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Skeletal Pathology in *Pan troglodytes schweinfurthii* in Kibale National Park, Uganda

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KEY WORDS skeletal pathology; body size; chimpanzees; poaching; primate health

ABSTRACT The ecological pressures shaping chimpanzee anatomy and behavior are the subject of much discussion in primatology and paleoanthropology, yet empirical data on fundamental parameters including body size, morbidity, and mortality are rare for wild chimpanzees. Here, we present skeletal pathology and body size data for 20 (19 crania, 12 postcrania) chimpanzees (*Pan troglodytes schweinfurthii*) from Kibale National Park, Uganda. We compare these data with other East African populations, especially Gombe National Park. Estimated body size for Kibale chimpanzees was similar to other East African populations and significantly larger than Gombe chimpanzees. The high rates of trauma and other skeletal pathology evident in the Kibale chimpanzee skeletons were similar to those in the Gombe skeletal sample. Much of the major skeletal trauma in the Kibale skeletons was attributable to falls, although other pathologies were noted as well, including apparent injuries from snares, degenerative arthritis, and minor congenital abnormalities. Am J Phys Anthropol 000:000–000, 2008. © 2007 Wiley-Liss, Inc.

Comparison of long-term data from multiple populations of wild chimpanzees (*Pan troglodytes*) suggests that differences in local ecology translate into long-term differences in overall health, body size, and life span (Teleki, 1989; Chapman et al., 1999; Hill et al., 2001). However, detailed information about mortality and morbidity in wild chimpanzee populations is limited by the challenges of observing and recording pathology in the field. A noninvasive technique to evaluate long-term stress on population health is the analysis of skeletal and dental remains (Lovell, 1990a,b, 1991). In this study, we present new metric and pathological data from skeletal remains from chimpanzees in Kibale National Park (KNP), Uganda, and compare this skeletal population to similar data from chimpanzees in Gombe National Park, Tanzania.

Studies of skeletal and dental pathology in human skeletal populations have been instrumental in evaluating the history of disease, chronic nutritional stress, changes in subsistence strategy, mortality trends, and interpersonal conflict (e.g., Cohen and Armelagos, 1984; Buikstra and Mielke, 1985; Owsley and Jantz, 1994; Milner, 1995). The past three decades have seen a dramatic increase in the application of paleopathological methodology and theory to the study of nonhuman primate skeletons to better understand morbidity in free-ranging populations (e.g., Lovell, 1990a,b, 1991; Carter, 1991; DeGusta and Milton, 1998; Jurmain, 2000). In several notable studies, comparisons between skeletal pathology and life histories of known individuals at Gombe National Park, Tanzania (Jurmain, 1989; Kilgore, 1989; Sumner et al., 1989; Zihlman et al., 1990; Morbeck et al., 1991; Jurmain, 1997; Morbeck, 1999), and Karisoke Field Station, Rwanda (Lovell, 1990b), have even provided the opportunity to assess how the skeleton records injury and illness during life in wild chimpanzees and gorillas. However, the lack of other skeletal collections for African apes from other well-studied populations has precluded comparisons of skeletal health between populations.

Here, we present pathology and metric data for a skeletal collection of wild chimpanzees in Kibale National Park, Uganda. Using established indicators of skeletal pathology, we examine the incidence and possible sources of morbidity and mortality in the Kibale chimpanzees. We also compare the rates of pathology in the Kibale sample to those reported for the Gombe chimpanzee skeletal collection. Given the ecological relevance of body size, we also compare estimated mass and stature in the Kibale chimpanzees against other populations. Results are applied toward establishing a more complete understanding of body size and the sources and rates of morbidity and mortality in East African chimpanzees.

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TABLE 1. *Summary of Kibale chimpanzee skeletal remains*

Specimen number	Age: Category[a]	Age: Years	Provenience	Date of death	Manner of death	Cranium	Mandible	Pectoral girdle L	Pectoral girdle R	Humerus L	Humerus R	Ulna & radius L	Ulna & radius R	Manus L	Manus R	Pelves L	Pelves R
Females																	
KFB 17[e]	YA		Ngogo		Unknown	1	–	–	–	–	–	–	–	–	–	–	–
KFB 106	PA		Ngogo	Mar 1994	Unknown	1	1	1	1	1	1	1	1	2	1	1	1
KFB 3[b]	OA		Kanyawara		Unknown	1	1	1	1	1	1	1	–	1	–	1	1
KFB 18[e]	OA		Kingo/Ngogo[f]		Unknown	1	–	–	–	–	–	–	–	–	–	–	–
KFB 150	OA	>31	Kanyawara	May 1997	Killed by farmer[c]	1	1	1	1	1	1	1	1	2	2	1	1
KFB 153	OA		Kanyawara		Old age	1	1	1	1	1	–	1	–	1	–	–	–
Males																	
KFB 156	YA		Kanyanchu	1999	Acute illness	1	1	1	1	1	1	1	1	1	1	1	1
KVC	YA		Kanyanchu		Unknown	1	1	–	–	–	–	–	–	–	–	–	–
KFB 105[e]	YA	~13	Kanyawara		Unknown	1	1	2	2	1	1	1	1	3	3	1	1
KFB 155	YA		Ngogo		Unknown	1	–	–	–	–	–	–	–	–	–	–	–
KFB 1[b]	PA		Ngogo		Unknown	1	1	1	2	1	1	1	1	3	3	1	1
KFB 107	PA		Kanyanchu	Mar 1994	Fall from tree	1	1	1	1	1	1	1	1	4	1	1	1
KFB 151	PA		Ruteete[f]	Sept 1998	Killed by villagers[c]	1	1	1	1	1	1	1	1	1	1	1	1
KFB 152	PA	20–25	Sebitole[f]	Aug 1998	Killed by conspecifics[d]	–	–	2	2	1	1	1	1	1	2	1	1
KFB 154	PA		Ngogo		Unknown	1	–	–	–	–	–	–	–	–	–	–	–
KFB 2[b]	OA		Kanyawara		Unknown	1	1	1	3	1	1	–	–	1	2	–	1
KFB 93	OA		Unknown		Unknown	1	–	–	–	–	–	–	–	–	–	–	–
Sex undetermined																	
KFB 4[b]	J	3–5	Ngogo		Unknown	1	1	–	–	1	–	–	–	–	–	–	–
KFB 5[e]	J	6–8	Ngogo		Unknown	1	–	–	–	–	–	–	–	–	–	–	–
KFB 20[e]	J	6–8	Ngogo		Unknown	1	–	–	–	–	–	–	–	–	–	–	–

Specimen number	Age: Category[a]	Age: Years	Provenience	Date of death	Manner of death	Femur L	Femur R	Tibia & fibula L	Tibia & fibula R	Pes L	Pes R	Spine C	Spine T	Spine L	Spine S	Ribs L	Ribs R
Females																	
KFB 17[e]	YA		Ngogo		Unknown	–	–	–	–	–	–	–	–	–	–	–	–
KFB 106	PA		Ngogo	Mar 1994	Unknown	1	1	1	1	1	1	1	1	1	1	1	1
KFB 3[b]	OA		Kanyawara		Unknown	1	1	1	1	1	1	3	1	1	1	1	1
KFB 18[e]	OA		Kingo/Ngogo[f]		Unknown	–	3	–	–	–	–	–	–	–	–	–	–
KFB 150	OA	>31	Kanyawara	May 1997	Killed by farmer[c]	1	1	1	1	1	1	2	2	1	1	1	1
KFB 153	OA		Kanyawara		Old age	–	–	–	2	–	–	1	1	1	1	2	2
Males																	
KFB 156	YA		Kanyanchu	1999	Acute illness	1	1	1	1	1	1	1	1	1	1	1	1
KVC	YA		Kanyanchu		Unknown	–	–	–	–	–	–	–	–	–	–	–	–
KFB 105[e]	YA	~13	Kanyawara		Unknown	1	1	1	1	1	1	1	1	1	1	1	1
KFB 155	YA		Ngogo		Unknown	–	–	–	–	–	–	–	–	–	–	–	–
KFB 1[b]	PA		Ngogo		Unknown	1	–	3	–	–	–	1	1	2	–	3	3
KFB 107	PA		Kanyanchu	Mar 1994	Fall from tree	1	1	1	1	4	1	1	1	1	1	1	1
KFB 151	PA		Ruteete[f]	Sept 1998	Killed by villagers[c]	1	1	1	1	1	1	1	1	1	1	–	–
KFB 152	PA	20–25	Sebitole[f]	Aug 1998	Killed by conspecifics[d]	1	1	1	1	1	2	1	1	1	1	1	1

