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Early Hominins and Paleoecology of the Koobi Fora Formation, Lake Turkana Basin, Kenya

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Introduction

The Koobi Fora Fm (Formation) east of Lake Turkana in northern Kenya is one of the most important paleoanthropological rock units in the world (Figure 26.1). Nearly 250 hominin specimens are documented from East Turkana, representing the species *Australopithecus anamensis*, *A. afarensis*, *Paranthropus boisei*, *Homo rudolfensis*, *H. habilis*, and *H. erectus* (or *ergaster*) (M.G. Leakey, 1970; R.E. Leakey, 1973, 1976; Day et al., 1976; M.G. Leakey and R.E. Leakey, 1978; Kimbel, 1988; Wood, 1991; M.G. Leakey et al., 1995, 2012; Spoor et al., 2007; Wood and Leakey, 2011). Spanning from about 4.3 Ma (million years ago) to about 0.7 Ma, the abundant paleontological and sedimentological records of the Koobi Fora Fm offers a rich picture of hominin evolution and paleoenvironments during the Pliocene and early Pleistocene. In this contribution we present a synthesis of previous paleoecological work at East Turkana and add new paleontological analyses relevant to understanding the ecology of early hominins.

The Lake Turkana Basin today is a hot and dry place, with mean annual temperature of 29.2°C (Passey et al., 2010) and mean annual precipitation of 180 mm/year (Cerling et al., 2003a). Turkana is a closed hydrological basin at low elevation. With the lake at ~400 m above sea level, Lake Turkana has the lowest elevation of the major rift valley lakes. Most of the water flowing into the lake (~80 percent) comes from the Omo River (Avery and Tebbs, 2018), originating in the Ethiopian highlands, with further contributions from the Turkwel River, originating on Mount Elgon, and the Kerio River flowing from high areas of western Kenya (Feibel et al., 1991). The predominant vegetation today east of Lake Turkana is composed of *Acacia–Commiphora–Salvadora* trees and bushes, with grasslands near the lake margins (Bamford, 2017).

Historically, the first reports of fossils found in the Turkana region are attributed to the French expedition led by Bourg de Bozas in 1902 and 1903, who discovered vertebrate fossils in the lower Omo Valley (Harris et al., 2006). These discoveries led to the subsequent expeditions by Camille Arambourg with the Mission Scientifique de l'Omo in 1932 and 1933 (Arambourg, 1947). In 1964, Bryan Patterson initiated systematic geological and paleontological surveys (continued from 1965 to 1972) between the Kerio and Turkwel rivers southwest of Lake

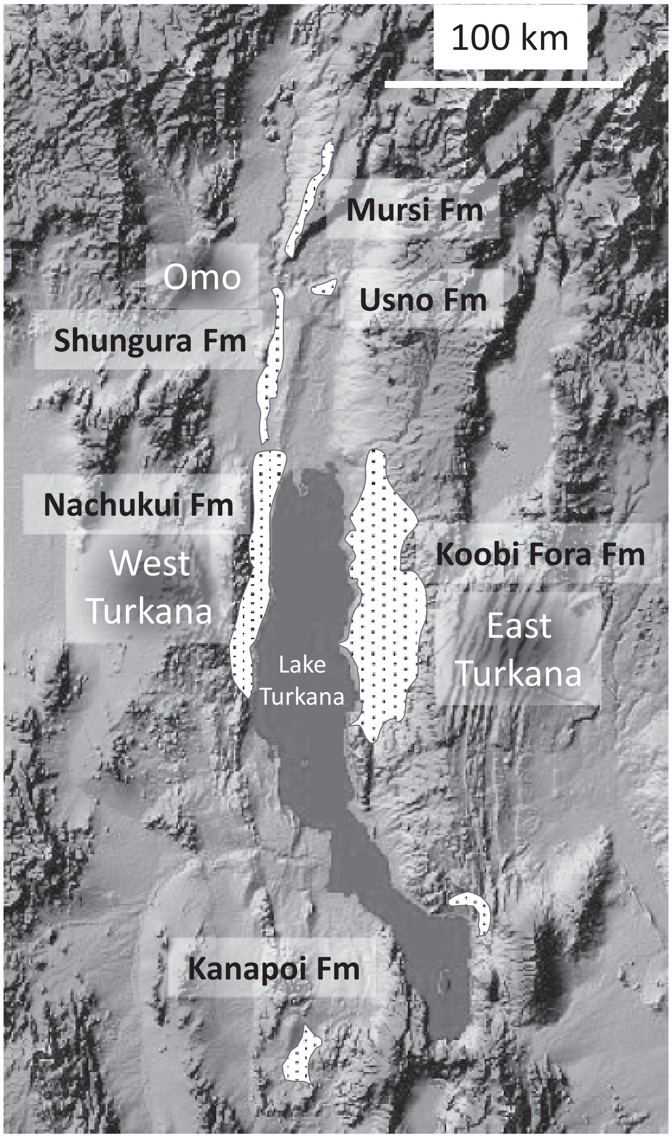

Figure 26.1 Map of the Omo-Turkana Basin including the lower Omo Valley of Ethiopia and the Lake Turkana Basin of Kenya. The Pliocene and Pleistocene Omo Group deposits include the Mursi, Nkalabong, Usno, and Shungura formations in Ethiopia, and the Koobi Fora, Nachukui, and Kanapoi formations in Kenya. The Nkalabong Formation is not known to be fossiliferous and is not shown on this map.

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Turkana, leading to the earliest reports of fossils from Kanapoi and Lothagam (Patterson, 1966; Patterson et al., 1970). In 1967, the International Omo Research Expedition (IORE) launched a long-term geological and paleontological project that conducted annual field seasons until 1976 (Howell, 1968, 1978a; Coppens et al., 1976; de Heinzelin, 1983b).

The East Turkana (then called East Rudolf) exposures came to the attention of Richard Leakey as he flew on his way to the Omo from Nairobi in 1967. The following year, Leakey began to explore the fossiliferous deposits east of Lake Turkana, accompanied by Bernard Wood, John Harris, Kamoya Kimeu, Bob Campbell, Paul Abell, and Margaret Leakey. Only a limited number of fossil specimens were collected in 1968, but the paleoanthropological potential of the region became clear. In 1969, Anna K. Behrensmeyer and Meave Leakey joined the team, and in 1970 Glynn Isaac agreed to lead archeological research at Koobi Fora (M.D. Leakey, 1978). Thus, Leakey established the East Rudolf Research Project (from 1969 to 1975) followed by the Koobi Fora Research Project (from 1975 to the present; Harris et al., 2006). In 1975 the government of Kenya changed the name of the lake from Lake Rudolf to Lake Turkana. Several researchers joined the team in the early 1970s, including geologists Carl Vondra, Bruce Bowen, Ian Findlater, and Thure Cerling; paleontologists Vince Maglio, Shirley Savage, Basil Cooke, Craig Black, Tim White, and Peter Williamson; paleoanthropologists Michael Day and Alan Walker; and archeologists Jack Harris and John Barthelme, among many others (M.D. Leakey, 1978). In 1979, Frank Brown, who had been working in the Omo since 1966, was invited to study the tuffs from the Koobi Fora region. Today, extensive research continues at East Turkana under the auspices of the National Museums of Kenya in collaboration with interdisciplinary teams from several institutions.

The Koobi Fora Formation

The Koobi Fora Fm, within the Turkana Depression, or the Omo-Turkana Basin, is part of the eastern branch of the East African Rift System (Brown and McDougall, 2011). Exposures of the Koobi Fora Fm occur from the Kenya/Ethiopia border in the north to the Loiyangalani area in the south. On the west side of the lake, West Turkana includes the sedimentary sequences of the Nachukui and Kanapoi Fms, while the lower Omo Valley on the Ethiopian side north of the lake encompasses the Shungura, Usno, Mursi, and Nkalabong Fms (Figure 26.1). These sedimentary sequences constitute the Omo Group (Figure 26.2), fossiliferous deposits associated with the ancient Omo river as well as its main tributaries (de Heinzelin, 1983b; Brown and McDougall, 2011; Feibel, 2011). In various parts of the Turkana Basin, Plio-Pleistocene deposits are covered by sediments of the younger Galana Boi Fm, which dates from the latest Pleistocene to the Holocene (Bowen and Vondra, 1973; Owen and Renaut, 1986; Beck et al., 2019).

The tectonic, sedimentary, and chronological framework of the Omo Group deposits, including the Koobi Fora Fm (Figure 26.3 and Table 26.1), has been well established after decades of research in the region, and it is concisely summarized by Brown and McDougall (2011) and Feibel (2011). The Koobi Fora Fm was formally defined by Brown and Feibel (1986: 299) as "sedimentary strata of the Koobi Fora region of Pliocene and Pleistocene age that lie disconformably or unconformably on, or are in fault contact with, Miocene and Pliocene volcanic rocks and/or associated sediments, and are disconformably overlain by the late Pleistocene and Holocene Galana Boi Beds of Bowen and Vondra (1973)." The formation, with a composite thickness of 565 m, is divided into eight members. The oldest is the Lonyumun Mb (Member), followed by the Moiti Mb, Lokochot Mb, Tulu Bor Mb, Burgi Mb, KBS Mb, Okote Mb, and Chari Mb. Each member, except for the Lonyumun, is defined by a volcanic ash layer at its base with the same name as the member (Figure 26.2): the Moiti Tuff defines the base of the Moiti Mb, the Lokochot Tuff defines the base of the Lokochot Mb, the Tulu Bor Tuff defines the base of the Tulu Bor Mb, etc. There is a major unconformity in the Burgi Mb, which is usually divided into a lower and upper Burgi Mb. The Koobi Fora Fm spans from about 4.3 Ma to 0.7 Ma.

The Koobi Fora Fm deposits represent fluvial, lacustrine, and deltaic paleoenvironments. The fossiliferous portions of the Koobi Fora Fm are primarily lake margin and fluvial, the latter laid down by the paleo-Omo river during times when a lake was either absent or restricted to portions of the rift basin. During times when the lake was absent, the river meandered through the basin and exited to the southeast via the Turkana River (inferred to have existed at times during the Pliocene and Pleistocene) through the Lamu embayment (Feibel, 1988, 1994). The paleo-Omo river originated in the Ethiopian highlands and is assumed to have been perennial, as it is today. Other rivers flowed into the basin from the south (paleo-Kerio River), west (paleo-Turkwel River), and the northeast. The fluvial sequences were interrupted episodically by lakes of varying size and duration. At various times during the Pliocene and Pleistocene the basin had hydrological connections to the Nile River drainage (Feibel, 2011). Thus, the rich geological, paleobotanical, and paleontological record of the Koobi Fora Fm includes elements from areas proximate to the depositional environments, e.g., the surrounding floodplains and lake shores, as well as elements transported downstream from more distant regions or reworked from previous deposits. The Appendix (Supplementary material) provides details of the Koobi Fora Formation exposures across Paleontological Collection Areas.

