5; I: cervical vertebra 6; J: thoracic vertebra 1; K: thoracic vertebra 3?; L: thoracic vertebra, last; M: lumbar vertebra 1; N: thoracic vertebra, mid to lower; O: thoracic vertebra 2; P: axis; Q: cervical vertebra 4; R: lt scapula glenoid; S: bone fragments; T: distal rt humerus; U: vertebra fragment; V: mandible fragment; W: vertebra fragment; X: bone fragment; Y: vertebra fragment; Z: mandible fragment; AA: incisor; AB: lt metatarsal 3; AC: lt metatarsal 4; AD: rt metatarsal 4; AE: rib fragment; AF: rib fragment; AG: rib fragment; AH: rib fragment; AI: rib fragment; AJ: rib fragment; AK: rib fragment; AL: rib fragment; AM: rib fragment; AN: rib fragment; AO: rib fragment; AP: rib fragment; AQ: rib fragment; AR: rib fragment; AS: cervical vertebra centrum; AT: cranium fragment; AU: manubrium fragment</td>
<td>4.3a-e; 4.5a-l</td>
<td></td>
</tr>
<tr>
<td>KBS 8B</td>
<td>KNM-ER 44462</td>
<td>rt horizontal mandibular ramus with p3-m1</td>
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### Specimen list for *cf. Torolutra* sp.

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<td>Upper Burgi 105</td>
<td>KNM-ER 4406</td>
<td>A-C: lt humerus, 3 pieces</td>
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<td>KNM-ER 5671</td>
<td>proximal rt femur lacking head and neck</td>
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<td></td>
</tr>
<tr>
<td>KNM-ER 5672</td>
<td>lt femur lesser trochanter and gluteal tuberosity</td>
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<td>KNM-ER 5673</td>
<td>distal lt humerus shaft fragment</td>
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<td>KNM-ER 5674</td>
<td>lt humerus shaft</td>
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263
Specimen list for cf. *Torolutra* sp. (cont.)

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<th>SPECIMEN DESCRIPTION</th>
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<td>KBS</td>
<td>103</td>
<td>KNM-ER 6076</td>
<td>A: proximal rt ulna; B: proximal rt humerus; C: proximal lt ulna; D: lt radius missing distal epiphysis; E: bone fragments (28); F: lt astragalus fragment; G: rt patella; H: lt patella fragment; I: thoracic vertebra centrum; J: lt navicular; K: proximal lt metatarsal 4; L: proximal phalanges (5); M: cervical vertebra centrum fragment; N: rt cuboid; O: proximal rt metatarsal 3; P: lt cuboid fragment; Q: distal ulna fragment; R: proximal rt metatarsal V; S: distal rt fibula; T: distal rt metatarsal; U: distal lt metacarpal V?; V: metatarsal? 1? lacking head; W: distal metapodial; X: lt entocuneiform</td>
<td>4.7a; 4.8a-d; 4.9a-c; 4.12a-h</td>
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<td>Okote</td>
<td>11</td>
<td>KNM-ER 44574</td>
<td>A: lt metacarpal 2 fragment; B: lt metacarpal 5</td>
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<td>Unknown</td>
<td>KNM-ER 48</td>
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<td>KNM-ER 75</td>
<td>proximal lt femur</td>
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<td>KNM-ER 76</td>
<td>distal lt femur</td>
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Specimen list for *Hydrictis gudho*

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<th>SPECIMEN DESCRIPTION</th>
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<tr>
<td>Upper Burgi</td>
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<td>KNM-ER 1486</td>
<td>neurocranium and posterior lt and rt mandibular rami with broken lt p4, m1, rt m1</td>
<td>4.13a-e</td>
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Specimen list for cf. *Hydrictis* sp.

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<th>SPECIMEN DESCRIPTION</th>
<th>FIGURE №</th>
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</thead>
<tbody>
<tr>
<td>Upper Burgi</td>
<td>105</td>
<td>KNM-ER 3778</td>
<td>A: cranium with broken P2-P4; B: rt ulna fragment of semilunar notch</td>
<td>4.14a-c</td>
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<tr>
<td>KBS</td>
<td>104</td>
<td>KNM-ER 395</td>
<td>cranium fragment with roots of lt P2-P3</td>
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Specimen list for cf. *Aonyx* sp.

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<tr>
<td>KBS</td>
<td>124</td>
<td>KNM-ER 5040</td>
<td>rt femur</td>
<td>4.15a-e</td>
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### Specimen list for Lutrinae gen. et sp. nov.