(continued)

TABLE 1. *(Continued)*

Specimen number	Age		Provenience	Date of death	Manner of death	Femur		Tibia & fibula		Pes		Spine				Ribs	
	Category[a]	Years				L	R	L	R	L	R	C	T	L	S	L	R
KFB 154	PA		Ngogo		Unknown	–	–	–	–	–	–	–	–	–	–	–	–
KFB 2[b]	OA		Kanyawara		Unknown	1	1	–	1	–	1	1	1	1	1	1	1
KFB 93	OA		Unknown		Unknown	–	–	–	–	–	–	–	–	–	–	–	–
Sex undetermined																	
KFB 4[b]	J	3–5	Ngogo		Unknown	–	2	–	–	1	1	–	3	–	–	1	1
KFB 5[e]	J	6–8	Ngogo		Unknown	–	–	–	–	–	–	–	–	–	–	–	–
KFB 20[e]	J	6–8	Ngogo		Unknown	–	–	–	–	–	–	–	–	–	–	–	–

1, 75% complete; 2, 25–75% complete; 3, <25% complete; – not present; 4, collected as soft-tissue specimen.
[a] J, Juvenile; YA, young adult; PA, prime adult; OA, old adult.
[b] Postcranial skeleton itemized in detail in Kerbis Peterhans et al. (1993, Table 2, p. 492).
[c] Death described by Wrangham (2001).
[d] Death described by Muller (2002).
[e] Included in Kerbis Peterhans et al. (1993).
[f] See Appendix for locale description.

MATERIALS AND METHODS

Study site

The skeletal remains of *Pan troglodytes schweinfurthii* analyzed in this study were collected in Kibale National Park, southwestern Uganda (Kerbis Peterhans et al., 1993). KNP is a mid-altitude tropical rain forest located north and east of the Ruwenzori Mountains, on the eastern edge of the Albertine Rift Valley. The Park covers 776 km^2 and is comprised of lowland rain forest, montane forest, mixed deciduous forest, papyrus swamp, and grasslands (Struhsaker, 1997). Separate chimpanzee populations in Kibale, Kanyawara (ca. 50 individuals (Wrangham et al., 1991)) and Ngogo (ca. 150 individuals (Watts and Mitani, 2000)), have been actively observed since 1976 (Ghiglieri, 1984; Struhsaker, 1997). Chimpanzees in the Kanyanchu community, near the Park headquarters, have also been observed by rangers over the past two decades, although this area was not an active research site during the period of this study. Kanyawara chimpanzees have been monitored continuously since 1987. Ngogo chimpanzees have been habituated to human observation since 1995 (Mitani et al., 2000).

Sample

Skeletal remains from 20 individuals were collected between 1987 and 2000 from multiple localities within the park (Table 1). Five sets of the skeletal remains were from known individuals. Twelve sets of remains include postcranial elements, while eight individuals are represented by only a cranium or skull. Postcranial skeletons, when present, are largely complete. Only two (KFB 4 and 153) of the 12 sets of postcranial remains are less than 50% complete (Table 1). Nine of these specimens (Table 1) were described briefly in a previous study on rainforest taphonomy (Kerbis Peterhans et al., 1993).

Chimpanzee remains were collected by researchers at Kanyawara whenever possible. Skeletons collected after 1993 were typically cleaned by natural decomposition. Dead chimpanzees were placed in plastic bags and buried at a marked location to ensure complete recovery. After at least six months the carcass was exhumed and cleaned. Skeletal elements were then soaked in a weak (~1%) chlorine solution for several hours to remove adhering soft tissue. Once dry, skeletons were stored at the Makerere University Biological Field Station in Kanyawara. Five sets of remains are on loan to the Field Museum of Natural History in Chicago, Illinois; these specimens retain their KFB (Kibale Forest Bone) numbers.

Age-class and sex of each individual were determined from skeletal and dental morphology and dental wear by M.L.C. and H.P. based on published standards (Schultz, 1940; Nissen and Reisen, 1949; Nissen and Reisen, 1964; Kerley, 1966; Dean and Wood, 1981; Anemone et al., 1991; Dean et al., 1992; Smith et al., 1994; Anemone et al., 1996; Zihlman et al., 2004). For individuals known only from skeletal material, sex was determined by canine size, supraorbital torus size, body size, and comparisons with known-sex skeletons. Juveniles (approximately 3–10 years) were individuals with unerupted third molars and had unfused long bone epiphyses. Young adults (approximately 10–20 years) had fully erupted third molars with minimal wear on all teeth. Further, all secondary ossification centers were fused to

TABLE 2. Skeletal measurements and body size estimates

				Femur (mm)		Tibia (mm)	Humerus (mm)		Radius (mm)
ID	Age	Sex	Mass[a] (kg)	Length	Head diameter	Length	Length	Head diameter	Length
a. Kibale chimpanzees									
KFB 3	Adult	F	34.9	282	31.3	242	285	35.0	272
KFB 106	Adult	F	37.2	302	30.2	245	309	37.9	275
KFB 150	Adult	F	42.1	313	32.4	263	293	38.9	269
KFB 153	Adult	F	33.3	–	–	–	294	34.7	257
KFB 1	Adult	M	46.6	291	33.1	267	317	41.7	265
KFB 2	Adult	M	46.5	290	34.5	262	301	36.7	–
KFB 105	Sub-Ad	M	47.1	324	35.8	267	320	38.4	271
KFB 107	Adult	M	35.2	274	32.1	234	280	34.4	249
KFB 151	Adult	M	43.1	278	34.0	234	286	37.9	264
KFB 152	Adult	M	39.6	278	32.0	237	284	37.7	263

					Maximum length							
		Body mass			Femur		Tibia		Humerus		Radius	
Population	Sex	Mean (kg)	SE	N	Mean	SE	Mean	SE	Mean	SE	Mean	SE
b. Comparisons with other populations												
Kibale	F	36.9	1.9	4	299.0	9.1	250.0	6.6	295.3	5.0	268.3	3.9
	M	43.0	2.0	6	289.2	7.5	250.2	6.8	298.0	7.1	262.4	3.6
Gombe[b,c]	F	31.3*	0.9	31	264.7*	4.7						
	M	39.0*	1.2	26	263.5*	3.5						
Mahale[d]	F	35.2	2.2	6								
	M	42.0	1.4	8								
Eastern Zaire[e]	F	34.3	1.9	9								
	M	42.8	1.6	3								
Pan troglodytes[f]	–				297.7	na	247.2	na	297.9	na	272.6	na

[a] Estimated from femoral head diameter using McHenry (1992) Hominoid equation.
[b] Body mass from Pusey et al. (2005).
[c] Femur length from Zihlman et al. (1990), $N = 6$ females, $N = 2$ males.
[d] Uehara and Nishida (1987).
[e] Rahm (1967).
[f] Shea (1984). Combined-sex sample. $N = 82$ for all elements.
* Smaller than other populations, $P < 0.05$.

the primary center. Prime adults (approximately 20–35 years) displayed third molars with moderate wear. Old adults (35+ years) were characterized by extreme wear on permanent dentition, tooth loss, and obliteration of ectocranial sutures. Note that absolute ages are approximate due to variation in dental eruption and attrition.

To determine body size, measurements were taken on available long bones. Lengths were measured using an osteometric board, and other measures were taken with calipers. Body mass was estimated from femoral head diameter using the Hominoid ordinary least squares equation presented in McHenry (1992).

Identification of skeletal pathology and taphonomy

Gross macroscopic observation served as the primary means for identification of abnormal lesions and taphonomic modification. Table 1 includes a general inventory of skeletal elements to demonstrate which bones and surfaces were available for pathological examination. Specimens were examined by M.L.C. and H.P. for signs of abnormal osteoclastic and/or osteoblastic response and degree of healing at death. Since skeletal pathology response in chimpanzees is comparable to that in humans (Barker and Herbert, 1972; Schmidt, 1978; Scott, 1992), observed skeletal lesions were assigned to the categories of trauma, arthropathy, bone formation, bone loss, or developmental abnormality, as per guidelines established by Buikstra and Ubelaker (1994) and Ortner (2003) for human skeletons, and pathologies were defined as follows.