The PaleoTurkana Database

Most fossil vertebrates collected from the Koobi Fora Fm and housed at the National Museums of Kenya (NMK) in Nairobi were incorporated into a database created by the first author in collaboration with A.K. Behrensmeyer (Smithsonian Institution), Meave Leakey (then at NMK, now at the Turkana Basin Institute), and Emma Mbua (NMK). Since 2004, a public version of the database has been available to the scientific community through the NMK, the Smithsonian Institution (Bobe, 2011), and the Turkana Basin Institute (Fortelius et al., 2016). In this chapter we use a current version of the database, the PaleoTurkana Database, maintained by the first author (Bobe

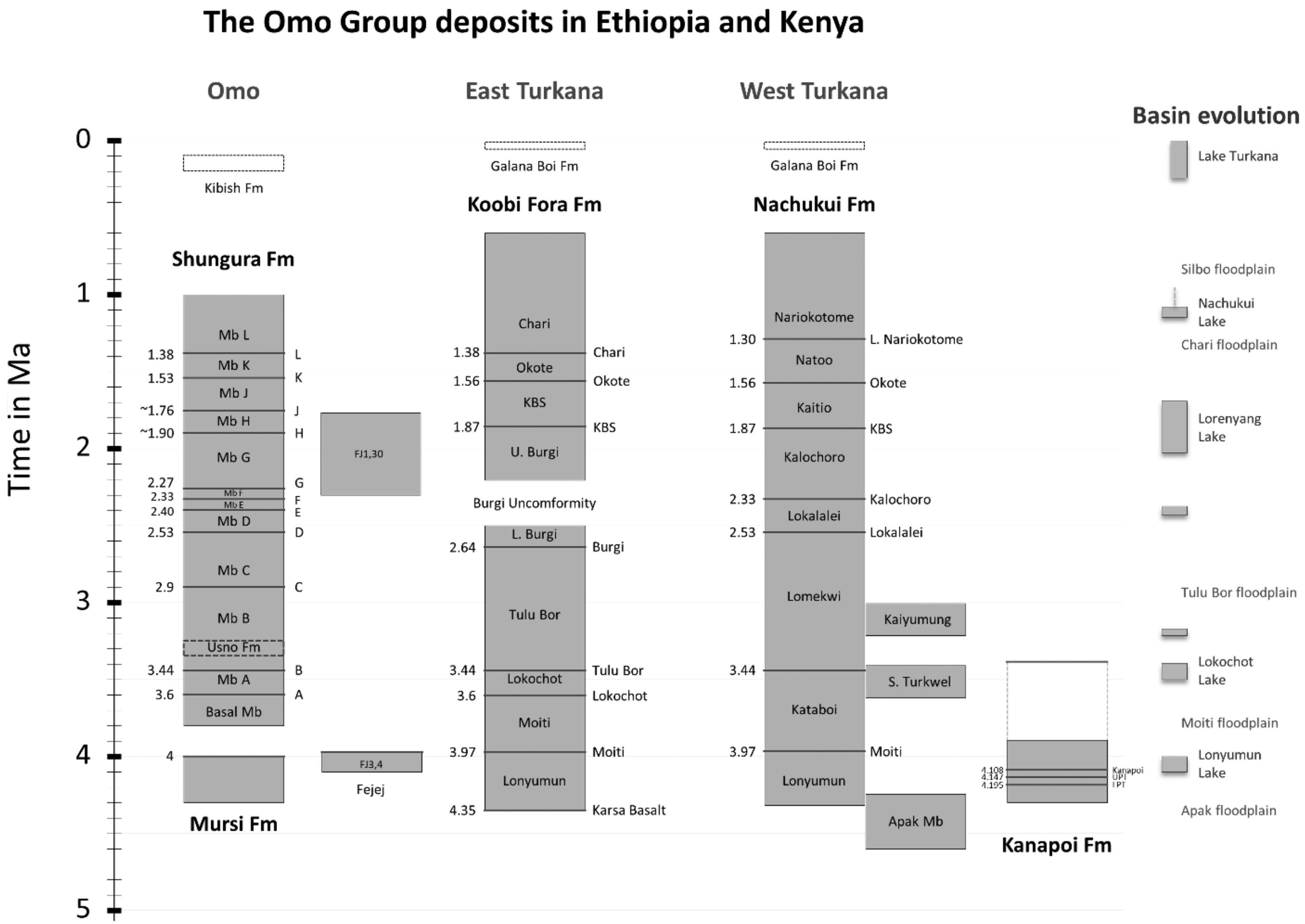

Figure 26.2 Schematic sequence of the Omo Group deposits including the Mursi, Usno, Shungura, Koobi Fora, Nachukui, and Kanapoi formations. Major tephra and basalts are indicated with horizontal lines, with their names on the right side of the column. Dates in Ma are indicated on the left of the column. The Kibish and Galana Boi formations constitute the Turkana Group deposits, and are depicted here in dashed rectangles. Major intervals in the evolution of the Omo-Turkana Basin are depicted on the right side of the figure.

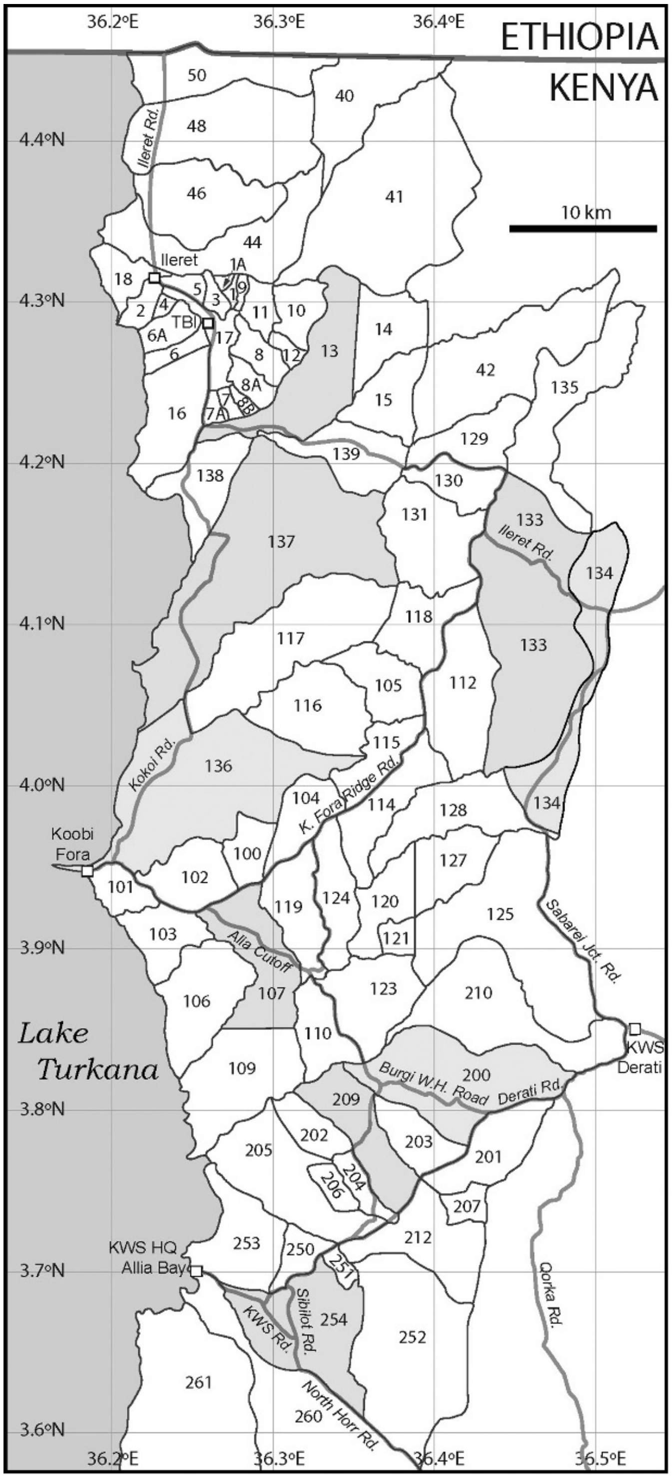

Figure 26.3 Map of paleontological collecting areas of the Koobi Fora Formation revised and modified by Frank Brown.

Table 26.1 Paleontological collection areas of the Koobi Fora Formation.

Area#	Area in km²
1	1.29
1A	0.93
2	5.88
3	3.63
4	1.53
5	3.65
6	5.62
6A	8.90
7	2.22
7A	2.49
8	9.24
8A	6.68
8B	1.68
9	1.43
10	12.50
11	7.52
12	3.12
13	47.40
14	23.30
15	21.80
16	34.40
17	11.30
18	11.90
40	41.70
41	116.00
42	58.00
44	49.20
46	42.40
48	69.00
50	33.80
100	12.20
101	11.40
102	22.30
103	19.30
104	18.80
105	20.90
106	37.10
107	38.30
109	46.60
110	18.50
112	42.40
114	28.10
115	17.80
116	37.90
117	69.88
118	25.60
119	24.70
120	19.40
121	5.68
123	32.00
124	22.10
125	82.70
127	22.90
128	37.40
129	35.30
130	15.60
131	39.20
133	115.00
134	46.70
135	37.80
136	103.00
137	140.00
138	25.90
139	27.20
200	65.70
201	26.50
202	13.00
203	17.50
204	7.84
205	47.90
206	6.28
207	6.63
209	31.70
210	60.20
212	36.50
250	9.45
251	3.74
252	85.80
253	32.80
254	54.00
260	67.20
261	86.20

and Carvalho, 2019). This database currently has about 12,000 records of fossil vertebrates from the Koobi Fora Fm. Table 26.2 provides a list of taxa known from the formation across geological members.

To determine taxonomic abundances, we use mNISP, a modified form of NISP (Number of Identified Specimens), whereby all specimens known to represent a single individual animal are counted as one, even if they have multiple records in

Table 26.2 Fossil mammals from the Koobi Fora Formation across members, with numbers representing modified numbers of identified specimens (mNISP) in the PaleoTurkana Database. P refers to specimens present but without abundance data. See main text for details.

	Lonyumun-Moiti	Lokochot	Tulu Bor	Upper Burgi	KBS	Okote	Chari
PRIMATES							
HOMINIDAE							
Hominini indet.	1	4	3	4	6	7	0
Australopithecus anamensis	46	0	0	0	0	0	0
Australopithecus afarensis	0	0	1	0	0	0	0
Paranthropus boisei	0	0	0	5	43	21	0
Homo indet.	0	0	1	26	29	10	0
Homo habilis	0	0	0	1	1	2	0
Homo rudolfensis	0	0	0	4	1	0	0
Homo erectus	0	0	0	4	9	11	0
CERCOPITHECIDAE							
Cercopithecidae indet.	2	0	0	0	0	1	3
Cercopithecinae indet.	70	24	6	27	24	18	0
Cercopithecus sp. indet. A	0	0	0	0	2	1	0
Cercopithecus sp. indet. B	0	0	1	0	0	0	0
cf. Papionini	3	0	0	1	0	1	0
Papionini indet.	16	11	1	1	7	11	0
Cercocebus indet.	0	0	0	0	0	1	0
cf. *Lophocebus*	0	0	0	0	0	6	0
Lophocebus cf. *albigena*	0	0	0	0	4	42	0
cf. *Parapapio*	40	0	0	1	1	2	0
Parapapio indet.	55	1	0	2	1	6	0
Parapapio cf. *ado*	52	1	1	0	0	0	0
Parapapio indet. A	0	0	0	3	1	2	0
Parapapio indet. B	7	3	0	0	1	0	0
Parapapio indet. C	0	1	0	0	0	1	0
cf. *Theropithecus* sp.	9	2	9	25	17	20	0
Theropithecus indet.	3	2	7	3	11	3	0
Theropithecus darti	0	1	0	0	0	0	0
Theropithecus brumpti	0	24	30	0	0	0	0
Theropithecus cf. *brumpti*	0	2	0	0	1	0	0
Theropithecus oswaldi	0	0	1	110	125	103	0
Theropithecus cf. *oswaldi*	0	0	0	10	9	4	1
cf. Colobinae	37	4	0	1	3	3	0
Colobinae indet.	19	6	0	8	17	15	0
cf. *Cercopithecoides*	40	4	2	0	0	0	0
Cercopithecoides williamsi	0	0	1	6	2	0	0
Cercopithecoides kimeui	0	0	2	6	6	0	0
Colobus indet.	0	0	0	0	0	2	0
Colobus freedmani	0	0	0	0	2	12	0
Paracolobus mutiwa	0	0	0	2	0	0	0
Rhinocolobus turkanaensis	0	2	0	10	14	0	0
cf. *Rhinocolobus*	0	4	0	1	8	2	0

Table 26.2 (cont.)