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<tr>
<td>Upper Burgi</td>
<td>102 (GAJ13)</td>
<td>KNM-ER 3881</td>
<td>lt femur</td>
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### Specimen list for Lutrinae gen. et sp. indet.

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<tr>
<td>Upper Burgi</td>
<td>130</td>
<td>KNM-ER 2036</td>
<td>A: proximal lt humerus; B: distal rt femur; C: proximal rt tibia; D: rt humerus shaft fragment; E: distal lt humerus shaft fragment; F: cranium frontal fragment; G: maxilla fragment with roots of ?I1, I2; H: cranium fragment with tooth root; I: sacrum; J: rt os coxae acetabulum fragment; K: distal rt metacarpal? IV?; L: rib fragment; M: middle thoracic vertebra centrum; N: lumbar vertebra centrum; O: thoracic vertebra centrum; P: sternebra fragment; Q: thoracic vertebra centrum fragment; R: middle caudal vertebra; S: middle caudal vertebra; T: vertebra neural spine; U: rt calcaneum distal fragment; V: cranium? fragments (4)</td>
<td>4.17a-j</td>
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### Specimen list for Mellivora sp.

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<tr>
<td>Upper Burgi</td>
<td>130</td>
<td>KNM-ER 3760</td>
<td>rt mandibular ramus fragment with m1</td>
<td>4.18a-c</td>
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<tr>
<td>Okote</td>
<td>8A</td>
<td>KNM-ER 44387</td>
<td>rt femur, os coxae fragments</td>
<td>4.19a-b</td>
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### Specimen list for Mustelidae indet. aff. Plesiogulo sp.

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<tr>
<td>Tulu Bor</td>
<td>203</td>
<td>KNM-ER 5476</td>
<td>distal lt femur</td>
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Specimen list for Mustelidae indet. aff. *Ictonyx* sp.

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<tr>
<td>Tulu Bor</td>
<td>117</td>
<td>KNM-ER 3097</td>
<td>rt calcaneum</td>
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Specimen list for Mustelidae indet.

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<tr>
<td>Lokochot</td>
<td>117</td>
<td>KNM-ER 3104</td>
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<tr>
<td>Upper Burgi</td>
<td>105</td>
<td>KNM-ER 1499</td>
<td>rt maxilla with broken P4</td>
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<tr>
<td></td>
<td>123</td>
<td>KNM-ER 44651</td>
<td>lt i3?</td>
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<td>KBS</td>
<td>103</td>
<td>KNM-ER 5422</td>
<td>phalanx, terminal</td>
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<tr>
<td></td>
<td>105</td>
<td>KNM-ER 3752</td>
<td>proximal rt ulna</td>
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<td>KNM-ER 4437</td>
<td>canine fragment</td>
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Specimen list for cf. *Agriotherium* sp.

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<td>Lonyumun/Tulu Bor</td>
<td>204</td>
<td>KNM-ER 3106</td>
<td>rt proximal fem fragment</td>
<td>5.3a-c</td>
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<tr>
<td>Tulu Bor</td>
<td>203</td>
<td>KNM ER 2012</td>
<td>A: rt distal femur fragment; B: rt proximal femur fragment</td>
<td>5.1a-b; 5.2a-b</td>
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Specimen list for cf. *Civettictis* sp.

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<td>KNM-ER 3749</td>
<td>splanchnocranium with roots of lt and rt P2-M1</td>
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<td></td>
<td>105</td>
<td>KNM-ER 1663</td>
<td>cranial fragment</td>
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<td>Chari</td>
<td>103</td>
<td>KNM-ER 5342</td>
<td>neurocranium</td>
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## Specimen list for *Pseudocivetta ingens*

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<tr>
<td>Upper Burgi</td>
<td>105 KNM-ER 3757</td>
<td>rt M1</td>
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<tr>
<td>KBS 8B</td>
<td>KNM-ER 44505</td>
<td>Skeletal parts including pelvis, vertebrae, metapodial, posterior part of rt m1</td>
<td>6.2a-c; 6.3a-b</td>
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<td></td>
<td>119 KNM-ER 2134</td>
<td>rt m1</td>
<td>6.1a-c</td>
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<td></td>
<td>130 KNM-ER 2011</td>
<td>isolated I3, lt? M1-M2</td>
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<td>Unknown</td>
<td>11 KNM-ER 44291</td>
<td>isolated lt P1?, P4?, M1, M2</td>
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## Specimen list for Viverridae indet. aff. *Civetictis* sp.