Arthropathy. Joint surfaces and margins were observed for abnormal bone proliferation or attrition following established guidelines (Rogers et al., 1987; Buikstra and Ubelaker, 1994). Changes at diarthodial joints were classified as either osteoarthritis (sclerosis, marginal osteophytosis, and/or eburnation) or erosive arthritis (osteolysis on subchondral bone surfaces, as observed in rheumatoid pathology) (Solomon, 2001; Ortner, 2003). Severity of observed changes was defined as none, mild (relatively small amounts of marginal osteophytosis or few erosive lesions in the subchondral surface), moderate (distinct formation of marginal osteophytes or substantial subchrondral pitting), or severe (extensive spicule formation, eburnation, polish with grooves, ankylosis, or severe osteolytic destruction of subchondral surface) (Rogers et al., 1987; Buikstra and Ubelaker, 1994; Ortner, 2003). Numerous specimens exhibited small pores on the subchondral surfaces of diarthrodial joints with no associated marginal proliferation or notable osteopenia. Such changes were classified as mild, although the etiology of lesion formation was not known.

Trauma. This category includes fractures (both healed and perimortem) and cranial lesions that are consistent with "probable bite wounds" observed in other studies of great ape skeletons (Lovell, 1990a,b, 1991; Jurmain, 1997). Inflammatory lesions not clearly caused by trauma are classified as bone formation. Perimortem

TABLE 3. Postcranial arthropathy in Kibale chimpanzees

Individual	Age	Cervical	Thoracic	Lumbar	Lumbosacral	Sacroiliac L	Sacroiliac R	Costo-vertebral L	Costo-vertebral R
a. Vertebral joints									
Females									
KFB 106	A	1	4t	1				4t	
KFB 3	OA		1	1					
KFB 150	OA	4t,o	4t,c	4t,c	4t,c				
KFB 153	OA			1					
Males									
KFB 107	A		1		4t	5t,a	5t		1
KFB 2	OA				4				

		Forelimb								Hind limb					
		Sterno-clavicular		Shoulder		Elbow		Wrists/Hands		Hips		Knee		Ankles/Feet	
Individual	Age	L	R	L	R	L	R	L	R	L	R	L	R	L	R
b. Peripheral synovial joints															
Females															
KFB 106	PA					1	1	5t	2						
KFB 3	OA					2	1	2	–			1		2t	2
KFB 150	OA	4	4	3	3	3	3	1	4t	2	2	4t	4	1	1
KFB 153	OA	3	3			2	–	2	–	–	–	–	–	–	–
Males															
KFB 156	J	–	–					4t							
KFB 105	YA	–	–							4d	4d				
KFB 1	PA					1	1			1	1		–		–
KFB 107	PA					1	1	1	1				1	–	3t
KFB 151	PA					2	2								
KFB 152	PA					2	2		4,5t					4t	1
KFB 2	OA	1	–	2	–	1	1	1	3t	–		1p	1p	–	1

–, Not present for observation; 1, minimal porosity on subchondral surface(s) without marginal osteophytosis; 2, mild changes (osteoarthritis with minimal pitting and marginal lipping); 3, moderate changes (moderate subchondral pitting and/or marginal lipping); 4, severe changes (significant subchondral porosity, eburnation, extensive marginal osteophytosis); 5, ankylosis.
a: early stages of ankylosis, c: erosion of centrum faces, d: presumed secondary to developmental abnormality, o: osteophytosis between C5 and C6, p: retropatellar arthritis, t: secondary to trauma.

damage to bones known to be due to injury is included in this category.

Bone formation and loss. Abnormal bone formation or degeneration is any hypertrophy or resorption away from a joint margin or surface. Whether the lesion was actively forming or breaking down, healed, or mixed at the time of death is noted. Lesions not associated with injury are classified as idiopathic inflammatory responses.

Developmental abnormalities. This category includes congenital defects and any morphological abnormalities that developed during growth and maturation.

RESULTS

Age and sex

Of the 20 individuals represented in the Kibale sample, six were females, 11 were males, and three were of unknown sex (Table 1). Individuals were distributed evenly across age classes, with four juveniles, five young adults, six prime adults, and six old adults. Males are predominantly represented in the younger age categories, and most of the old adults are female. Nearly all of the postcranial material is from adults; only one of the six juveniles is represented by a relatively complete skeleton. A brief description of each specimen, including age class, sex, nature of death and recovery, and evidence of pathology, is given in Appendix.

Body size

Size estimates for Kanyawara chimpanzees fall within the range reported for other wild populations (Table 2). As expected, mean estimated body mass was significantly greater for males (mean 43.0 kg, standard deviation ±4.8, $N = 6$) than females (36.9 ± 3.8 kg, $N = 4$) ($P < 0.05$, Student's one-tailed t-test). Estimated body mass was not significantly different than reported from direct measurements of bodyweight in other populations ($P > 0.05$, Student's two-tailed t-test) with the exception of Gombe. Body mass and femur length were both greater for the Kibale sample than has been reported for Gombe ($P < 0.05$; Students two-tailed t-test). Estimated sexual dimorphism (female/male body mass) for Kanyawara (1.17) is also similar to other sites, including Gombe.

Pathology

Arthropathy. Degenerative joint disease was observed in 15 of the 20 individuals in this sample, although most cases were mild (Table 3). Nearly all moderate to severe cases were related to trauma. The only cases of moderate or severe osteoarthritis not clearly secondary to trauma were observed in two old adults, both females (see Fig. 1). Kibale chimpanzees experienced more extensive joint

Fig. 1. Extensive skeletal pathology in an old adult female, KFB150. **A**: Osteoarthritis evident in the proximal ulnae, proximal clavicle, and acetabulum. Note enthesophyte in obturator foramen. The manus shows signs of healed traumatic injury. **B**: The left knee, showing (in caudal and medial views) severe osteoarthritis, possibly secondary to fracture of the tibial plateau. **C**: Superior and lateral views of a cervical, thoracic, and lumbar vertebra, showing severe osteoarthritic changes, including subchondral porosity and lipping in the centra. Scale is the same for all panes.

disease in their extremities than in their spines (Table 3), which is consistent with other studies (Jurmain, 2000). Degenerative arthritis was more prevalent in joints of the forelimbs than of the hind limbs.

Most individuals showed signs of at least mild TMJ arthropathy (Table 4). Of 19 individuals represented by crania, four (three old adult females and one young adult male) had severe degenerative arthritis at the temporomandibular joints (TMJ) (Table 4). One of these individuals, KVC1, had a fractured mandible that undoubtedly influenced the ipsilateral degradation of his right TMJ (see Fig. 2). TMJ degeneration in the three other individuals was apparently unrelated to trauma.

TABLE 4. Arthropathy in the temporomandibular joint (TMJ) in Kibale chimpanzees

		TMJ	
Individual	Age	L	R
Females			
KFB 106	PA	1	1
KFB 154	PA	1	1
KFB 3	OA	4	4
KFB 18	OA	4	2
KFB 150	OA		4
KFB 153	OA	1	1
Males			
KFB 156	J		
KVC1	YA		4t
KFB 105	YA		
KFB 1	PA		
KFB 107	PA	1	1
KFB 151	PA	1	1
KFB 2	OA		
KFB 93	OA		1

1, minimal porosity on subchondral surface(s) without marginal osteophytosis; 2, mild changes (osteoarthritis with minimal pitting and marginal lipping); 4, severe changes (significant subchondral porosity, eburnation, extensive marginal osteophytosis); t, secondary to trauma.