	Lonyumun-Moiti	Lokochot	Tulu Bor	Upper Burgi	KBS	Okote	Chari
RODENTIA							
THRYONOMYIDAE							
Thryonomis indet.	0	0	0	0	0	3	0
MURIDAE							
Aethomys indet.	0	0	0	0	0	6	0
Arvicanthis indet.	0	0	0	0	7	0	0
Mus indet.	0	0	0	0	5	0	0
Praomys cf. *minor*	0	0	0	0	24	0	0
Thallomys quadrilobatus	0	0	0	0	10	0	0
HYSTRICIDAE							
Hystrix indet.	1	1	0	0	0	1	0
DIPODIDAE							
Jaculus orientalis	0	0	0	0	0	3	0
SCIURIDAE							
Sciuridae indet.	1	0	0	0	0	0	0
CARNIVORA							
Carnivora indet.	0	0	2	8	1	1	0
CANIDAE							
cf. Canidae	0	0	0	0	1	0	0
Lupulella sp.	0	0	0	6	2	0	0
Vulpes sp.	0	0	0	0	1	0	0
MUSTELIDAE							
Mustelidae indet.	0	1	0	2	2	1	1
Enhydriodon afman	0	1	0	0	0	0	0
Enhydriodon cf. *afman*	1	0	2	1	0	0	0
cf. *Torolutra* sp.	0	0	0	9	1	1	0
Torolutra cf. *ougandensis*	0	0	0	2	1	0	0
cf. *Hydrictis*	0	0	0	1	1	0	0
Hydrictis gudho	0	0	0	1	0	0	0
cf. *Aonyx*	0	0	0	0	1	0	0
Lutrinae gen. sp. nov.	0	0	0	1	0	0	0
Lutrinae indet.	0	0	0	1	0	0	0
Mellivora indet.	0	0	0	1	0	1	0
aff. *Plesiogulo*	0	0	1	0	0	0	0
aff. *Ictonyx*	0	0	1	0	0	0	0
URSIDAE							
cf. *Agriotherium* sp.	1?	0	2	0	0	0	0
VIVERRIDAE							
cf. *Civettictis*	0	0	0	4	0	0	1
cf. *Pseudocivetta* sp.	0	0	0	1	2	0	0
Pseudocivetta ingens	0	0	0	1	3	0	0
aff. *Genetta*	0	0	0	1	0	0	0
Genetta genetta/maculata	0	0	0	2	0	2	0
Genetta nyakitongwer	0	0	0	0	1	0	0
Viverridae indet. sp. A	0	0	0	1	0	0	0

Table 26.2 (cont.)

	Lonyumun-Moiti	Lokochot	Tulu Bor	Upper Burgi	KBS	Okote	Chari
Viverridae indet. sp. B	0	0	1	0	1	0	0
Viverridae indet.	1	1	0	0	1	1	0
HYAENIDAE							
Hyaenidae indet.	0	1	1	1	1	0	0
Hyaenidae indet. sp. A	0	0	0	0	0	1	0
Crocuta indet.	0	1	0	2	1	2	0
Crocuta eturono	0	0	1	0	0	0	0
Crocuta dietrichi	0	0	0	2	0	0	0
Crocuta cf. *dietrichi*	0	1	0	4	0	0	0
Crocuta ultra	0	0	0	2	8	9	0
Crocuta cf. *ultra*	0	0	0	1	6	3	0
Hyaena sp.	0	1	0	0	0	4	0
Hyaena cf. *makapani*	0	0	0	3	1	0	0
Hyaena cf. *hyaena*	1?	0	1	0	1	0	0
cf. *Parahyaena*	0	0	0	0	0	1	0
FELIDAE							
Felidae indet.	0	0	1	3	1	0	0
Homotherium sp.	3	1	4	10	7	1	0
cf. *Meganterion* sp.	0	0	0	0	2	1	0
Megantereon whitei	0	0	0	0	1	2	0
Dinofelis indet.	0	0	0	0	2	0	0
Dinofelis petteri	1	0	1	5	1	0	0
Dinofelis aronoki	0	0	0	1	1	0	0
Dinofelis piveteaui	0	0	0	0	0	9	0
Machairodontinae indet.	0	0	0	1	0	0	0
Panthera pardus	0	0	0	3	1	0	0
Panthera leo	0	0	0	5	1	11	0
Acinonyx sp.	0	0	0	2	0	0	0
Acinonyx sp. nov.	0	0	0	0	2	1	0
Caracal or *Leptailurus*	0	0	4	0	0	0	0
ARTIODACTYLA							
BOVIDAE							
Bovidae indet.	353	0	3	0	13	15	1
Tragelaphini sp.	P	6	12	12	35	14	0
Tragelaphus kyaloi	P	1	0	0	0	0	0
Tragelaphus nakuae	0	0	0	16	7	0	0
Tragelaphus rastafari	0	20	27	1	0	0	0
Tragelaphus strepsiceros	0	0	0	37	79	19	0
Bovini sp.	0	0	0	4	2	0	0
Simatherium cf. *khollarseni*	0	4	25	0	0	0	0
Pelorovis oldowayensis	0	0	0	2	12	7	0
Pelorovis turkanensis	0	0	0	6	52	8	1
Aepyceros sp.	P	0	0	3	7	1	0
Aepyceros shungurae	0	16	4	0	0	0	0
Aepyceros melampus	0	0	0	33	71	5	0

Table 26.2 (cont.)

	Lonyumun-Moiti	Lokochot	Tulu Bor	Upper Burgi	KBS	Okote	Chari
Reduncini sp.	P	1	25	55	66	15	0
Kobus sp.	0	0	0	1	1	2	0
Kobus ancystrocera	0	0	9	6	43	0	0
Kobus ellipsiprymnus	0	0	0	0	5	0	0
Kobus aff. *kob*	P	1	4	0	0	0	0
Kobus kob	0	0	0	2	28	48	0
Kobus aff. *leche*	0	0	0	3	15	1	0
Kobus oricornus	P	6	30	0	0	0	0
Kobus sigmoidalis	P	2	13	104	82	3	0
Menelikia leakeyi	P	0	13	0	0	0	0
Menelikia lyrocera	P	0	2	23	78	2	0
Hippotragus gigas	0	0	0	3	2	0	0
Oryx sp.	0	0	0	2	12	0	0
Alcelaphini sp.	P	0	0	8	39	7	1
Beatragus antiquus	0	0	0	2	8	2	0
Beatragus cf. *hunteri*	0	0	0	0	0	0	1
Connochaetes aff. *gentryi*	0	7	3	0	0	0	0
Connochaetes gentryi	0	0	0	12	16	6	0
Damaliscus indet.	0	1	0	0	0	3	0
Damaliscus cf. *eppsi*	0	0	4	0	0	0	0
Damaliscus eppsi	0	0	0	3	66	7	0
Damaliscus cf. *niro*	0	0	0	0	3	0	0
Damaliscus sp. nov.	0	0	0	0	0	1	0
Megalotragus sp.	0	1	6	0	0	0	0
Megalotragus isaaci	0	0	0	34	38	9	0
Parmularius sp.	0	0	0	0	1	0	0
cf. *Parmularius angusticornis*	0	1	1	0	0	0	0
cf. *Parmularius altidens*	0	0	0	0	1	0	0
Caprini indet.	0	0	0	0	1	0	0
Antilopini indet.	P	0	0	0	0	0	0
Antidorcas recki	0	0	3	14	49	3	0
Gazella sp.	P	1	0	12	15	1	0
Gazella aff. *granti*	0	0	0	0	1	1	0
Gazella cf. *janenschi*	0	0	0	3	5	0	0
Gazella praethomsoni	0	4	4	18	11	2	1
Raphicerus	0	0	0	1	5	0	0
Madoqua	0	0	0	0	2	0	0
GIRAFFIDAE							
Giraffa indet.	33	5	10	8	39	8	0
Giraffa jumae	4	1	2	1	6	2	0
Giraffa pygmaea	1	4	1	9	19	3	0
Giraffa stillei	9	3	1	8	16	0	0
Sivatherium maurusium	3	2	3	8	32	0	0
HIPPOPOTAMIDAE							
Hippopotamidae indet.	118	0	0	0	0	0	0

Table 26.2 (cont.)

	Lonyumun-Moiti	Lokochot	Tulu Bor	Upper Burgi	KBS	Okote	Chari
aff. *Hippopotamus* cf. sp. Hadar	5	0	0	0	0	0	0
aff. *Hippopotamus protamphibius*	0	8	18	0	0	0	0
aff. *Hippopotamus aethiopicus*	0	0	0	3	25	13	0
aff. *Hippopotamus karumensis*	0	0	0	37	50	13	0
Hippopotamus gorgops	0	0	0	6	17	6	1
SUIDAE							
Nyanzachoerus kanamensis	105	1	10	0	0	0	0
Notochoerus jaegeri	8	0	0	0	0	0	0
Notochoerus euilus	25	1	58	0	0	0	0
Notochoerus scotti	0	0	4	104	6	0	0
Kolpochoerus limnetes	0	1	7	152	138	19	0
Metridiochoerus andrewsi	0	0	0	66	217	1	0
Metidiochoerus compactus	0	0	0	0	10	65	0
Metridiochoerus modestus	0	0	0	1	4	1	0
Metridiochoerus hopwoodi	0	0	0	2	27	6	0
CAMELIDAE							
Camelus	0	0	4	0	0	0	0
PERISSODACTYLA							
EQUIDAE							
Equidae indet.	45	0	3	3	1	2	0
Eurygnathohippus sp.	0	0	1	3	10	0	0
Eurygnathohippus cornelianum	0	0	0	1	0	0	0
Eurygnathohippus cf. *ethiopicum*	0	0	1	22	24	4	0
Eurygnathohippus hasumense	1	1	18	1	0	0	0
Equus sp.	0	0	0	15	80	7	0
Equus koobiforensis	0	0	0	36	23	1	0
Equus cf. *tabeti*	0	0	0	0	2	4	0
Equus cf. *grevyi*	0	0	0	0	0	8	0
Equus cf. *burchelli*	0	0	0	0	0	1	0
RHINOCEROTIDAE							
Rhinocerotidae indet.	11	0	0	0	0	0	0
Ceratotherium praecox	2	0	3	0	0	0	0
Ceratotherium simum	0	0	0	8	21	1	0
Diceros bicornis	0	0	0	1	9	0	0
PROBOSCIDEA							
DEINOTHERIIDAE							
Deinotherium bozasi	13	1	16	12	12	0	0
ELEPHANTIDAE							
Elephas recki	23	0	0	0	2	0	0
Elephas recki atavus	0	0	0	9	18	0	0
Elephas recki brumpti	0	0	26	0	0	0	0
Elephas recki ileretensis	0	0	0	0	17	0	0
Elephas recki recki	0	0	0	0	0	10	0
Elephas recki shungurensis	0	0	7	33	0	0	0
Loxodonta adaurora adaurora	8	0	0	0	0	0	0

Table 26.2 (cont.)