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<th>FIGURE №</th>
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<tbody>
<tr>
<td>Upper Burgi</td>
<td>102 KNM-ER 878</td>
<td>lt horizontal mandibular ramus with roots of p4-m1</td>
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<tr>
<td></td>
<td>123 KNM-ER 44717</td>
<td>rt P4</td>
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<tr>
<td>Unknown</td>
<td>KNM-ER 7726</td>
<td>m1 fragment</td>
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## Specimen list for Viverridae indet aff. *Genetta* sp.

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<td>Upper Burgi</td>
<td>105 KNM-ER 5677</td>
<td>A: neurocranium; B: rt maxilla fragment with I3?; C: distal scapula</td>
<td>6.12</td>
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## Specimen list for cf. *Pseudocivetta* sp.

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<tr>
<td>Upper Burgi</td>
<td>KNM-ER 2014</td>
<td>A: proximal phalanx; B: proximal phalanx, proximal end; C: proximal phalanx distal end</td>
<td>6.6a-c</td>
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<td>KBS 10</td>
<td>KNM-ER 5339</td>
<td>cranium with lt and rt I1-P4</td>
<td>6.4a-c</td>
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<tr>
<td></td>
<td>KNM-ER 5340</td>
<td>lt? m2 and M2</td>
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<tr>
<td>KBS/Okote 103</td>
<td>KNM-ER 3763</td>
<td>proximal rt tibia</td>
<td>6.5</td>
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### Specimen list for *Genetta genetta or Genetta maculata*

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<tr>
<td>Upper Burgi</td>
<td>130</td>
<td>KNM-ER 3123</td>
<td>lt maxilla with P3-P4 and dp4?</td>
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<tr>
<td></td>
<td>123</td>
<td>KNM-ER 44716</td>
<td>lt maxilla with P3, roots of P4, M1</td>
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<tr>
<td>Okote</td>
<td>8</td>
<td>KNM-ER 979</td>
<td>Palate with lt C, P2-P4, rt P1-M2</td>
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<tr>
<td></td>
<td>8A</td>
<td>KNM-ER 44365</td>
<td>lt mandible fragment with m1</td>
<td>6.9a-c</td>
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### Specimen list for *Genetta nyakitongwer*

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<th>SPECIMEN DESCRIPTION</th>
<th>FIGURE №</th>
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<tr>
<td>KBS?</td>
<td>104</td>
<td>KNM-ER 46408</td>
<td>lt mandibular ramus with p1 alveolus, broken p2, p3-m1, broken m2</td>
<td>6.10a-c</td>
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### Specimen list for Viverridae indet. sp. A

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<th>FIGURE №</th>
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<tbody>
<tr>
<td>Upper Burgi</td>
<td>Unknown</td>
<td>KNM-ER 702</td>
<td>rt humerus shaft</td>
<td>6.13a-c</td>
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### Specimen list for Viverridae indet. sp. B

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<th>FIGURE №</th>
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<tbody>
<tr>
<td>Tulu Bor</td>
<td>116</td>
<td>KNM-ER 3754</td>
<td>proximal lt femur</td>
<td>6.14a1-d1</td>
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APPENDIX 1

Specimen list for Viverridae indet cf. sp. B

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<tr>
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<tr>
<td>KBS</td>
<td>105</td>
<td>KNM-ER 3797</td>
<td>proximal lt femur</td>
<td>6.14a2-d2</td>
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Specimen list for Viverridae indet sp. C

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<tr>
<td>Upper Burgi</td>
<td>130</td>
<td>KNM-ER 2034</td>
<td>proximal lt femur</td>
<td>6.14a3-d3</td>
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Specimen list for cf. Viverridae indet A

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<tr>
<td>Unknown</td>
<td>Unknown</td>
<td>KNM-ER 1347</td>
<td>proximal lt femur</td>
<td>6.16a4-d4</td>
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Specimen list for Viverridae indet. or Herpestidae indet.