Trauma. The rate of traumatic injury was high, with 13 of the 20 individuals (65%) examined in this study showing some evidence of healed trauma, most commonly bites and fractures (Table 5, Fig. 2). This percentage would undoubtedly have been higher if more individuals were represented by postcrania. Healed traumatic injuries (including fractures, a finger amputation, and a bite wound) were present in 11 of the 12 individuals (92%) represented by postcranial remains (Table 5). Considering only fractures of long bones, 4 of 11 (36%) individuals were affected. All four of these individuals had additional healed fractures elsewhere (e.g., ribs and hands) in the skeleton. The most commonly fractured part of the body was the hand, with seven of eight (88%) of individuals affected. Fractures of the feet and forearms were markedly less common, and no incidence of femur, humerus, or clavicle fracture was noted. Four of the Kibale chimpanzees had suffered three or more fractured bones.

Trauma was observed in eight of the 19 crania in the sample, with healed cranial fractures observed in three of these (16%). For example, the young adult male KVC1 had a healed fracture of his right mandibular condyle, and the adult male KFB 107 had a fractured right zygomatic arch. Seven of 19 individuals (5/6 females and 2/11 males) had at least one small, shallow, circular depressed lesion on the cranium that was a possible healed bite wound (canine puncture). Most of these lesions were on the cranial vault, but at least one individual had a maxillary lesion. One individual, KFB 106, an adult female, had five of these suspected bite wounds.

Notably, KFB1, an adult male, had a small fragment of tooth enamel embedded in his left distal ulna. Bone was well healed around the fragment, and radiographic examination confirmed that the fragment was small. Further analysis of the enamel is needed to determine if the animal was bitten by another chimpanzee or a different species.

Bone formation and loss. Bone formation in the Kibale chimpanzee skeletons is present as either perios-

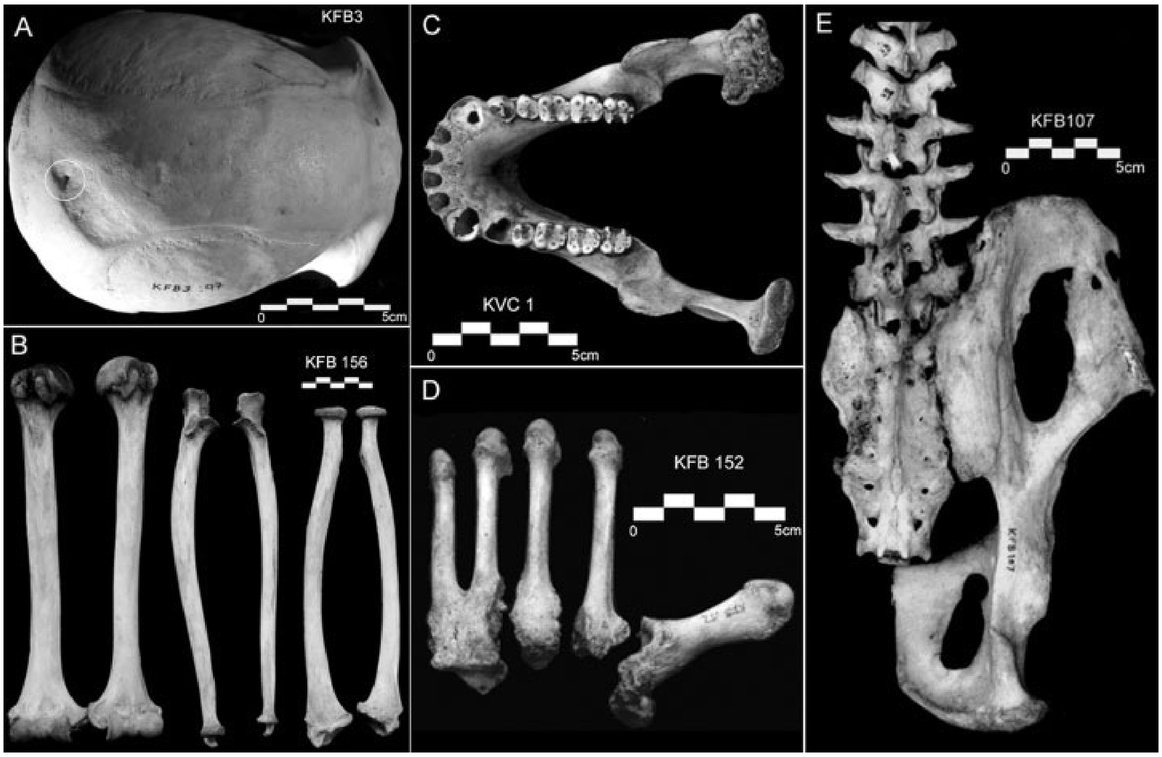

Fig. 2. Examples of healed traumatic injury in the Kibale chimpanzees. **A**: Depressed lesion (probable bite wound), indicated with white circle, on cranial vault of KFB 3. **B**: Upper limbs long bones of KFB156 showing the smaller left arm, which resulted from a left hand injury. **C**: The mandible of KVC1, showing the fractured and extensively modified right ramus and condyle. **D**: Fused metatarsals and distal tarsal row (all cuneiforms and cuboid) of KFB 152. **E**: Extensively remodeled right pelvis of KFB107, the probable result of a fall from height.

TABLE 5. Frequency of antemortem trauma (healed or partially healed) by location, right and left combined

	Number of elements	No. of affected	%	Number of individuals	No. of affected	%
Cranium	19	8	42.1	19	8	42.1
Mandible	12	2[a]	16.7	12	2[a]	16.7
Clavicle	19	0	0.0	10	0	0.0
Scapula	19	0	0.0	11	0	0.0
Humerus	22	0	0.0	12	0	0.0
Radius	19	2	10.5	10	2	20.0
Ulna	19	2	10.5	10	2	20.0
Manus	15	7	46.7	8	7	87.5
Pelvis	19	1	5.3	10	1	10.0
Femur	19	0	0.0	10	0	0.0
Tibia	17	1	5.9	9	1	11.1
Fibula	18	0	0.0	10	0	0.0
Pes	18	2	11.1	10	2	20.0
Whole Body	–	–	–	12	11	91.7

Frequencies are given with respect to the number of elements in the sample, and with respect to the number of individuals represented
[a] Includes one case of infection with unknown etiology.

titis (subperiosteal bone deposition) or enthesophytes (ossified tendons or ligaments). All lesions are focal. Five adults (KFB 1, 105, 106, 107, and 152) exhibited periostitis, all related to traumatic injuries. Three individuals exhibited enthesophytes, with two individuals showing ossified obturator ligaments. Four Kibale individuals (KFB 3, 150, 152, and 154) showed signs of idiopathic bone loss not definitively related to trauma (see Fig. 1).

Developmental abnormalities. There are four examples of developmental anomalies in the Kibale sample. KFB 151, an adult male, had an accessory navicular present in both feet, the first documented example of this type of epigenetic skeletal trait in a chimpanzee. This same individual also had bilateral os acromiale, and mild scoliosis in the lower thoracic/upper lumbar region. Another individual, KFB 105, had a tripartite os acromiale, and mild scoliosis which may be related to a very rare congenital hip dysplasia, coxa valga (see Fig. 3). This is the first documentation of coxa valga in apes, and the etiology is unknown.

Fig. 3. Developmental abnormalities in KFB105. Coxa valga is evident in both proximal femurs, affecting the femoral neck angle and orientation of the femoral heads. Inset shows normal femur for comparison. The lumbar spine shows mild scoliosis, possibly secondary to the femoral abnormality. The acetabula show osteoarthritic changes (including lipping) secondary to coax valga.

TABLE 6. Frequency of moderate to severe degenerative joint disease in Kibale versus Gombe chimpanzee skeletons

	Kibale			Gombe[d]		
Joint[a]	N[b]	n[c]	%	N[b]	n[c]	%
Cervical[e]	10	0	0.0	11	1	9.1
Thoracic[e]	10	0	0.0	11	1	9.1
Lumbar[e]	10	0	0.0	11	0	0.0
TMJ	19	3	15.8	17	0	0.0
Sternoclavicular	10	2	20.0	na[f]	na[f]	–
Shoulder	11	1	9.1	11	0	0.0
Elbow	11	1	9.1	11	0	0.0
Wrist/Hand	11	0	0.0	11	0	0.0
Hip	10	0	0.0	11	0	0.0
Knee	10	1	10.0	10	0	0.0
Ankle/Foot	10	0	0.0	10	0	0.0

Males and females combined. Juveniles and DJD secondary to trauma excluded.
[a] DJD includes both right and left sides.
[b] Number of individuals with observable parts; regions at least 50% complete to be included.
[c] Number of individuals showing moderate to severe lesions in region.
[d] From Jumain (2000)
[e] Apophyseal joints only; vertebral osteophytosis not observed in either population.
[f] Not available (na).