	Lonyumun-Moiti	Lokochot	Tulu Bor	Upper Burgi	KBS	Okote	Chari
Loxodonta adaurora kararae	0	0	0	6	0	0	0
Loxodonta exeptata	0	0	12	0	0	0	0
TUBULIDENTATA							
ORYCTEROPODIDAE							
Orycteropus indet.	0	1	0	1	3	1	0

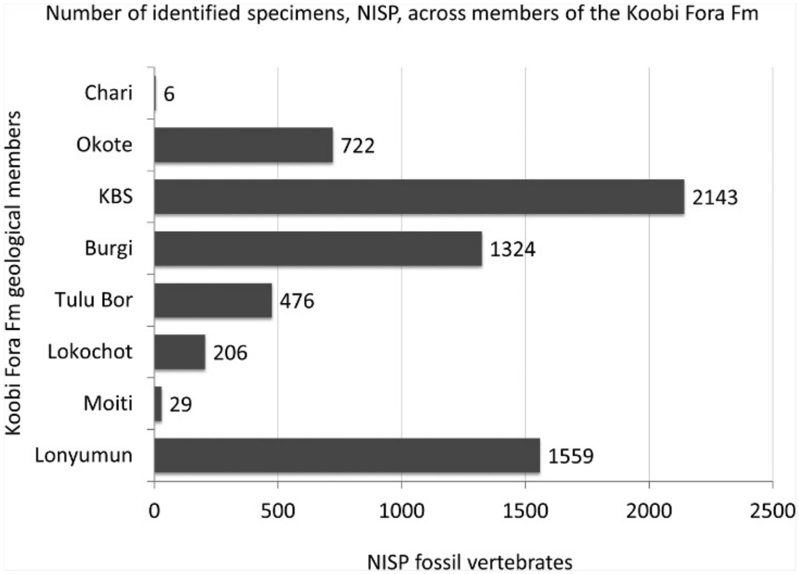

Figure 26.4 Abundance of fossil mammals (NISP) per geological member of the Koobi Fora Formation.

the database. For example, the newly described partial skeleton KNM-ER 47000 is represented by nine records in the database (partial scapula, humeral fragments, ulna, etc.; Richmond et al., 2020), but as all specimens belong to a single individual animal, it is counted as one in Table 26.2. Faunal abundances in Table 26.2 indicate the number of fossils in the database, but not necessarily relative abundances of these taxa in the exposures. Some taxa (e.g., Primates) have been more thoroughly collected, studied, identified, and published than others (e.g., Hippopotamidae) and their abundances in Table 26.2 will be inflated relative to other taxa. The numbers provided here are not adjusted for collection efforts and taphonomic factors that undoubtedly play an important role affecting the abundance data. Even considering these caveats, however, it still is clear that fossil vertebrates are unevenly distributed across members of the Koobi Fora Fm (Figure 26.4). Some of the lower members, i.e., Moiti, Lokochot, and Tulu Bor, have lower sample sizes than the upper members (Table 26.2). Many specimens from these lower members have yet to be fully studied and published, but ongoing work on these fossils will significantly improve our understanding of the interval between about 4 Ma and 3 Ma (Villaseñor, 2017; Dumouchel, 2018). Thus, for the lower part of the Koobi Fora sequence we focus on those taxa that have been well published: hominins (Leakey and Leakey, 1978; Wood, 1991; Leakey et al., 1995; Ward et al., 2001), cercopithecids (Jablonski and Leakey, 2008), and carnivores (Werdelin and Lewis, 2013b).

Paleoenvironments and Fossil Mammals

The hydrology of the Omo-Turkana Basin and its evolution during the late Cenozoic has played a central role in shaping the water balance and vegetation of the region. A brief outline of key intervals in the history of the basin is sketched in Figure 26.2, derived from the work of Craig Feibel and Frank Brown (Brown and Feibel, 1991; Feibel et al., 1991; Feibel, 1999a). Alongside changes in basin evolution, the region has been affected by frequent volcanism in the form of volcanic ashes (Feibel, 1999b) and lava flows (Haileab et al., 2004). Some tephra in the Koobi Fora Fm were the result of massive eruptions that likely blanketed large areas of eastern Africa (e.g., Moiti Tuff, Tulu Bor Tuff, Chari Tuff), while others corresponded to smaller, and sometimes frequent and complex episodes of deposition by fluvial systems (e.g., Okote Tuff Complex). Figure 26.5 presents the number of separate tephra per unit of time in the Omo-Turkana Basin from 4.2 Ma to 1.0 Ma (after an illustration by Feibel, 1999b) with data published by McDougall and colleagues (McDougall, 1985; McDougall

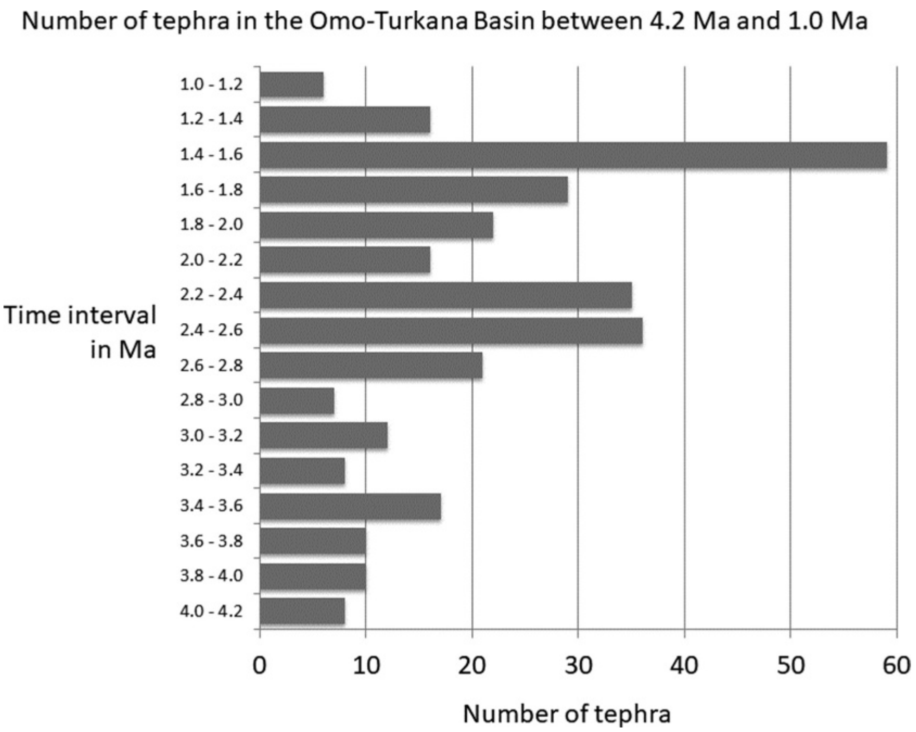

Figure 26.5 Number of tephra in the Omo-Turkana Basin between 4.2 to 1.0 Ma. Data compiled and redrawn from McDougall et al. (2012) and Feibel (1999b). Some of these tephra are airfall deposits from massive volcanic eruptions that likely produced major disruptions of regional ecosystems

et al., 1985; Brown et al., 2006; Brown and McDougall, 2011; McDougall and Brown, 2006, 2008; McDougall et al., 2012). There were three increasingly higher peaks of tephra deposition in the basin with intervals of about 1 million years: first at about 3.5 Ma, then at about 2.5 Ma, and finally at about 1.5 Ma. Whether these peaks relate to broader-scale tectonic cycles remains to be determined. The magnitude and frequency of volcanism in the region provided some degree of environmental disruption and heterogeneity that influenced the vegetation and fauna at various times (Bobe and Carvalho, 2019).

Temperatures in the Turkana Basin appear to have been relatively stable over the past 4 Myr, with surface temperatures during soil formation typically above 30°C (Passey et al., 2010). Along with consistently high temperatures, water deficit in the basin (a measure of aridity) shows no discernible trends over the past 4.4 Myr (Blumenthal et al., 2017). Nevertheless, stable carbon isotopes from paleosols are indicative of an overall shift toward increasingly C_4 environments in the region between 4.2 and 1 Ma (Wynn, 2004; Levin et al., 2011). Thus, there seems to be a decoupling between long-term changes in aridity, which were minimal, and the documented increase in C_4 vegetation in the region. The vegetation history of the basin can be well summarized by stable carbon isotopes from pedogenic carbonates as published by several colleagues (Wynn, 2000; Cerling et al., 2003b, 2011b; Quinn et al., 2007; Levin et al., 2011; Quinn and Lepre, 2020). The pedogenic carbonate isotope data from the basin between about 4.3 Ma and 1 Ma is synthesized in Figure 26.6. Stable carbon isotopes have also been obtained from dental enamel from a range of fossil mammals in the Turkana Basin (Cerling et al., 2003a, 2011a, 2013a, 2013b, 2015; Patterson et al., 2017a, 2017b, 2019). Here we illustrate previously published data from hominins (Figure 26.7) and from the cercopithecid genus *Theropithecus* (Figure 26.8).

In our discussions we use the term megaherbivore to refer to herbivorous mammals estimated to weigh 1000 kg or more (Owen-Smith, 1988). Today there are six species of megaherbivores in Africa: elephants – *Loxodonta africana* and *Loxodonta cyclotis*; rhinocerotids – *Ceratotherium simum* and *Diceros bicornis*; giraffe – *Giraffa camelopardalis*; and hippos – *Hippopotamus amphibius.* However, in the past African megaherbivores were significantly more abundant and diverse (Faith et al., 2018).

Below we summarize the geology and reconstructed paleoenvironments for each of the Koobi Fora Fm members, based on sedimentological, faunal, and stable isotopic evidence. By presenting the data on a member by member basis, we are dealing with samples that are time-averaged and derive from different depositional environments. Thus, these samples do not necessarily represent paleocommunities except in a very broad sense. We suggest that further taphonomic work is needed to evaluate the ideas, paleoenvironmental reconstructions, and faunal associations tentatively presented here (Behrensmeyer, 1985).

Lonyumun Member: 4.3–3.97 Ma

The Lonyumun Mb is composed of sediments deposited over Miocene and early Pliocene volcanic rocks, and capped by the base of the Moiti Tuff, dated to 3.97 Ma (McDougall et al., 2012).