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<tr>
<td>KBS</td>
<td>119</td>
<td>KNM-ER 5235</td>
<td>splanchnocranium with roots of I1-P2</td>
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<tr>
<td>Okote</td>
<td>7A</td>
<td>KNM-ER 43965</td>
<td>cranial fragments including occipital and parietals, lumbar vertebra</td>
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<td>SPECIMEN DESCRIPTION</td>
<td>FIGURE №</td>
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<tr>
<td>Tulu Bor 117</td>
<td>KNM-ER 3748</td>
<td>rt mandibular ramus with roots of p4-m1</td>
<td>7.1a-c</td>
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<th>FIGURE №</th>
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<tr>
<td>Tulu Bor-KBS 102</td>
<td>KNM-ER 2119</td>
<td>lt metacarpal 2</td>
<td>7.2a</td>
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<td>KBS 12</td>
<td>KNM-ER 699</td>
<td>lt metacarpal 4</td>
<td>7.3</td>
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<th>FIGURE №</th>
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<tr>
<td>Upper Burgi 130</td>
<td>KNM-ER 3753</td>
<td>lt p2</td>
<td>7.4a-b; 7.5a-k; 7.6a-g; 7.7a-e; 7.14a</td>
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<tr>
<td>131</td>
<td>KNM-ER 721</td>
<td>A: thoracic vertebra 12; B: lumbar vertebra 1; C: lumbar vertebra 4; D: thoracic vertebra 4; E: lumbar vertebra 2; F: thoracic vertebra 11; G: thoracic vertebra 7/8; H: mandible with lt il-m2, rt il-m1; I: rt os coxae lacking pubis; J: proximal lt tibia; K: axis; L: atlas; M: ilium fragment; N: lt scapula; O: sacrum; P: thoracic vertebra 10; Q: distal lt humerus; R: thoracic vertebra 5; S: lumbar vertebra 5; T: rt calcaneum; U: thoracic vertebra 13; V: caudal vertebra 2?; W: proximal rt metacarpal 4; X: proximal rt metacarpal 5; Y: distal lt metacarpal 4?; Z: distal rt metacarpal 5; AA: humerus? shaft fragment; AB: caudal vertebra 4?; AC: rib fragments (36); AD: thoracic vertebra 14/15; AE: bone fragments; AF: caudal vertebra 5?; AG: caudal vertebra 3?</td>
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<tr>
<td>Upper Burgi? 15?</td>
<td>KNM-ER 3109</td>
<td>rt mandibular ramus with p2, p3 roots, damaged p4, m1</td>
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### Specimen list for Crocuta cf. C. dietrichi

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<td>Lokochot</td>
<td>117 KNM-ER 3103</td>
<td>distal rt tibia</td>
<td>7.8b-c</td>
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<tr>
<td>Upper Burgi</td>
<td>100 KNM-ER 3761</td>
<td>rt metacarpal 2</td>
<td>7.2b</td>
</tr>
<tr>
<td></td>
<td>104 KNM-ER 361</td>
<td>neurocranium</td>
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<td></td>
<td>105 KNM-ER 1541</td>
<td>rt cranium fragment with P3-P4</td>
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<td>116 KNM-ER 3745</td>
<td>A: distal rt femur; B: lt horizontal mandibular ramus with roots of p2-m1</td>
<td>7.8a</td>
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<tr>
<td>Unknown</td>
<td>130 KNM-ER 654</td>
<td>lt tibia shaft</td>
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### Specimen list for Crocuta ultra

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<th>FIGURE №</th>
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<tr>
<td>Upper Burgi</td>
<td>10 KNM-ER 970</td>
<td>A: proximal rt ulna; B: proximal lt ulna; C: proximal rt radius; D=E: proximal let radius; F: distal rt humerus; G: lt calcaneum; H: rt navicular; I: rt cuboid; J: proximal rt metatarsal III; K: lt scapholunar; L: rt scapholunar; M: proximal lt metacarpal 5; N+AB: rt metacarpal 5; O+S: rt metacarpal 3; P+AA: proximal rt metacarpal 2; Q: lt cuneiform; R: terminal phalanx digit 3, manus?; T: middle phalanx; U: lt mesocuneiform; V: lt femur greater trochanter fragment; W: proximal rt metatarsal 5; X: terminal phalanx digit 2?; Y: terminal phalanx fragment; Z: lt terminal phalanx digit 1, manus; AC: distal rt metacarpal 4?; AD: lt pisiform, ventral part; AE: lt proximal phalanx digit 1, manus; AF: middle phalanx fragment, manus; AG: proximal phalanx digit 3 or 4 fragment; AH: rt pisiform fragment; AI: proximal rt metacarpal 4; AJ: distal lt metacarpal 1; AK: rt ilium fragment; AL: ischium fragment; AM: rt ulna shaft fragment; AN: scapula fragment; AO: distal rt fibula; AS: middle phalanx; AT: lt petrosal; AU: distal rt metacarpal I; AV: rt ectocuneiform</td>
<td>7.2c; 7.12a-p; 7.14b; 7.16c;</td>
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<td>Upper Burgi?</td>
<td>102 KNM-ER 2008</td>
<td>lt ulna lacking olecranon and distal end</td>
<td>7.15a, b</td>
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<tr>
<td>Upper Burgi/KBS</td>
<td>104 KNM-ER 896</td>
<td>A: rt horizontal mandibular ramus with c-m1; B: rt mandibular condyle</td>
<td>7.9a-c</td>
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<tr>
<td>KBS</td>
<td>8B KNM-ER 44433</td>
<td>lt p3</td>
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<td>103 KNM-ER 358</td>
<td>lt horizontal mandibular ramus with c-p4, broken m1</td>
<td>7.11a-c</td>
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Specimen list for *Crocuta ultra* (cont.)