TABLE 7. Summary comparison of size and skeletal pathology in Kibale and Gombe chimpanzees

Category	Kibale chimpanzees	Gombe chimpanzees
Average body size		
Male	43.0 kg (estimate)	39.0 kg[b]
Female	36.9 kg (estimate)	31.3 kg[b]
Arthropathy[a]		
Postcranial	2/12 (16.7%)	1/11 (9.1%)[c]
Temporomandibular	3/19 (15.8%)	0/14 (0%)[c]
Postcranial trauma		
Long bones	4/11 (36.4%)	4/13 (30.8%)[c]
All	10/11 (90.9%)	7/13 (53.8%)[c]
Cranial trauma		
Healed Fractures	3/19 (15.8%)	2/14 (14.3%)[c]
Possible Bite Wounds	7/19 (36.8%)	2/14 (14.3%)[c]
Killed by Humans	3	0
Chronic Infection	0	2 (poliomyelitis)[d]

Rates of pathology are per individual.
[a] Unrelated to trauma.
[b] Pusey et al. (2005).
[c] Jurmain (2000).
[d] Morbeck et al. (1991).

DISCUSSION

Patterns of morbidity and mortality in Kibale chimpanzees

As in other wild primate populations, Kibale chimpanzees exhibit a high rate of skeletal pathology. Over half of the individuals in this sample, and nearly all of the complete skeletons, exhibited signs of healed fractures and other traumatic injury. Degenerative bone pathology is also very common, with 75% of all individuals showing at least minor joint damage somewhere in the skeleton. Trauma was an important factor here as well, with most instances of joint degeneration apparently secondary to traumatic injury.

Known causes of death for Kibale chimpanzees were varied but often violent, including attacks by conspecifics, killing by humans, and falling from the canopy. The incidence of trauma related to falls is consistent with the hypothesis that avoiding falls from the canopy is an important selection pressure shaping chimpanzee locomotor anatomy (Pontzer and Wrangham, 2004). Several chimpanzees died from acute illness, but there is no evidence for chronic infectious disease or inflammation in the Kibale skeletons. All postcranial lesions noted in the Kibale skeletons are localized periostitis, mostly associated with fracture healing. Kibale chimpanzees do suffer from dental pathology, including alveolar inflammation and associated osteomyelitis, which will be addressed in a future study.

In both humans and apes, cranial trauma shows sex-specific patterns and is therefore hypothesized to be correlated with interpersonal violence (Walker, 1989; Jurmain and Kilgore, 1998). Jurmain and Kilgore (1998) found that females have injuries to the cranial vault, while males experience facial trauma. The Kibale chimpanzee sample provides partial support for this observation. Cranial fractures in Kibale chimpanzees follow this trend, but the pattern of probable puncture lesions that might represent healed bite marks does not.

Body mass

Body mass estimates and long bone lengths (an index of stature) for the Kibale sample, while larger than individuals in Gombe, appear similar to other populations (Table 2). In contrast, mean body mass reported for Gombe chimpanzees (Pusey et al., 2005) is significantly lower than values reported for other populations ($P < 0.05$ all comparisons, Student's two-tailed t-test, Table 2) and reported femur length (Morbeck and Zihlman, 1989) is significantly less than that for the Kibale sample. This may suggest low levels of food availability at Gombe

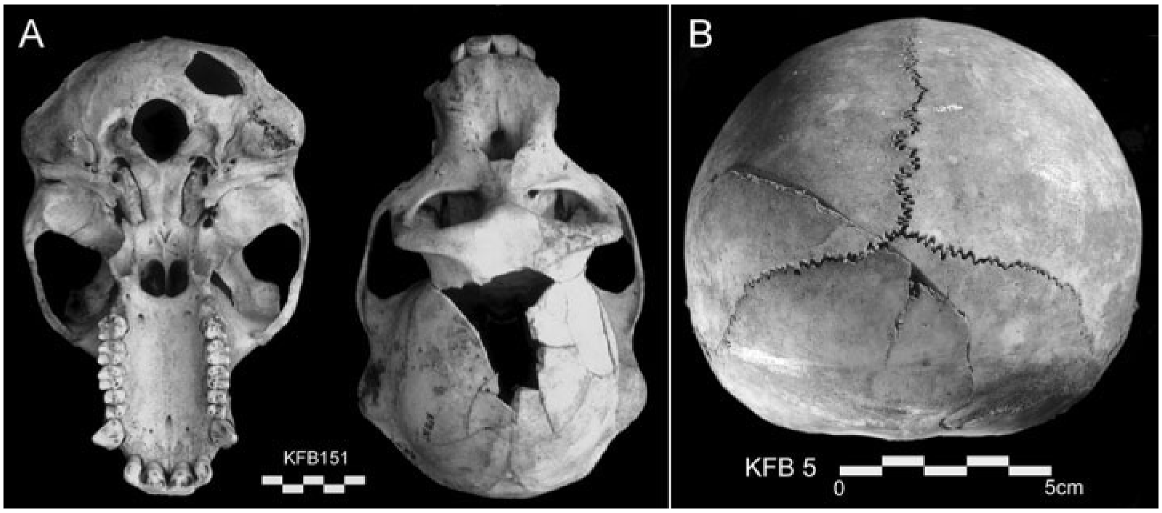

Fig. 4. Perimortem trauma in two Kibale chimpanzees. **A**: Gun shot trauma to the skull of KFB 151. **B**: Sharp force trauma (probable machete) in KFB 5.

(Pusey et al., 2005). In any case, these size differences suggest that reported body mass estimates for *Pan troglodytes schweinfurthii* based on the Gombe population (e.g. Smith and Jungers, 1997) may be slightly lower than is common for this subspecies and underscores the importance of site-specific data for metric comparisons.

Comparison with Gombe chimpanzees

Rates of skeletal pathology in the Kibale collection were broadly similar to those previously reported for Gombe skeletons, but there are suggestive differences. Though skewed by data contributed from one old individual in each sample, Kibale chimpanzees show a higher frequency of osteoarthritis in 4 of 10 joints, while Gombe chimpanzees show a higher frequency of cervical and lumbar arthritis (Jurmain, 2000). The greatest difference in the incidence of degenerative arthropathy was in the temporomandibular joints (16% Kibale versus 0% Gombe) (Table 6), although this could be due to interobserver differences in diagnosis. Patterns in skeletal trauma were also similar between the two assemblages (Table 7), especially in terms of long bone fractures (36% of individuals in Kibale versus 30.8% in Gombe) and cranial trauma (16% Kibale versus 14% Gombe) (Jurmain, 1997). There is a substantial difference, however, in the incidence of injuries to hands and feet. Adding these injuries to the incidence of postcranial fractures, Kibale chimpanzees show a much higher rate of injury than seen at Gombe (91% Kibale versus 53.8% Gombe).

The similarity in the incidence of fractures and other major trauma may point to similarities in the rates and sources of morbidity for Gombe and Kibale chimpanzees. In particular, both assemblages demonstrate the morbidity and mortality associated with falls from the canopy. At Gombe, there are documented cases of chimpanzees falling to their death from trees (Teleki, 1973; Goodall, 1986), and Jurmain (1997) attributes severe fractures in this sample to falls from great heights. In the Kibale specimens, KFB 107 almost certainly died after falling from a tree. Further, the partially healed, extensive trauma evident in his pelvis and lumbar region indicates that his fall was not his first.

Several individuals, mainly older chimpanzees, in both the Kibale and Gombe collections had enthesophytes at various locations of the skeleton. While the etiology of ossified connective tissue is not certain, it is usually associated with trauma, aging, and/or excessive use of muscles (Roberts and Manchester, 2005). Incidence of abnormal bone loss was also similar between populations. Jurmain (1989) mentions two Gombe individuals with abnormal bone loss: Charlie, an adult male, had porotic lesions on the subchondral surfaces of his right tibiotalar joint, which is supposed to be a "possible fungal or bacterial infection" (p. 234), and Gilka, a young adult female, who had erosive lesions in her manual phalanges, indicative of osteomyelitis. Destructive lesions are similar in frequency (three of 20 individuals) in the Kibale sample but are not clearly diagnostic of a particular disease process.