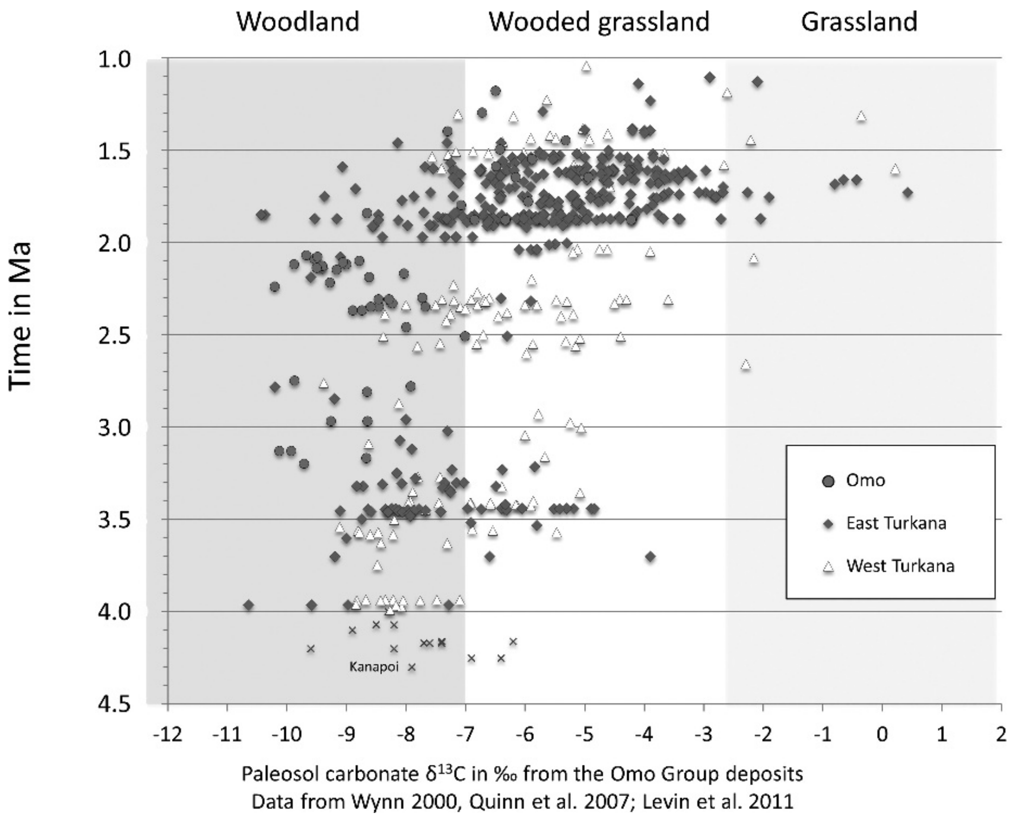

Figure 26.6 Paleosol carbonate $\delta^{13}C$ in ‰ from the Omo Group deposits reflecting C_3 and C_4 vegetation in the Omo-Turkana Basin from 4.3 Ma to 1.0 Ma. Data from Quinn et al. (2007) and Levin et al. (2011). (A black and white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

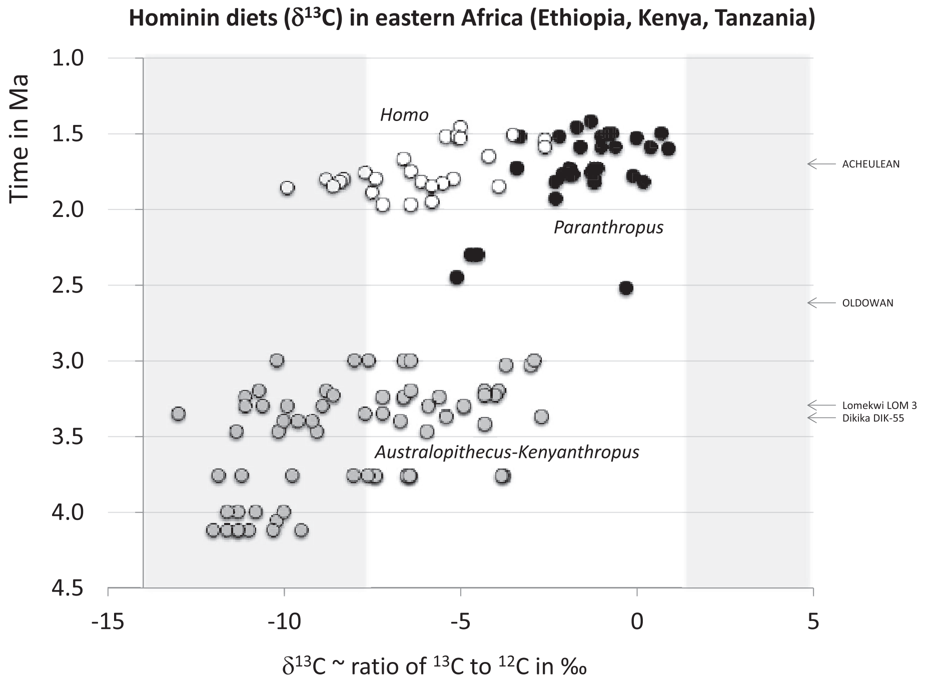

Figure 26.7 Stable carbon isotopes, $\delta^{13}C$ in ‰, in hominin dental enamel in East African sites (Ethiopia, Kenya, Tanzania) from 4.2 Ma (*Australopithecus anamensis*) to 1.5 Ma (*Homo* and *Paranthropus*).

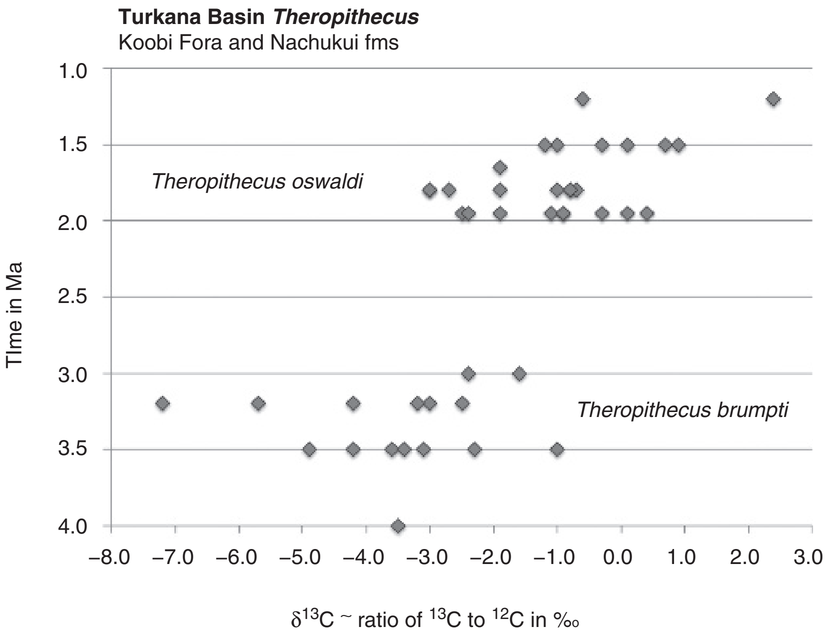

Figure 26.8 Stable carbon isotopes, δ^{13}C in ‰, in *Theropithecus* dental enamel in the Turkana Basin (Koobi Fora and Nachukui formations) from 4 Ma to 1.2 Ma.

The type section is defined in Area 260, where it is 36.8-m thick (Brown and Feibel, 1986). This member is exposed in areas 13–15, 40–41, 117, 129, 133, 136–139, 200, 212, 251–252, 254, 260–261, and in the Loiyangalani region. Fossiliferous sediments of this age range are also well represented in the Apak Mb of the Nachukui Fm at Lothagam, in the Kanapoi Fm, and in the Omo Mursi Fm. In the lower part of the Lonyumun Mb about 4.3 Ma fluvial deposits of the Apak floodplain record the onset of sediment accumulation associated with the integrated Omo Group, but by 4.1 Ma a major freshwater lake formed and covered most of the basin: the Lonyumun Lake lasted for about 100 ky (Feibel et al., 1991; Feibel, 2011). By about 4 Ma, the extensive flood basalts of the Gombe Group intruded into the Lonyumun Mb landscape (Haileab et al., 2004), and the lake was replaced by a depositional system dominated by a large river (Figure 26.2; Feibel et al., 1991). Pedogenic carbonates from paleosols in the Allia Bay region indicate that woodland was the dominant type of vegetation during this time (Levin et al., 2011; Figure 26.6), but stable isotopes from mammalian dental enamel indicate that grasses were also widely available (Cerling et al., 2015).

The richest faunal sample from the Lonyumun Mb comes from the very top of the sequence, just below (or within) the Moiti Tuff at Locality 261–1 (in Area 261), the site of *Australopithecus anamensis* at Allia Bay (Leakey et al., 1995). Specimens in the 261–1 excavation derive from a densely packed bone bed, about 20 cm thick, with abundant but abraded and fragmentary bones and teeth (Coffing et al., 1994; Hagemann, 2010). This means that many of the specimens from the bone bed have only been identified to order or family rather than to genus or species. There are about 2000 specimens of fossil fish, with the lungfish *Protopterus* being particularly abundant and indicating floodplain, swampy habitats. Other fishes including *Gymnarchus*, *Hydrocynus*, *Sindacharax* are indicative of fluvial settings (Coffing et al., 1994). The reptiles, Trionichidae (soft-shelled turtles), *Crocodylus*, and *Euthecodon* are all indicative of aquatic conditions. The horned crocodile *Crocodylus thorbjarnarsoni* is documented at the nearby site of Kanapoi and in later intervals at Koobi Fora (Brochu, 2020), and it is also likely that it was one of the top predators at Allia Bay. The primate and carnivoran faunas from Allia Bay are well studied and published (Jablonski and Leakey, 2008; Werdelin and Lewis, 2013b), while other taxa including bovids and suids are currently under review (Dumouchel, 2018). All hominins are attributed to the species *Australopithecus anamensis*, which, with a total of 46 specimens (Table 26.2), is relatively abundant at 261–1. This hominin is also present in the older deposits of the nearby site of Kanapoi (Ward et al., 2001). Comparisons between 261–1 and Kanapoi are difficult because the two sites are taphonomically very different: Allia Bay 261–1 hominins derive from a fluvial channel bone bed (Coffing et al., 1994), whereas Kanapoi hominins come primarily from paleosols (Wynn, 2000).

Among Allia Bay monkeys, cercopithecines are about 2.5 times more abundant than colobines, with *Parapapio* as the dominant primate. This is the only member of the Koobi Fora Fm in which *Parapapio* is more abundant than *Theropithecus*. Sometime after 3.9 Ma, *Theropithecus* became the dominant cercopithecid genus in the basin. Both *Australopithecus* and *Theropithecus* co-occurred at Allia Bay, as they did at Kanapoi. Among carnivores, *Homotherium* was a ubiquitous predator in the Turkana Basin during this time, both at Kanapoi and Allia Bay (Werdelin and Lewis, 2013b). Bovids are currently under review, so here we report taxonomic presence or absence. As at Kanapoi, Tragelaphini was the most abundant bovid tribe at Allia Bay 261–1, followed by Alcelaphini. Most of the suids belong to the species *Nyanzachoerus kanamensis*, with a few specimens of *Notochoerus jaegeri* and *Not. euilus*. Hipparionin equids were common. The diversity of megaherbivores in the

Allia Bay deposits appears lower than at Kanapoi, where there were 10 species of mammals weighing over 1000 kg. However, the lower diversity at Allia Bay could result from the fragmentary nature of the fossils, which limits identification to species. Overall, the paleoenvironments of *A. anamensis* at East Turkana appear to have been similar to those of the well-studied site of Kanapoi, with a mix of woodlands and grasslands and abundant freshwater in rivers and/or lakes (Bobe et al., 2020a).

Moiti Member: 3.97–3.6 Ma

The Moiti Tuff, well-dated to 3.97 Ma, defines the base of the Moiti Mb, and the base of the Lokochot Tuff, dated to 3.6 Ma, caps the member. The type section of the Moiti Mb is defined at Jarigole in Area 261, where it measures 59.9 m in thickness (Brown and Feibel, 1986). Outcrops of the Moiti Mb occur in areas 13, 40–41, 129, 133–134, 200, 205, 212, 250–252, 254, and 260–261. The Moiti Tuff is the earliest of the major volcanic eruptions to blanket the Turkana Basin, measuring up to 17 m in parts of the Allia Bay Region (Brown and Feibel, 1991). This ash layer is also found in the Gulf of Aden about 1600 km to the northeast, indicating that it was the product of a massive volcanic eruption (Sarna-Wojcicki et al., 1985). Paleogeographically, this interval was dominated by a large meandering river flowing across the Moiti Floodplain from about 4 Ma to 3.6 Ma, with no evidence of lacustrine sediments (Figure 26.2; Feibel et al., 1991; Feibel, 2011). The fossil record of the Moiti Mb is relatively sparse, except for the very base of this member at Locality 261–1, where a dense concentration of bones occurs below or within the base of the Moiti Tuff, as discussed in the section above. Paleosols from this level indicate a mixture of woodlands and wooded grasslands (Figure 26.6; Levin et al., 2011). Fossil samples other than those from Locality 261–1 show a dominance of Reduncini among the bovids.