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<td>A: rt horizontal mandibular ramus fragment with roots of c-p3; B: rt horizontal mandibular ramus fragment with roots of p4-m1; C: proximal rt femur; D: rt p4 crown; E: cervical vertebra ventral half of centrum; F: distal tibia; G: middle phalanx; H: distal metatarsal 3?; I: rib fragment; J: mandible fragment; K: mandible fragment</td>
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<td>A: damaged cranium with lt C-P4, rt I1-P4; B: lt horizontal mandibular ramus with c-m1; C: premolar fragment; D: rib and skull fragments; E: rib and skull fragments; F: rib and skull fragments; G: rib and skull fragments; H: rib and skull fragments; I: rib and skull fragments; J: rib and skull fragments</td>
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<td>A: rt i3; B: lt c; C: lt i2; D: canine fragment; E: lt p2; F: lt p3; G: lt p4; H: lt m1; I: rt p2; J: rt p3; K: rt p4; L: rt m1; M: distal rt metatarsal 4; N: distal rt metatarsal 3; O: proximal rt radius; P: lt middle phalanx; Q: caudal vertebra; R: caudal vertebra; S: caudal vertebra; T: caudal vertebra; U: rt femur head; V: lt os coxae fragment; W: patella; X: ilium fragment; Y: bone fragments large; Z: bone fragments small</td>
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### Specimen list for *Crocuta* *cf*. *C. ultra*

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<td>A: distal femur; B: femur shaft fragment; C: femur shaft fragment; D: proximal tibia; E: os coxae acetabulum and ilium; F: proximal rt radius; G: rt navicular; H: proximal lt metacarpal 2; I: mandible fragment with lt roots of p3-p4, rt roots of c-p3; J: proximal rt ulna lacking olecranon; K: rt calcaneum; L: cervical vertebra fragments (2); M: rib fragments; N: rt astragalus; O: bone fragments</td>
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### Specimen list for *Crocuta* *sp.*

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### Specimen list for *cf. Crocuta*

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### Specimen list for *Hyaena cf. H. makapani*

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<td>KNM-ER 3766</td>
<td>cranium and mandible with lt and rt 11-M1, 11-m1</td>
<td>7.22a-d; 7.24a-j; 7.25a-e</td>
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<td>131</td>
<td>KNM-ER 1548</td>
<td>A: cranium with lt and rt 11-M1; B: mandible with lt i2-m1, rt i1-m1; C: atlas; D: rt scapula; E: lt proximal radius; F: lt humerus distal and shaft; G: proximal lt ulna; H: thoracic vertebra 13?; I: thoracic vertebra 10?; J: thoracic vertebra 11?; K: thoracic vertebra 12?; L: caudal vertebra; M: caudal vertebra; N: caudal vertebra; O: caudal vertebra; P: caudal vertebra; Q: rib fragments; R: rib fragments; S: rib fragments; T: rib fragments; U: rib fragments; V: rib fragments; W: rib fragments; X: rib fragments; Y: rib fragments; Z: rib fragments; AA: rib fragments (5); AB: rt scapholunar; AC: rt unciform; AD: rt magnum; AE: rt trapezoid; AF: rt trapezium?; AG: rt metacarpal 4; AH: rt metacarpal 3; AI: rt metacarpal 2; AJ: rt metacarpal 5; AK: distal rt metatarsal 4?; AL: distal rt metatarsal 2?; AM: distal rt metatarsal 3?; AN: distal rt metatarsal 5?; AO: middle phalanx digit 5; AP: proximal lt tibia; AQ: fibula? shaft fragment; AR: proximal rt femur shaft; AS: distal lt radius; AT: distal rt humerus; AU: sesamoids (17); AV: rib fragments (8); AW: lt middle phalanx digit 2; AX: rt middle phalanx digit 2; rt middle phalanx digit 3; rt middle phalanx digit 4; BA: lt middle phalanx digit 3; BB: lt middle phalanx digit 4; BC: lt middle phalanx digit 5; BD: lt terminal phalanx digit 3; BE: lt terminal phalanx digit 4; BF: rt terminal phalanx digit 4; BG: rt terminal phalanx digit 3; BH: lt terminal phalanx digit 2?; BI: terminal phalanx; BJ: lt terminal phalanx digit 5; BK: rt terminal phalanx digit 2?; BL: caudal vertebra; BM: vertebra fragment; BN: bone fragments; BO: lt proximal phalanx digit 3; BP: rt proximal phalanx digit 2; BQ: lt proximal phalanx digit 3; BS: lt proximal phalanx digit 4; BT: rt proximal phalanx digit 4; BU: lt proximal phalanx digit 5; BV: rt proximal phalanx digit 5; BW: distal rt ulna</td>
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APPENDIX 1