Both skeletal assemblages provide evidence of detrimental contact with local humans but in different ways. The Gombe skeletons include individuals who suffered from poliomyeltitis, supposedly contracted through human contact in the 1960s (Morbeck et al., 1991). Although there is concern that Kibale chimpanzees are exposed to human diseases and parasites (Ashford et al., 2000; Krief et al., 2005; Muehlenbein, 2005), the skeletal remains show no evidence of chronic inflammation. However, the Kibale skeletal assemblage includes an individual who was killed by local villagers for disturbing their livelihoods (KFB 151), as well as a young animal (KFB 5) apparently killed by a machete for unknown reasons (see Fig. 4). Though local farmers do not hunt or eat primates, farmers will kill animals that raid their crops (Naughton-Treves, 1998). Chimpanzees are regularly injured by wire snares set illegally for game animals and suffer mutilated fingers and toes, as well as amputated hands and feet (Muller, 2000; Wrangham, 2001). Similar human impact has been observed in other East African chimpanzee communities (Waller and Reynolds, 2001) but is not observed in the Gombe sample.

CONCLUSION

This study presents new data on skeletal pathology and morphometrics from a sample of chimpanzee skeletons from Kibale National Park, Uganda. Our data are consistent with the high rates of skeletal pathology observed in other chimpanzee populations, suggesting this pattern of illness and injury is common for East African chimpanzees. Like chimpanzees in Gombe National Park, Tanzania, Kibale chimpanzees experience a high rate of traumatic injury. Nearly all the individuals in the Kibale sample showed signs of healed trauma and secondary degenerative joint disease. In addition to death from humans, illness, and attacks from conspecifics, falls from the canopy appear to be an important source of morbidity and mortality for Kibale chimpanzees, as in Gombe.

It should be noted that skeletal analyses present an incomplete account of illness and injury. A limited number of infectious pathogens cause skeletal lesions, and acute episodes of physiologic stress rarely affect the skeleton, especially macroscopically. However, skeletal remains of free-ranging primates are a valuable source of information about physiological stress on the individual and population as well as body size and ontogeny. Only concerted efforts to collect additional carcasses will generate large enough skeletal assemblages to allow statistically robust testing of hypotheses regarding population health and adaptation to different and changing environments. Future research on larger collections will shed new light on the sources of morbidity and mortality in wild chimpanzees.

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APPENDIX: BRIEF DESCRIPTIONS OF EACH SPECIMEN

Females

KFB 17 (young adult female, Ngogo) is represented by the cranium. The left zygomatic process was cut off of the temporal bone anterior to the articular tubercle; the process is separated anteriorly at the unfused zygomaticotemporal suture. A small (0.4 cm) cut mark is present on the inferior border of the left temporal process. The left medial and lateral pterygoid plates of the sphenoid bone are partially crushed; there had been soft tissue on the bone. A tiny cut on the left palatine bone is in line with the cut on the temporal bone. The cut marks were made with a sharp instrument, but whether they were made prior to death is difficult to assess. Two small (0.5 cm diameter) depressions or pits are visible on the cranial vault. One is on the superior left frontal, and the other is 2.5 cm laterally on the left parietal. These are consistent with a healed bite wound, but the etiology is unknown.

KFB 106 (adult female, Kanywara) is represented by the complete skeleton. The fresh carcass was found in March 1994, buried at the research camp to clean the skeleton, and subsequently excavated in June 1994.

The most notable pathology is a dislocation of the right rib 11, which formed a new articular facet on a large ventral osteophyte of T10. Numerous arthritic and inflammatory responses to this dislocation are evident in the vertebrae and ribs. The head of rib 11 is grossly enlarged with corresponding arthritic changes. Mild osteoarthritic lipping is present at several rib facets of the thoracic vertebrae, marginal bodies of T8 and T11, and the zygopophyses of L2 and L3. Severe osteophytosis and inflammation are present on the right side of T9 and T10.

Evidence of traumatic injury throughout the skeleton may be related to the thoracic injury. There is a healed fracture of the left distal ulnar diaphysis. Inflammation of the proximal 2/3 of the diaphysis and slight shortening of the length signify a healed fracture of the left metacarpal III. Ankylosis (joint fusion) and abnormal angulation between the middle and distal phalanges of one finger may be secondary to fracture and healing; the head of the distal phalanx shows marked degeneration. A single puncture on the ischiopubic ramus of the right hip bone occurred peri- or postmortem. Five small depressions located on the frontal and both parietal bones, on the cranial vault, might represent healed wounds.

Other, potentially unrelated arthritic pathologies are evident as well. Erosive pitting characterizes the left superior surface of the centrum of C3. Mild arthrosis is seen on the lateral margins of mandibular condyles, dorsal margins of trochlea of right humerus, left distal radius, and styloid processes of both distal ulnae. Mild arthritic lipping lines the joint surfaces of numerous carpals, secondary to trauma. Two healed lesions of periostitis are present: one, on the dorsal diaphysis of the right metacarpal II; the other, on the lateral side of the distal diaphysis of the left metatarsal II.

KFB 150 (adult female, Kanyawara) is represented by a cranium, mandible, and nearly complete postcranial skeleton. This old female, identified as a member of the Kanywara community, Ngonya, was killed by farmers in 1996 in the Kanyawara area. The estimated year of birth for this individual was 1965, based on behavioral observation and appearance in the field. However, given the extensive tooth wear and osteoarthritis, this individual may well have been older than 31 years at death.

Osteoarthitic wear is evident throughout the postcranium and involves nearly every visible joint surface (see Fig. 1). Vertebral bodies show extensive wear on the articular surfaces, with lipping present in the cervical and lower thoracic/upper lumbar regions and on the superior surface of the sacrum. Mild arthrosis is evident in the phalangeal joints and the cuneiform-metatarsal I and trapezium-metacarpal I articulations. Moderate arthrosis with some lipping is evident on the following joint surfaces: glenoid (scapula), acromioclavicular, humero-ulnar, radio-ulnar (both proximal and distal), and acetabulum. Severe arthrosis, with extensive wear and lipping, is evident in the articulation between the manubrium and clavicle, the femur and tibia, and the proximal tibia and fibula (proximally). The tibial plateaus, medial condyle of the left femur, and lateral condyle of the right femur all have exposed trabecular bone with burnishing. The left knee in particular shows extensive wear, possibly partially as a result of trauma, with the posterior portion of the tibial plateau worn well below the original articular surface and the exposed trabecular bone burnished. The proximal tibio-fibular articulation shows lipping and osteophytic deposits on the tibia. The right temporomandibular joint shows extensive wear, with trabecular bone visible over most of the glenoid fossa. This wear is consistent with severe wear on the right mandibular condyle.

Evidence of traumatic injury is minimal. The cranium shows a small (1 cm diameter) healed lesion on the right parietal, as well as perimortem cut marks on the right parietal and the anterior surface of the left maxilla. The right metacarpal IV and V are fused, possibly as a result of injury. One proximal hand phalanx shows wear and osteophytic growth consistent with trauma on its distal articular surface; similar pathology is evident on the proximal articual surfaces of two intermediate phalanges.

The right scapula shows a small (1 cm diameter) idiopathic lesion near the tip of the inferior angle (left scapula is incomplete) on the ventral surface, similar to KFB 152. The olecranon fossa of the left humerus is patent. Postmortem skeletal damage is minimal; he right femur sustained a midshaft fracture, and the left scapula was fractured across the body so that only the superior portion is present.

KFB 153 (adult female, Kanyawara) is represented by a cranium, mandible, and partial skeleton. This old adult female died from an apparent respiratory disease in 2000 and is believed to be the known individual "Josta" from the Kanyawara community. Remains were recovered several days after death, after apparently being scavenged, and consequently not all body parts were recovered. Upon recovery, remains were buried at the research camp and were excavated in June 2001. No evidence of scavenging is visible on the bones. The estimated age of birth for this individual is 1960, based on observations and appearance in the field.