Lokochot Member: 3.6–3.44 Ma

The Lokochot Mb ranges from the base of the Lokochot Tuff, dated to 3.6 Ma, to the base of the Tulu Bor Tuff, dated to 3.44 Ma (McDougall and Brown, 2008). Its type section as defined in Area 261 measures 34.4 m (Brown and Feibel, 1986). This member is also exposed in areas 13, 40–41, 117, 129, 133–134, 136–139, 204–206, 210, 212, and 250–253. A major lake, Lake Lokochot, was the dominant paleogeographic feature during this interval. This was a relatively shallow lake with fluctuating margins that persisted for about 60 ky (Feibel, 2011; Figure 26.2). Although the published paleontological record of the Lokochot Mb is relatively sparse (Figure 26.4), significant fieldwork in recent years has added important new faunal samples to the collections, including hominins, but these fossils are still under study (Villaseñor, 2017) so they are not discussed here. So far only four hominins have been published from the Lokochot Mb, and these are considered Hominini indet. The holotype of the hominin *Kenyanthropus platyops*, KNM-WT 40000, derives from sediments of Lokochot age west of Lake Turkana (Leakey et al., 2001). At Koobi Fora, *Theropithecus brumpti* became the most abundant primate during this time. Stable carbon isotopes from dental enamel indicate that *Theropithecus* was a mixed feeder of C_3 and C_4 vegetation during this time (Figure 26.8; Cerling et al., 2013c). As with the Moiti Mb, the Lokochot pedogenic carbonates indicate a mixture of woodlands and wooded grasslands in the region (Figure 26.6). The Lokochot Mb correlates with Mb A of the Shungura Fm, where suids were the most abundant family of mammals (Bobe and Behrensmeyer, 2004). The higher abundance of suids in the Shungura Fm and monkeys in the Koobi Fora Fm may relate to differences in depositional environments between the Omo and East Turkana. Taphonomic factors remain to be fully analyzed.

Tulu Bor Member: 3.44–2.63 Ma

The Tulu Bor Mb spans from the base of the Tulu Bor Tuff to the base of the Burgi Tuff. At the type section in Areas 202 and 204, it measures 86.2 m in thickness (Brown and Feibel, 1986). This member is exposed in areas 13, 40, 116–117, 129–130, 133, 136–139, 202, 204–209, 212, 250, 260–261, and in the Loiyangalani Region. The Tulu Bor Tuff is a major marker bed for dating and correlations. It occurs from the Gulf of Aden in the north to the Lake Baringo basin in the south, and it is found in sedimentary sequences in the Afar (where it is called the Siki Hakoma Tuff), the lower Omo Valley (where it is called Tuff B), and the Turkana Basin (Figure 26.9; Brown, 1982; WoldeGabriel et al., 2013). This tuff provides an unparalleled opportunity for extensive faunal and sequence correlations across eastern Africa (Bobe et al., 2007b; Villaseñor, 2017).

By 3.4 Ma, the Lokochot Lake no longer existed, and the region was dominated by a large river that exited the basin through a southeast outlet toward the Indian Ocean (Bruhn et al., 2011). The Tulu Bor Floodplain characterized the paleogeography of the basin for about one million years (Feibel, 2011). Pedogenic carbonates indicate woodlands and wooded grasslands in the region (Levin et al., 2011), while dental enamel isotopes provide evidence of both woodland and grassland dietary resources for mammals (Cerling et al., 2013a). Important new paleontological collections from this time are currently under study by A. Villaseñor and colleagues, and these include new hominins as well as abundant fossil mammals. On the west side of the lake, the paratype of *Kenyanthropus platyops*, KNM-WT 38350, derives from strata equivalent to the lower Tulu Bor Mb (Leakey et al., 2001), and in temporal association with the earliest known archeological site at Lomekwi 3 (Harmand et al., 2015). Although rare, *Australopithecus afarensis* (KNM-ER 2602) has been identified in the Tulu Bor Mb (Kimbel, 1988). The most abundant species in the lower Tulu Bor Mb are *Notochoerus euilus*, *Theropithecus brumpti*, *Kobus oricornus*, *Tragelaphus rastafari*, and *Elephas recki*, in that order (Harris, 1983, 1991; Jablonski and Leakey, 2008). The upper part of the Tulu Bor Mb has a sparse fossil record, but it may hold one of the earliest specimens of the genus *Homo*, KNM-ER 5431 (Wood, 1991). The earliest record of *Paranthropus* also dates to this time, about 2.7 Ma, in Mb C of the Shungura Fm in the Omo (Suwa et al., 1996; Bobe and Carvalho, 2019).

Figure 26.9 The Tulu Bor Tuff, dated to 3.44 Ma, caps this sequence with Lokochot Member sediments below, in Area 117 of the Koobi Fora exposures. The Tulu Bor Tuff is a widespread volcanic ash layer, found from the Gulf of Aden in the north to the Tugen Hills in the south. It is a major marker in the correlation of sedimentary sequences in the Afar region, the lower Omo Valley, the Turkana Basin, and the Tugen Hills. In this view, it forms the white, erosion-resistant layer capping the ridge.

Burgi Member: 2.63–1.87 Ma

The Burgi Mb is defined by sediments from the base of the Burgi Tuff, dated at 2.6 Ma, to the base of the KBS Tuff, dated at 1.87 Ma (Brown and Feibel, 1986; McDougall and Brown, 2008). Burgi sediments occur in areas 10, 12–13, 40–41, 44, 48, 50, 100, 102, 104–105, 110, 114–118, 123, 125, 127, 129–131, 134, 136, 139, 200, 202–203, 207, 210, and in the Loiyangalani Region. A major unconformity – the Burgi Unconformity – separates the lower Burgi Mb (Feibel, 2011), with a sparse fossil record, from the upper Burgi Mb, which has a rich fossil record in its uppermost sediments. The type section of the lower Burgi in Area 207 measures 26.9 m in thickness, whereas the upper Burgi type section in Area 102 measures 120.1 m (Brown and Feibel, 1986). The longest lived of the late Cenozoic Turkana Basin lakes, the Lorenyang Lake, developed in the later stages of the Burgi Mb, and remained in place in varying configurations until about 1.5 Ma. The gigantic crocodile *Crocodylus thorbyarnarsoni* was abundant in the rivers and lake of this period: measuring over 6 m in length (larger than any living crocodile) it would have been a formidable predator of water-dependent hominins and other vertebrates (Brochu and Storrs, 2012). During much of this time, the basin continued to have a hydrological outlet to the Indian Ocean through the Turkana River, as attested by the presence of stingrays in the upper Burgi, KBS, and Okote Mbs (Feibel, 1994). Pedogenic stable isotopes (Quinn et al., 2007; Levin et al., 2011) and fossil wood (Braun et al., 2010; Bamford, 2011) indicate that during the upper Burgi times the vegetation in the region continued to be a mix of woodlands and wooded grasslands with an ample supply of fresh water.

By 2.3 Ma, species of *Homo* and *Paranthropus* appear to have been well-established in the Omo-Turkana Basin, with three or four hominin species co-occurring by 2 Ma (Bobe and Carvalho, 2019; Grine et al., 2019). Key hominin fossils from the upper Burgi Mb include the lectotype of *Homo rudolfensis*, KNM-ER 1470 (Figure 26.10A) and the KNM-ER 1813 cranium usually referred to *Homo habilis* (Figure 26.10B). The earliest records of *H. erectus* are from the upper Burgi with specimens KNM-ER 1481, 1812, 2598, and 3228. In the upper Burgi Mb, specimens of *Homo* are more abundant than those of *Paranthropus* (Table 26.2). The earliest well-documented archeological site at East Turkana is in the upper Burgi Mb and dates to 1.95 Ma (Braun et al., 2010), although there are earlier Oldowan sites both in the Omo Shungura Fm (Howell, 1987) and west of the lake in the Nachukui Fm (Roche et al., 1999). These sites prior to 2 Ma have low densities of artifacts and appear restricted to specific points in the landscape with an intersection of key ecological resources (Rogers et al., 1994).

Upper Burgi cercopithecids are represented by *Parapapio*, *Theropithecus*, *Rhinocolobus*, *Cercopithecoides*, and *Paracolobus*, with *Theropithecus* as the most abundant primate. Koobi Fora carnivorans reach a peak of species richness in the upper Burgi Mb, with at least 18 documented species (Table 26.2; Werdelin and Lewis, 2013b). Reduncini are the most abundant bovids, followed by Tragelaphini, Alcelaphini, Antilopini, and Aepycerotini, in order of diminishing abundance. Among suids, the genus *Kolpochoerus* is most abundant, followed by *Notochoerus* and *Metridiochoerus*. The earliest record of *Equus* in Africa is in Shungura Mb G, at about 2.3 Ma (Eisenmann, 1976b), and by upper Burgi times, around 2 Ma, *Equus* is about twice as abundant as *Eurygnathohippus*. The megaherbivore fauna is dominated by *Elephas recki* and hippopotamids.

KBS Member: 1.87–1.56 Ma

KBS Mb sediments span from the base of the KBS Tuff, dated to 1.87 Ma, to the base of the Okote Tuff, dated to 1.56 Ma. This member outcrops in areas 1–1A, 6, 8–8A, 9–13, 16, 41, 44, 48,