KBS 101 KNM-ER 1666 A: bone fragments; B: lt metacarpal V; C: proximal rt metatarsal 3; D: rib fragments (3); E: fibula fragment; F: bone fragments; G: axis fragment; H: thoracic vertebra 13; I: bone fragments; J: lt P4; K: lt p4; L: rt p4 fragment; M: lt m1; N: canine fragment; O: rt m1 fragment; P: incisors (2); Q: tooth fragment; R: tooth fragment; S: ?p4 fragment; T: thoracic vertebra 4; V: rt mandible fragment; W: mandibular condyle fragment; X: lt ulna distal 2/3; Y: lt mandibular fragment with posterior root of p4, roots of m1; Z: rt mandibular condyle fragment; AA: cervical vertebra, caudal process fragment; AB: cervical vertebra 4/5 fragment; AC: cervical vertebra 3; AD: rt metatarsal 2; AE: distal lt metacarpal 2AF: mid-cervical vertebra anterior part of centrum; AG: axis spinous process tip; AH: lt ischium fragment; AI: lt os coxae acetabulum fragment; AK: vertebra fragments (8); AL: vertebra fragments (5); AV: vertebra fragment; AW: rt I3; AX: cranium fragment; AY: incisor; AZ: incisor; BA: innominate fragment; BB: premolar fragment; BC: incisor; BD: bone fragments (81); BE: thoracic vertebra centrum (last?) BF: lumbar vertebra 4 centrum

Unknown Unknown KNM-ER 2239 rt ulna proximal and shaft

Specimen list for *Hyaena* cf. *H. hyaena*

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<td>KBS 133 (FxJ24)</td>
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<td>lt horizontal mandibular ramus with c-m1</td>
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Specimen list for *Hyaena* sp.

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Specimen list for cf. *Parahyaena* sp.

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Specimen list for Hyaenidae indet. sp. A

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Specimen list for *Hyaenidae* indet.

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### Specimen list for *Megantereon whitei*

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<td>KNM-ER 701</td>
<td>A: rt horizontal mandibular ramus with m1; B: lt distal p4; C: lt? distal? p3; D: lt c; E: lt i3 fragment; F: lt i1; G: lt i1 root and i2; H: rt i2; I: rt P4; J: rt? C; K: lt? C; L: lt i2 and I3; M: bone fragments (19)</td>
<td>8.11d-f</td>
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<td>9A</td>
<td>KNM-ER 793</td>
<td>A: damaged cranium with lt I1-I3, C root, P3-M1, rt I1-I3, C root, P3 alveolus, P4-M1; B: rt hemimandible with i1, i3-m1; C: bone fragments (13)</td>
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### Specimen list for cf. *Megantereon* sp.