While much of the postcranial skeleton is missing, the available elements show evidence of minor osteoarthritis throughout. The temporomandibular joints are pitted, consistent with minor pitting of mandibular condyles. Mild wear and lipping is present in the left humero-ulnar, left radio-ulnar (proximal and distal), and clavicle-manubrium joints (right forelimb is missing). Similarly, the L1 zygopophyseal joint shows mild wear.

Evidence of trauma is minimal. The left metacarpal IV and V show evidence of healed midshaft fractures. The cranium shows a small (1 cm diameter) healed lesion on the left parietal, just medial to the temporal line. The pelvis and lower extremities are missing except for the right fibula, which shows no evidence of pathology.

KFB 18 (old adult female, Kingo/Ngogo) is represented by the cranium and femur fragment, thought to be a member of the Kingo chimpanzee community, which ranged near a village of the same name, immediately south of the Ngogo community, near the southern border of KNP. The femur fragment shows considerable gnawing damage (Kerbis Peterhans et al., 1993). On the right side of the cranium, there are smooth incisions, possibly related to the manner of death, on the temporal and zygomatic processes which resulted in the removal of the entire zygomatic arch. The deepest and longest cut lies posterior to the left mastoid process; the second lies anterior to the foramen magnum; and the third lies anteriomedial to the carotid canal of the right petrous temporal. Areas of crushed bone are noticeable on the posterior maxilla, pterygoid plates, and medial to the temporomandibular joint. The left side of the cranium shows definitive evidence of scavenger activity. The left zygomatic arch is absent. Multiple small puncture marks are scattered on the left basicranium, the left orbital floor, and left nasal cavity wall. Severe osteoarthitic lipping and erosive degeneration are present at the left temporomandibular joint. Only mild arthritic changes are observable at the right joint. Two small depressions on the right parietal bone, 2.0 cm apart, are similar to those seen on the cranium of KFB 17.

KFB 3 (old adult female, Kanyawara) is represented by the complete skull and nearly complete postcranial skeleton of an old adult female chimpanzee from Kanyawara. The fresh carcass was found and retrieved in March 1988. Although no bones show evidence of gnaw marks, the carcass had been scattered by a scavenger (Kerbis Peterhans et al., 1993).

Severe osteoarthritic degeneration is present at the temporomandibular joints. Both right and left glenoid fossae show extensive remodeling and marginal lipping. The mandibular condyles are significantly flattened; lateral, anterior, and medial margins of the condyles are sharply defined by arthritic lipping. The posterior margins of the articular surfaces are porous. Mild arthritic degenerative lesions are present on articular surfaces of most long bones, tarsals, metatarsals and phalanges (both manual and pedal). Mild arthrosis is observable on many zygopophyses of the thoracic and lumbar vertebrae. Enthesopthytes (ossified tendons and ligaments) are also evident in the pronounced bony ridges along the ventral margins of a manual phalanx and partially ossified obturator ligaments in both innominate bones.

A probable infection in the right maxillary sinus resulted in the partial erosion of the orbit floor. The opening in the maxilla lies medial to the inferior orbital canal and has smooth (sclerotic) borders. The only possible evidence of infection in the postcranial bones is idiopathic lytic lesions along the dorsal margins of the proximal fibular facets on both tibiae.

There are signs of traumatic injury in two places. The left second metatarsal shows acute angular deformation at the distal third of the diaphysis with slight hypertrophic osseous response around the metatarsal head. The most remarkable lesion is a well-healed depressed lesion located at the posterior third of the right parietal bone (Fig. 2A). The depressed region is roughly oval in shape (maximum length = 30.2 mm; maximum width = 13.4 mm) and reaches across the sagittal suture to the left parietal bone. Osseous remodeling has resulted in a rerouting of the right superior temporal line and a sharpened ridge of bone along this muscle attachment site.

Males

KFB 105 (young adult male, Kanyawara) is a nearly complete chimpanzee skeleton thought to be the known individual "Ruwenzori." In August 1992, the fresh carcass of a young male, assumed to be Ruwenzori, was recovered and cleaned. The bones display no evidence of scavenging. Small cut marks on several hand bones probably result from defleshing the remains.

The most remarkable pathological condition is bilateral coxa valga (see Fig. 3). Both proximal femora are deformed, with corresponding arthritic changes in both acetabula. The femoral necks are narrow and elongated, and the angle between the neck and femoral diaphysis is greatly increased on both sides. The angle between the femoral neck and greater trochanter is correspondingly decreased. The right femoral head has an abnormal porous lesion in the normal location of fovea capitis; a porous lesion extends down the inferior border of the neck. The left femoral head is normal, with only a small region of porotic bone on the neck. The etiology of this condition is uncertain. Field assistants do not recall that Ruwenzori had an abnormal gait. Perhaps as a result of the femoral abnormality, several intervertebral joints show early stages of osteoarthritic change. Osseous buttressing is evident in L4, possibly a response to slight asymmetry in the transverse processes.

In addition to signs of infection on the mandible, a small, healed lesion of idiopathic periostitis is located directly superior to glabella, and a small, active periostitic lesion can be found in the center of the right scapular blade. Two small depressions (2.5 cm apart) on the right parietal bone might represent healed wounds. Left ribs 11, 12 and 13 show peri- or postmortem linear breakage close to their sternal ends.

KFB 156 (young adult male, Kanyanchu) is represented by a cranium, mandible, and nearly complete skeleton. This member of the Kanyanchu chimpanzee community and died of an unknown illness in 1999. The corpse was wrapped in plastic and buried soon after death and was excavated in July 2001.

Severe trauma is evident in the left hand. Metacarpals II and III show numerous osteophytic lesions and reactive bone, and metacarpal V is severely atrophied. Apparently as a consequence of this injury, the left forelimb, including the clavicle, humerus, ulna, radius, carpals, and metacarpals are noticeably less robust than those of the right forelimb: the diameters of the left humerus and ulna are approximately 15% smaller than the right at midshaft. Further, the left ulna and radius are approximately 3% shorter than the right (Fig. 2B).

Kanyachu Visitors Center 1 (adult male) is represented by a cranium and mandible of unknown provenience. The right temporomandibular joint shows evidence of healed trauma, with the right ramus having been fractured (Fig. 2C). The fracture has shortened the ramus, and the resulting morphology of the condyle is irregular and characterized by rough, reactive bone. A portion of the articular surface of the original condyle is evident in the healed fracture. The right glenoid fossa is expanded and rough. The left zygomatic arch was broken postmortem.

KFB 1 (adult male, Ngogo) is represented by the complete skull and partial postcranial skeleton of an adult male chimpanzee from Ngogo. Field assistants found the fresh carcass 10 m from a distressed adult female chimpanzee in December 1987. Collection efforts in the following two months recovered skeletonized remains that an unknown scavenger had scattered. Gnaw marks are present on many bony elements. A broken wire snare was found near the remains (Kerbis Peterhans et al., 1993).

Extreme arthrosis is evident on the inferior surface of the left acromion (lateral margin) and on the intercondylar ridges of both distal humeri. There are ridges of arthritic lipping along the inferior border of the superior portions of both acetabular articular surfaces. The only evidence of inflammation is a small circular lesion of idiopathic healed periostosis on the dorsomedial border of the distal third of the right radius. The most interesting pathological condition of KFB 1 is a healed bite wound, which resulted in a small chip of enamel being embedded in the distal diaphysis of the left ulna. Sclerotic bone surrounding the enamel fragment indicates that the wound fully healed from the insult.

KFB 107 (adult male, Kanyanchu) is represented by a complete skeleton. The fresh carcass was found on March 17, 1994, and buried near the Park headquarters at Kanyanchu. Field assistants first observed this animal at Kanyanchu on March 31, 1993. Due to vocalizations and location of the carcass, field assistants suspect that the chimpanzee was killed by a fall out of a tree during an aggressive encounter with other chimpanzees. Before burial, the right hand and left foot were removed for preservation in fluid. The right mandibular ramus has been severed postmortem by an unknown agent.