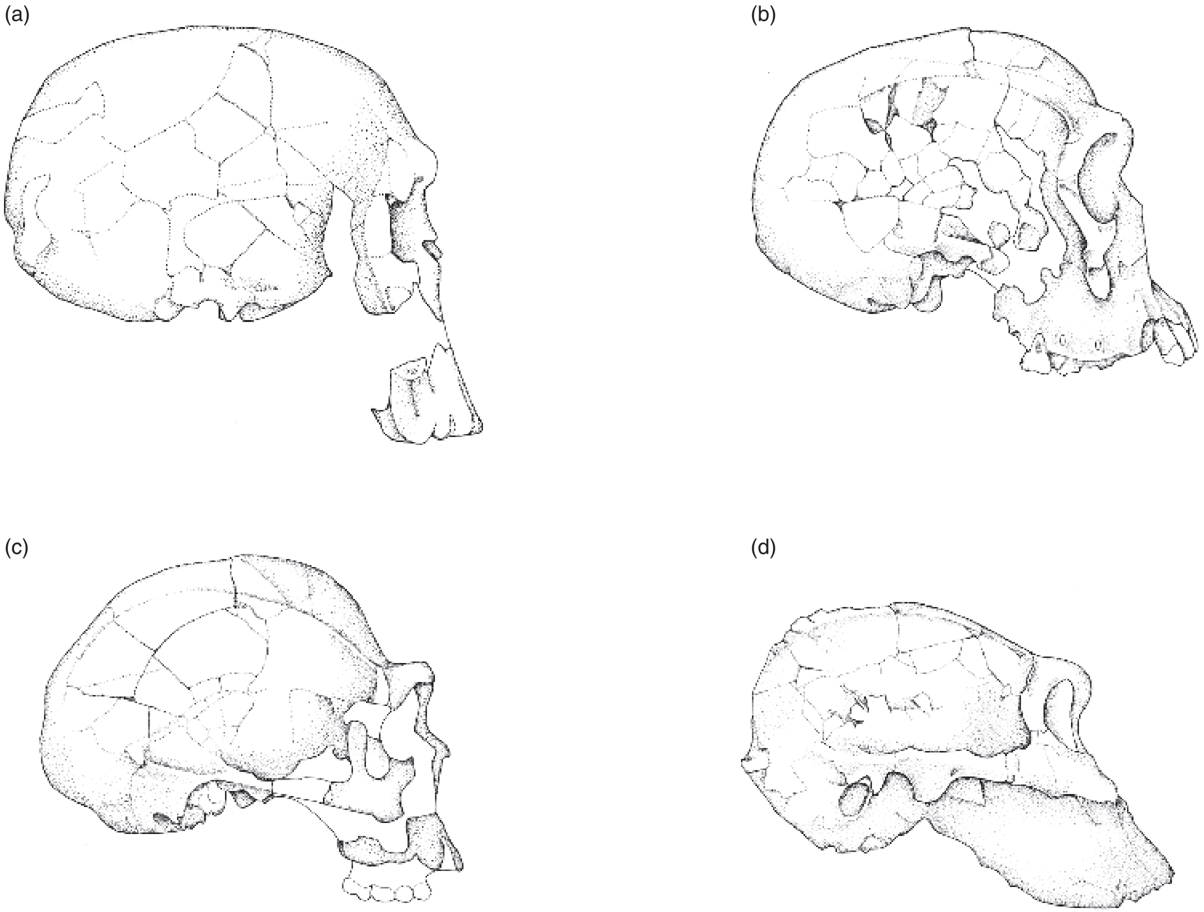

Figure 26.10 Illustration of hominin species co-occurring in the upper Burgi and KBS members of the Koobi Fora Formation. Lateral views of (A) *Homo rudolfensis* specimen KNM-ER 1470, (B) *Homo habilis* specimen KNM-ER 1813, (C) *Homo erectus* specimen KNM-ER 3733, (D) *Paranthropus boisei* specimen KNM-ER 406. Artwork by Vanessa Cannon.

50, 101–112, 114–115, 117–134, 200, and in the Loiyangalani Region. During this time the Lorenyang Lake dominated the basin. Stable carbon isotopes from pedogenic carbonates in the KBS Mb are more enriched than in the upper Burgi Mb, indicating a modest but significant shift toward greater expansion of C_4 vegetation in the region (Patterson et al., 2019). Nevertheless, throughout the interval encompassed by the upper Burgi, KBS, and Okote Mbs there was environmental heterogeneity in the East Turkana region (Behrensmeyer, 1985; Quinn et al., 2007; Patterson et al., 2017a). KBS is the only member in the Koobi Fora Fm with a substantial sample of micromammals, and these indicate relatively arid environments with some riverine forests and arid scrub (Black and Krishtalka, 1986). The basin retained a mix of woodlands, wooded grasslands, and extensive mesic grasslands, as attested by the isotopic signatures and the overall composition of the fauna. The KBS Mb has the highest abundance of fossil vertebrates in the Koobi Fora Fm (Figure 26.4). The well-known hominin specimens KNM-ER 3733 (*Homo erectus*) and KNM-ER 406 (*Paranthropus boisei*) derive from this member (Figure 26.10C,D). The last appearance record of *H. rudolfensis* is in the KBS. Unlike in the upper Burgi Mb, in the KBS Mb specimens of *Paranthropus* are more abundant than specimens of *Homo* (Table 26.2). Within the genus *Homo*, there is a shift in isotopic signature indicating significantly greater consumption of C_4 resources beginning about 1.65 Ma, in the upper part of the KBS Mb (Patterson et al., 2019). Archeological sites at Koobi Fora become more common than in previous members (Figure 26.11; Bunn, 1997; Braun and Harris, 2009), and the earliest record of Acheulean technology is documented on the west side of the lake at Kokiselei locality KS4, dated to 1.76 Ma (Lepre et al., 2011). Monkeys are represented by *Cercopithecus*, *Lophocebus*, *Parapapio*, *Theropithecus*, *Colobus*, *Rhinocolobus*, and *Cercopithecoides*, with *Theropithecus* far outnumbering other primate genera. Among carnivorans, species richness is lower than in the upper Burgi Mb both in absolute terms (16 vs. 18 species) and relative to sample size (Werdelin and Lewis, 2013b). The most abundant bovid tribes are Reduncini, Alcelaphini, Tragelaphini, Antilopini, and Aepycerotini, in that order. Among suids, *Metridiochoerus* became more abundant than *Kolpochoerus*, and *Notochoerus* became rare (Patterson et al., 2017b). The most common suid species was *Metridiochoerus andrewsi*. Among equids, specimens of *Equus* are three times more abundant than those of *Eurygnathohippus*. The megaherbivore fauna was dominated by hippopotamids, *Elephas*, *Giraffa*, *Sivatherium*, and *Ceratotherium*.

Okote Member: 1.56–1.38 Ma

The Okote Mb is defined as those sediments from the base of the Okote Tuff to the base of the Chari Tuff, dating from 1.56 Ma to 1.38 Ma (Brown and Feibel, 1986). The type section in Area 131

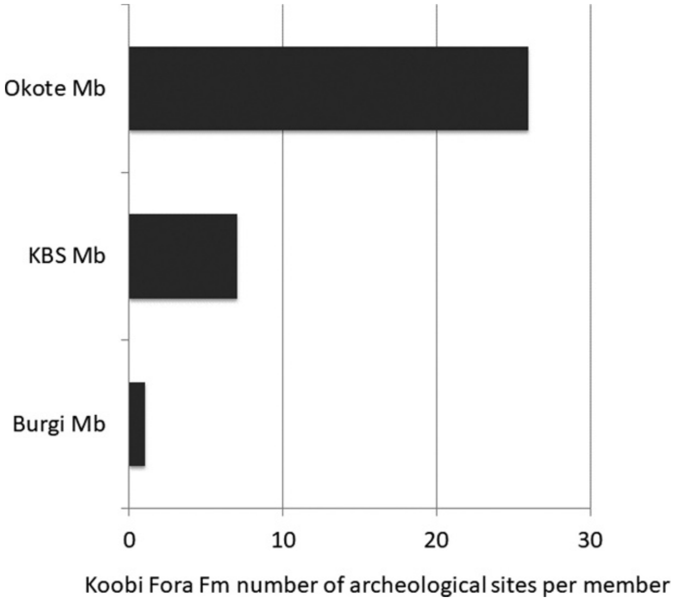

Figure 26.11 Number of archeological sites per member of the Koobi Fora Formation. Data from Isaac (1997) and Braun et al. (2009).

measures 21.6 m, and Okote exposures occur in areas 1–4, 6–6A, 7A, 8–11, 16, 44, 46, 101, 103–105, 112, 118–119, 128–134, and 200. The Okote sediments include very complex fluvial deposits, with brief lacustrine intervals constrained to only parts of the basin (Behrensmeyer and Isaac, 1997). The time interval around the Okote Mb has the highest number of tephra in the Omo-Turkana Basin from 4 Ma to 1 Ma (Figure 26.5). It is likely that frequent volcanism added to the environmental heterogeneity of the basin during this time (Feibel, 1999b; Bobe and Carvalho, 2019). Stable carbon isotopes indicate heterogeneous vegetation dominated by wooded grasslands (Figure 26.6). The paleobotanical record of the Okote Mb includes over 100 specimens of silicified wood from the site FwJj14 in Area 1A. This site is of particular importance because of the well-preserved hominin trackways attributed to *Homo erectus* (Bennett et al., 2009), as well as a newly described upper limb skeleton attributed to *Paranthropus boisei* (Lague et al., 2019b; Richmond et al., 2020). The vessel structure and configuration of the fossil wood specimens from this site indicate large to medium trees from mesic, megathermal environments with no water stress (Bamford, 2017). The most common genus identified from the fossil wood is *Drypetes*, indicative of dense, semideciduous forests. Other taxa indicate gallery forest, Miombo and wooded grasslands, and mangroves. Several of the wood specimens identified derive from genera that are not found in Kenya today but occur in Central and West Africa (Bamford, 2017).

In the Okote Mb, specimens of *Homo* are slightly more abundant than those of *Paranthropus*. The last appearance of *Homo habilis* is documented in the Okote Mb (Spoor et al., 2007), as *Homo erectus* becomes the increasingly dominant species within the genus. At the site FxJj 14E in Area 1A there is a series of hominin trackways produced by at least 20 individuals tentatively attributed to *Homo erectus* (Bennett et al., 2009; Hatala et al., 2016, 2017). These hominin tracks are comparable in morphology, and similar in age, to those found in the 1970s at the site GaJi 10 in Area 103 (Behrensmeyer and Laporte, 1981), about 45 km to the south of FxJj 14E. The site FxJj 14E also produced the newly described partial upper limb skeleton of *Paranthropus boisei*, KNM-ER 47000 (Richmond et al., 2020), which indicates that this species spent at least some time in the trees (Green et al., 2016; Lague et al., 2019a, 2019b).

The abundance of archeological sites is significantly greater than in any of the earlier members (Figure 26.11). Archeological sites are also more widely distributed in relation to paleogeographic and environmental settings (Rogers et al., 1994), with most sites having abundant lithic materials and a few including fossil bones (Harris and Isaac, 1976; Isaac, 1978a; Isaac and Harris, 1978; Harris and Isaac, 1997; Stern et al., 2002; Braun et al., 2008; Merritt, 2017; Presnyakova et al., 2018). It is noteworthy that the fauna from archeological sites has a higher proportion of Alcelaphini than in the general landscape, suggesting that hominins may have had a preference for hunting or scavenging bovid remains in relatively open environments (Patterson et al., 2017b). Okote sediments also contain the earliest evidence of possible hominin control of fire at the FxJj 20 site complex in the Karari Ridge (Hlubik et al., 2017, 2019).

The sample of Okote cercopithecids includes the genera *Cercopithecus*, *Cercocebus*, *Lophocebus*, *Parapapio*, *Theropithecus*, and *Colobus*. The dominant primate was *Theropithecus oswaldi*, a C_4 grazer (Figure 26.8; Cerling et al., 2013b), but other common monkeys, e.g., *Lophocebus* cf. *albigena* and *Colobus freedmani*, are consistent with the arboreal vegetation inferred from the fossil wood specimens (Bamford, 2017). *Parapapio* was still present during Okote times but in very small numbers. It is noteworthy that the large colobines that were present in earlier members (*Rhinocolobus*, *Paracolobus*, *Cercopithecoides*) all appear to have gone extinct by the time of the Okote Mb. Carnivoran species richness is lower in the Okote Mb than in the Burgi or KBS Mbs, both in absolute terms and relative to sample size (Werdelin and Lewis, 2013b). The broad decline in the functional and taxonomic diversity of African carnivorans was well underway by the time of the Okote Mb, e.g., the last occurrence of *Homotherium* (Werdelin and Lewis, 2013a), but the abundance of *Crocuta* increased relative to earlier members. The bovid fauna is dominated in abundance by Reduncini, followed by Alcelaphini, Tragelaphini, and Bovini, in that order. Among suids, the most abundant species is *Metridiochoerus compactus*, followed by *Kolpochoerus limnetes*. Among equids, the genus *Equus* is five times more abundant than *Eurygnathohippus*. Thus, from the upper Burgi to the Okote Mb, *Equus* became increasingly more abundant in relation to *Eurygnathohippus*. The megaherbivore fauna is dominated by *Hippopotamus*, *Elephas*, and *Giraffa*. The megaherbivore fauna is less diverse in the Okote than in earlier members.