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<td>KNM-ER 1662</td>
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<td>A: rt astragalus trochlea; B: lt magnum; C: lt unciniform; D: lt metacarpal I; E: rt metacarpal I fragment; F: rt? scapholunar fragment; G: metapodial heads; I: rt proximal phalanx digit 5, proximal part; J: rt trapezoid; K: metapodial shaft fragments; L: distal? tibia? fragment; M: femur condyle; N: bone fragments</td>
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### Specimen list for *Dinofelis petteri*

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<td>117</td>
<td>KNM-ER 2612</td>
<td>damaged cranium with lt and rt canine roots and nearly complete lt P3-P4, partial rt P3-P4</td>
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<td>KNM-ER 3880</td>
<td>partial skeleton—A: cranial fragments; B: rt I3; C: proximal rt ulna; D: distal lt radius; E: proximal rt humerus; F: proximal rt radius; G: distal lt radius shaft fragment; H: thoracic vertebra 1; I: cervical vertebra 5; J: cervical vertebra 7?; centrum; K: thoracic vertebra 2/3; L: cervical vertebra 3; M: cervical vertebra 6; N: cervical vertebra 4; O: axis; P: vertebrae (22); Q: rt mandibular horizontal ramus with i1-m1; R: lt mandibular horizontal ramus with p3-m1; S: cranial fragment; T: cranial fragment; U: zygomatic arch fragment; V: phalanx, proximal end; W: bone fragments; X: I</td>
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### Specimen list for *Dinofelis aronoki* (cont.)

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| KNM-ER 6112 | Unknown | rt metacarpal II |
| KNM-ER 987 | Unknown | lt femur |
### Specimen list for *Dinofelis piveteaui*

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<td>8.18; 8.19; 8.20</td>
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<td>KNM-ER 6024</td>
<td>lt humerus</td>
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<td>KNM-ER 40482</td>
<td>partial skeleton—A: lt maxilla fragment with P3-P4; B: rt maxilla fragment with P3-P4; C: lt horizontal mandibular ramus with c-m1; D: rt horizontal mandibular ramus with broken p3 and m1; E: frontal fragment; F: premaxilla with lt and rt I1-I3; G: rt C; H: lt C root; I: i3?; J: rt calcaneum; K: rt astragalus; L: distal lt radius fragment; M: lt metatarsal V; N: rt metacarpal V; O: distal rt metacarpal IV fragment; P: rt proximal phalanx digit 1; Q: caudal vertebra; R: lt middle phalanx digit 3/4; S: lt proximal phalanx digit 3, pes?; T: lt proximal phalanx digit 5, pes; U: bone fragment; V: cervical vertebra centrum; W: bone fragment; X: cervical vertebra fragment; Y: distal rt metatarsal V fragment; Z: cranial? fragment; AA: pisiform; AB: distal part of middle phalanx digit 2/5; AC: sesamoid; AD: proximal part of terminal phalanx; AE: rib fragment; AF: rib fragment; AG: rib fragment; AH: ssamoid fragment; AI: rt patella fragment; AJ: rt ulna shaft fragment; AK: rt ulna shaft fragment; AL bone fragments; AM: distal lt humerus; AN: rt os coxae fragment; AO: axis; AP: lumbar vertebra 3; AQ: rt metatarsal III; AR: rt metatarsal II; AS: lt patella fragment; AT: vertebrae (2); AU: vertebral centra fragments (5); AV: vertebra fragments (20); AW: rib fragments (12); AX: long bone shaft fragment; AY: bone fragments (16)</td>
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Specimen list for *Dinofelis piveteaui* (cont.)

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Specimen list for *Dinofelis sp.*

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### Specimen list for Machairodontinae indet.

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### Specimen list for Panthera pardus

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<td>A: proximal lt tibia; B: rt os coxae fragment; C: rt astragalus; D: lt calcaneum; E: metacarpal?; F: pisiform; G: caudal and cervical vertebrae; H. bone fragments (8)</td>
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<td>rt horizontal mandibular ramus with p4-m1, isolated rt c, lt m1</td>
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Specimen list for *Acinonyx* sp. nov.

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<td>A: proximal lt ulna; B: proximal rt ulna; C: proximal lt radius fragment; D: proximal rt radius fragment; E: lt scapula glenoid; F: distal lt humerus lateral shaft fragment; G: distal lt humerus medial fragment; H: distal lt humerus lateral fragment; I: rt humerus shaft fragment; J: rt humerus shaft fragment; K: lt humerus head; L: distal rt femur; M: distal lt humerus fragment; N: rt femur greater trochanter; O: proximal lt tibia; P: lt tibia distal end; Q: rt tibia distal end; R: distal lt tibia shaft; S: rt calcaneum; T: rt astragalus trochlea; U: lt scapholunar; V: distal fibula fragment; W: rt patella; X: carpal? fragment; Y: cranial fragment; Z: rt humerus lateral shaft fragment; AB: lumbar vertebra 4 centrum; AC: thoracic vertebra centrum; AD: axis spinous process; AE: thoracic vertebra centrum; AF: thoracic vertebra centrum; AG: lumbar vertebra anterior centrum; AH: thoracic vertebra centrum; AI: thoracic vertebra centrum; AJ: lumbar vertebra centrum posterior fragment; AK: thoracic vertebra centrum; AL: axis fragment; AM: cervical vertebra centrum; AN: vertebra fragment; AO caudal vertebra; AP: caudal vertebra fragment; AQ: caudal vertebra fragment; AR: vertebra fragment; AS: lumbar vertebra fragment; AT: cervical vertebra fragment; AU: vertebra fragment; BB: bone fragments (31); CC: bone fragments (27); CD: sesamoid; CE: femur midshaft fragment</td>
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Specimen list for cf. *Acinonyx* sp.