Destruction and remodeling of the pelvic girdle indicates that this individual was partially recovered from a severe trauma, consistent with a fall from great height, experienced sometime prior to death (Fig. 2E). The iliac blade of the right hip bone shows the most damage. A central opening in the ala is slightly larger than the obturator foramen; its superior margins are sharp, while the inferior margin is smooth. The cranial half of the right sacroiliac joint is ankylosed. The auricular surface of the left hip bone shows that the joint was in early stages of ankylosis at death. The medial margins of the left ilium show buttressed, smooth undulations and three abnormal foramina, which may represent callus formation. Other evidence of trauma, perhaps related to the pelvic injury, are two large lesions of active periostitis distal to the callus of a healed fracture in the left distal radial diaphysis. Also, a probable healed fracture is evident on the right zygomatic arch, as well as a healed fracture of the left rib 8. There is breakage of the partial ankylosis at the pubic symphysis, which may have occurred during the presumed fatal fall.

Arthrosis is present on the mandibular condyles, multiple zygopophyses of upper and middle thoracic vertebrae, several articular facets of proximal right ribs, the intercondylar ridges of both distal humeri, the ventral margin of the left radial head, and the distal articular surfaces of both radii. Osteoarthritis, as marginal osteophytic lipping, is present in the semilunar notches of both proximal ulnae, on the medial condyle of the right femur, the left proximal fibula, all articular surfaces of the manual first digit, right talar head, and numerous foot bones, secondary to trauma. Bilateral diarthrodial joint porosity of the postzygopophyses of L4 and prezygopophyses of S1 is severe and is secondary to pathological changes in the pelvic girdle.

KFB 151 (adult male, Ruteete) is represented by a cranium, mandible, and nearly complete postcranium. This adult male was killed by humans, reportedly for raiding crops and attacking villagers, near the village of Ruteete, a village approximately 5–8 km east of the Kanyawara community range, near the KNP border.

The cranium shows an apparent gunshot wound to the head, entering the back of the skull via the right occipital, posterior to the foramen magnum and inferior to the nuchal torus, and exiting near the frontal-parietal suture near midline (Fig. 4A). Other evidence of perimortem trauma is minor. A laceration is evident on the anterior surface of the left maxilla. The right scapula has a deep laceration on the scapular spine, and the right articular surface of the manubrium is severed. Evidence of antemortem trauma is also minor, with one intermediate phalanx (hand) severed at midshaft.

The temporomadibular joint shows some pitting bilaterally, consistent with pitting on the mandibular condyles. The left distal radio-ulnar articulation shows evidence of inflammation and wear, possibly resulting from trauma as no other arthrosis is evident.

Two cases of genetic or developmental abnormalities are present in this individual. First, minor scoliosis is evident in the lower thoracic/upper lumbar region (T10–14, L1), the mediolateral wedging of the vertebral bodies. Second, an accessory navicular is present bilaterally. Neither condition appears to have affected function.

KFB 152 (adult male, Kanyawara) is represented by a nearly complete postcranial skeleton. This adult male from a neighboring community was killed by Kanyawara chimpanzees near the village of Sebitole, a village near the KNP border. The cranium and mandible, as well as the atlas (C1) were missing at the time of analysis. Cut marks on the axis (C2) are consistent with decapitation postmortem.

Evidence of trauma is limited to the distal extremities. The lateral portion of the left distal radius shows a healed lesion. There is also evidence of trauma to the right hand. The right lunate, triquetral, and pisiform are deformed and burnished, consistent with healed, severe trauma. The right metacarpals are less robust than those of the left hand, consistent with a healed traumatic injury to the right hand leading to compromised function. In the lower extremities, articular surfaces of the tarsals show wear and pitting bilaterally. The left foot shows evidence of severe, healed trauma: the distal tarsal row is fused to the proximal metarsal articulations, and metatarsals IV and V are fused proximally (Fig. 2D). The proximal metatarsal articulations are pseudoarthroses, characterized by irregular and rugous bone that would not have permitted movement between metarsals proximally. The talar surface of the left tibia is less keeled than in the right tibia, possibly as a consequence of the injury to the left foot.

Other lesions are minor. Ideopathic lesions are evident on the ventral surface of the inferior angle of the scapula near the tip, bilaterally, similar to KFB 150. This specimen also has similar lesions at the base of the acromion. Finally, two small osteophytic calluses are present, one (0.5 cm diameter) on the dorsal surface of the left radius near midshaft and the other (0.5 cm diameter) on the posterior surface of the distal articular surface of the humerus near its medial margin.

KFB 154 (adult male) is represented by a cranium of unknown provenience. All teeth have been lost postmortem, but the size of the sockets for the canines, size of the skull, and size of the supraorbital torus indicate that this individual was an adult male. Postmortem damage is moderate, with left and right mastoids and zygomatic arches fractured and missing. Further, the surface of the bone shows mild weathering. A healed laceration (3 cm) is visible on the superior surface of the right supraorbital torus. Another smaller lesion (0.5 cm diameter) is visible on the left parietal just medial to the temporal line.

KFB 155 (adult male, Ngogo) is represented by a cranium collected in Ngogo. The surface of the bone in and around the orbits is slightly porous, but this is not severe. No other pathology is apparent.

KFB 93 (old adult male, unknown provenience) is represented by the cranium. Osteoarthitic changes in the cranium are observed as mild arthritic lipping on the medial margins of both occipital condyles and mild arthrosis in the glenoid fossa of the right temporal bone.

KFB 2 (old adult male, Kanyawara) is represented by the complete skull and relatively complete postcranial skeleton of an old adult male chimpanzee from Kanyawara. The remains were recovered in February 1988. The bones show gnawing damage (Kerbis Peterhans et al., 1993).

Degenerative disease is evident on most joint surfaces. Moderate arthrosis-trophic degeneration of joint surfaces without osteoarthritic lipping is evident on the left sternoclavicular joint, the glenoid fossa of the left scapula, the intercondylar ridges on both distal humeri, the patellar trochleae of both distal femora, and numerous intertarsal joints. Severe porotic lesions on the right capitate and hamate represent arthritic changes caused by trauma. Mild osteoarthritis (pitting associated with marginal lipping) is present at the humeroulnar joints, radiocarpal joints, and at most interphalangeal joints (both manual and pedal). Severe marginal osteoarthritis, possibly secondary to traumatic insult, is evident at the proximal joint surface of the left second metacarpal (MTCL II). Similarly, severe osteoarthritic change is evident on the right MTCL IV (both proximal and distal ends) and MTCL V, undoubtedly related to trauma. MTCL IV also shows diaphyseal inflammation. The only sign of vertebral arthritis is severe bilateral diarthrodial joint porosity of the postzygophophyses of L5 and prezygopophyses of S1 (see Fig. 3).

Angular deformation, in conjunction with osteoarthritis and diaphyseal inflammation, suggests that the right MTCL IV and V were once fractured, although the resulting calluses are well healed. This individual also had a partially ossified obturator ligament on his right pelvis (left was not recovered), and other enthesophytes on this bone suggestive of a healed injury. A large bony spicule extends from below the anterior inferior iliac spine, directly above the proximal attachment of the rectus femoris muscle.

Juveniles

KFB 4 (juvenile, 3–5 years, Ngogo) is represented by a complete skull (all teeth present) and fragmentary skeleton (mainly ribs and diaphyseal fragments). A field assistant found the scattered remains at Ngogo. Most elements were gnawed (Kerbis Peterhans et al., 1993). These remains show no sign of illness or injury.

KFB 5 (juvenile, 6–8 years, Ngogo) is represented by only a cranium. The dry specimen was found in 1987 (Kerbis Peterhans et al., 1993). The inferior margins of the basicranium were gnawed. The fragmentary postcranial bones show no pathological lesions. The cranium, however, shows the probable cause of death, a deep laceration to the posterior occiput (Fig. 4B). The cleft (63 mm long) runs from the squamous occipital to the posterior left parietal bone. The beveled margins of the cut are sharp and continuous with peripheral cracks that were secondarily produced by the force of the initial impact. The morphology of the cleft suggests that soft tissue covered the skull upon impact.

KFB 20 (juvenile, Ngogo) is represented by the cranium. Sharp cut marks are present on the left maxilla, on the labial aspect of alveolar bone at the level of I2 and C, and through the centers of the empty crypts of both I1's. No other pathology is evident.

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