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<td>KNM-ER 3740</td>
<td>A: distal femur shaft; B: femur head fragment; C: rt maxilla fragment with broken P3; D: distal tibia shaft fragment; E+F: rt metatarsal IV ventral proximal articulation; G: vertebra fragment; H: bone fragment; I: fibula shaft fragment; J: rib fragment; K: rib fragment; L: rib 1 fragment; M: rib fragment</td>
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<td>Upper Burgi/KBS 123</td>
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### Specimen list for *Caracal* sp. or *Leptailurus* sp.

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<td>Tulu Bor</td>
<td>117</td>
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### Specimen list for Felinae indet.

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### Specimen list for Felidae indet.

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### CANIDAE

#### Upper dentition

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#### Forelimb

| Canidae | Radius Max Length | Radius Functional Length | Radius Max Head Width | Radius Min Head Width | Radius Medial shaft ML Width | Radius Distal Max Width | Ulna Medial Process Length | Ulna Mid trochlear notch Articular Width | Ulna Medial Shaft AP Width | Ulna Mid Trochlear Notch Height | Ulna Olecranon Process Length | Ulna Midshaft ML Width | Ulna Midshaft AP Width | Metacarpal Midshaft Length | Metacarpal Midshaft ML Width | Metacarpal Midshaft DV Width | Metacarpal Donal ML Width | Metacarpal Donal DV Width | Metacarpal Proximal ML Width | Metacarpal Proximal DV Width |
|---------|------------------|-------------------------|-----------------------|-----------------------|----------------------------|------------------------|-------------------------------|---------------------------------|----------------------------|---------------------------------|--------------------------|------------------------|------------------------|-----------------|-------------------|-----------------|-----------------|----------------------|-----------------|
| *Lupulella sp.* |     |     |     |     |     |     |     |      |      |     |     |     |     |     |     |     |     |     |     |     |     |     |
| ER 3741A| 145.9 | 141.9| 15.3| 11.3| 11.2| 6.8 | 24.2| 12.9  | 59.0  | 5.5  | 5.3  | 6.7 | 49.7 | 6.6 | 5.0 | 7.3 | 8.4 |     |     |     |     |
| ER 3741B|     |     |     |     |     |     |     |      |      |     |     |     |     |     |     |     |     |     |     |     |     |     |
| ER 3741C|     |     |     |     |     |     |     |      |      |     |     |     |     |     |     |     |     |     |     |     |     |     |
| ER 3741D|     |     |     |     |     |     |     |      |      |     |     |     |     |     |     |     |     |     |     |     |     |     |
| ER 3741G|     |     |     |     |     |     |     |      |      |     |     |     |     |     |     |     |     |     |     |     |     |     |
| ER 45536|     |     |     |     |     |     |     |      |      |     |     |     |     |     |     |     |     |     |     |     |     |     |
**MUSTELIDAE**

**Lower dentition**

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**Upper dentition**

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### Humerus

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ER 5895T: 17.0, 10.0, 15.2, 36.1

ER 3751: 29.0, 30.3, 26.0

ER 389: 110.7, 110.7, 28.9, 30.2, 20.6, 25.0, 11.0, 18.0, 17.6, 10.2, 17.5, 37.7

ER 4406A, B, C: 31.5, 33.6, 21.7, 26.2

ER 6076B: 36.0, 23.3, 30.0

ER 2036A: 27.8, 29.7, 21.9, 23.1
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# Metacarpals

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**Os coxae, patella, and tibia**

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**Tarsus**

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**Mustelidae indet. aff. Ictonyx sp.**

| ER 3097                  | 41.7                 | 21.4                     |                          |                  |                       |                     |                   |                  |                |                |                |
### Metatarsals

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### Phalanges

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#### Lower Dentition

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