Chari Member: 1.38–0.7 Ma

The base of the Chari Mb is defined by the base of the Chari Tuff, dated to 1.38 Ma, and the top is estimated to be 0.7 Ma. The

Chari Mb is 42.7 m thick at the type section (Brown and Feibel, 1986). Exposures of this member occur in areas 1, 2–7, 7A, 16, 44, 46, 112, 128, 130–131, 133–134, and 138. Most of the deposition of the Koobi Fora Fm during this time took place in the northern areas. The Chari Tuff was deposited in a fluvial context that marked the onset of Chari Floodplain, dominated by a large meandering river and episodic lacustrine intervals (Feibel et al., 1991). The Chari Tuff is the result of a massive volcanic event, as it is found throughout the Turkana Basin (= Tuff L in the Shungura Fm) and as far north as the Gulf of Aden. Other major markers within the Chari Mb include the Gele Tuff (1.25 Ma), the Silbo Tuff (0.75 Ma), and the Matuyama/Bruhnes Chron boundary (0.78 Ma). The lower part of the Chari Mb correlates with Mb L of the Shungura Fm, and with the upper Natoo/lower Nariokotome Mbs of the Nachukui Fm. Sedimentation of the Koobi Fora Fm, and the Omo Group, ended by about 0.7 Ma (Feibel et al., 1989, 1991). Although fossil mammals are sparse in the Chari Mb, there are sand sequences that contain abundant fossil fish, ostracods, and bivalves. In the Omo, the Shungura Mb L mammalian fauna is dominated by hippopotamids, Reduncini, and to a lesser extent by Alcelaphini, indicating extensive grasslands in the vicinity of a major river in the Chari Floodplain. It is most likely that *Paranthropus* went extinct during the time of the Chari Mb, but better samples are needed to establish the timing of this extinction event.

Patterns of Faunal Associations

The best sampled and most continuous part of the Koobi Fora Fm is from the upper Burgi Mb to the Okote Mb, i.e., from about 2 Ma to 1.4 Ma. The fossil record of the upper Burgi, KBS, and Okote Mbs has been more thoroughly studied and published, and here we present new analyses of faunal associations based on these upper members. Ever since the first coefficient of association between species was devised by pioneer ecologist Stephen Alfred Forbes (Forbes, 1907), numerous quantitative metrics have been defined, aiming at clarifying how species combine themselves into larger communities (Dice, 1945). We use a version of Table 26.2 that includes only genera across the upper Burgi, KBS, and Okote Mbs to detect patterns of association in relation to taxonomic abundance data. All extremely rare genera ($N \leq 10$) were excluded from the following analysis. To reveal faunal patterns, we employed APRIORI (Agrawal et al., 1993), an *if A then B* algorithm for mining association rules, typically used to analyze transaction data for retail markets and online e-commerce stores (Hahsler, 2017; Hahsler and Karpienko, 2017). Instead of looking at transactions per se, we transformed our count data (a proxy for the abundance of taxa) of genera across geological members into "association" data. The data transformation involved three steps: first the data set was double-standardized per *max* value of each column (member) and per the *sum* of each row (genus; Legendre and Gallagher, 2001); second, a Euclidean distance matrix D_{mn} was calculated; and third, a matrix X_{ij}, where each value *ij* is a binarized logical solution for $D_{mn} < \overline{D}_n$. This Boolean matrix X_{ij} can then be fed into the APRIORI algorithm to understand associations *if i then j* between any paleotaxa *i* and *j*. Then, the associations calculated were analyzed, scored and ranked by the following thresholds:

$$Support = \frac{\#\ of\ Associations\ between\ A\ and\ B}{Total\ \#\ of\ Associations} = P\left(A \cap B\right) \qquad \text{(eq. 1)}$$

$$Confidence = \frac{\#\ of\ Associations\ between\ A\ and\ B}{Total\ \#\ of\ Associations\ with\ A} = \frac{P\left(A \cap B\right)}{P(A)} \qquad \text{(eq. 2)}$$

$$Lift = \frac{Confidence}{Expected\ Confidence} = \frac{P\left(A \cap B\right)}{P(A) \times P(B)} \qquad \text{(eq. 3)}$$

Here we introduce FARUBO, a flexible web application for rule-based learning and visualization of paleofaunal associations, available through the "osteomics" web platform. FARUBO (http://osteomics.com/FARUBO) was fully developed in R using shiny, arules and arulesViz packages (Hahsler et al., 2005, 2011; Hahsler, 2017; R Core Team, 2019). FARUBO is designed with a side panel for interactive functionalities and a main panel with three menu tabs: "Data Exploration," "Paleofaunal Network," and "Clustered Rules." The side panel allows users to control interactively all parameters as minimum thresholds (eqs. 1–3). The fourth parameter of the side panel, "Rules length," allows one to define the number of taxa in the left-hand side (LHS) of the if–then rule, while the last parameters are all related to filtering taxa for the analyses. Regarding the main panel, the first tab "Data Exploration" is the landpage; it summarizes all rules being generated in real-time by the web application and it allows users to download them anytime as a .csv table. In the "Paleofaunal Network" tab, interactive networks of associations can be visualized; in the default display, circle size increases with support and circle shading saturates (to red) with confidence, while the rules' number decreases with lift. If hundreds or thousands of rules are being generated the graph visualization gets too convoluted, and therefore users can alternatively use the "Clustered Rules" tab to see a summarized visualization of the rules. The current version of the webapp loads with the hominins as required RHS (right-hand side) taxa, but this is also an option that can be manipulated in the side panel. *Homo* associations tend to rank higher than *Paranthropus* in terms of Support and Confidence, but lower in terms of Lift. This is due to *Paranthropus* being comparatively underrepresented in the upper Burgi Mb, which leads to lower expected confidence.

For the results presented here, we defined the same minimum thresholds of support = 0.4, confidence = 0.6, and lift = 1, as in the web application defaults, resulting in 23 association rules. The top 10 identified rules (Figure 26.12) show the major importance and representativeness of *Theropithecus* (9/10 rules) overall for hominin assemblages, with *Metridiochoerus* following closely (but more relevant toward *Paranthropus*). Indeed, the best rule in terms of lift (1.938) was (*Metridiochoerus*, *Theropithecus*) ⇒ (*Paranthropus*)

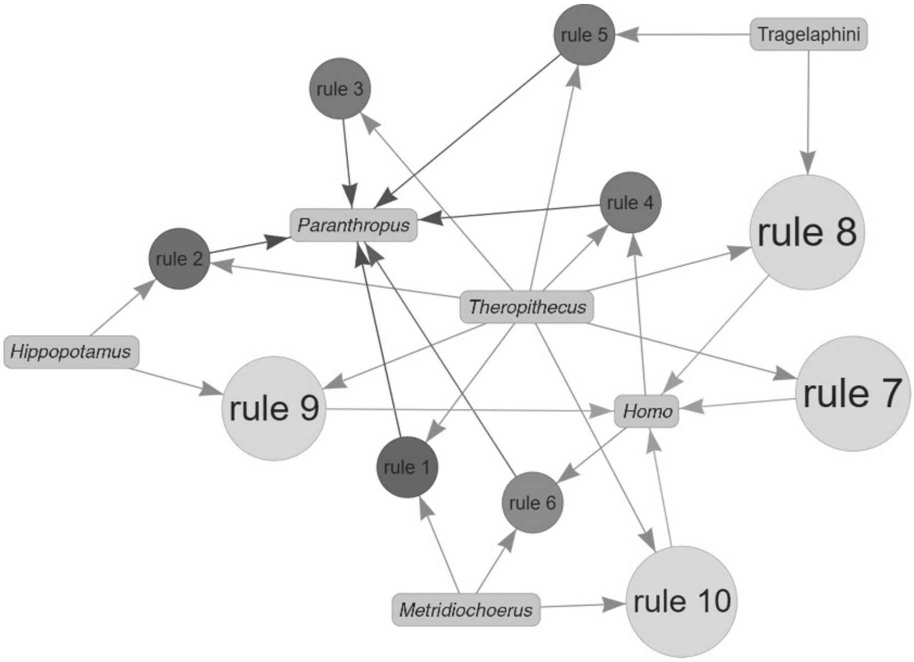

Figure 26.12 Faunal associations in the Koobi Fora Formation upper Burgi, KBS, and Okote members with abundance data at the genus level. Extended Hominin graph model showing the top 10 rules (by lift). Parameters: minimum support = 0.4; minimum confidence = 0.6; minimum lift = 1; maximum length = 3; RHS = c("*Paranthropus*," "*Homo*"); maximum rules displayed = 10.

with 81.3 percent confidence, while the top five rules for *Homo* all contained *Theropithecus* in the LHS. From this, their combined potential as paleontological predictors for hominins in the region can be inferred. Both *Theropithecus* and *Metridiochoerus* are more abundant than hominins, and thus are easier to detect during paleontological surveys.

The fossil record indicates that *Theropithecus* was a successful primate lineage, comparable to some early hominins in terms of geographic range and terrestriality (Elton, 2006). At the site of Olorgesailie in Kenya, there is direct evidence of coexistence and interactions between *Theropithecus* and Pleistocene hominins from cut-marked bones of *T. oswaldi* (Shipman et al., 1981). Additionally, *Theropithecus* has been central as a comparative model for hominin locomotor evolution (Jolly, 1970; Wrangham, 1980; Kingdon, 2003) and behavioral adaptations (e.g., diet) to changing habitats and climate (Dunbar, 1983; Foley, 1993). As for *Metridiochoerus* and its stronger association to *Paranthropus*, we tentatively attribute this to overlapping habitat preferences, and to possibly similar strategies of resource exploitation. It is known that in eastern Africa grasses were an important component of both of their diets, and *Metridiochoerus* species (advanced forms of the genus) have been interpreted as indicators among suids of seasonal grassland habitats (Bobe and Behrensmeyer, 2004). However, taphonomic factors likely play a role: *Paranthropus* and *Metridiochoerus* teeth are both abundant in the fluvial deposits of the KBS Mb, where their durable teeth may survive better during fluvial transport.

Also important are the hominin associations to *Hippopotamus* and *Tragelaphus* most likely demonstrating the importance of close sources of fresh water and trees in the life history of hominins. Furthermore, if we look at the lower-ranking rules, we see that *Crocuta* is also associated with *Homo* in multiple rules (but with lower support values), and other bovid tribes such as Reduncini and to a lesser extent Bovini also show some degree of association to the hominins (not depicted), which further illustrates the complexities of the environmental context.

It is also possible to look exclusively at paired associations, that is, associations that do not need combined taxa to be detected. As an example, if one is only interested in pair relationships related to hominins, the maximum value of the "Rules length" parameter should be kept at 2 in FARUBO, and "*Homo*" and "*Paranthropus*" have to be selected in "Require taxa in RHS." Considering only pair relationships, the association of *Crocuta* with *Homo* becomes more evident (lift = 1.192; Figure 26.13), and this might indicate commonalities in the way both taxa exploited resources, as the *Homo* lineage is thought to have increasingly adopted meat and marrow into its diet by opportunistic scavenging and eventually by hunting (Moleón et al., 2014). Further relaxing the minimum support value in FARUBO will allow users to detect a few more interesting pair associations with *Homo* that might also indicate some ecological overlaps, notably *Dinofelis* and *Parapapio* at 29 percent support and *Panthera* (25.8 percent).

The evolutionary and ecological significance of these associations needs further work to assess the role of collection biases and taphonomic factors such as the durability of teeth and mandibles in different depositional contexts (Behrensmeyer, 1975, 1978b, 1985). Thus, these associations are best considered as tentative hypotheses to be tested with further taphonomic analyses.

Summary and Conclusions

In this chapter we have focused on the fauna and paleoenvironments of the Koobi Fora Fm (Formation) from about 4.3 Ma to about 1 Ma. It is important to keep in mind that Koobi Fora

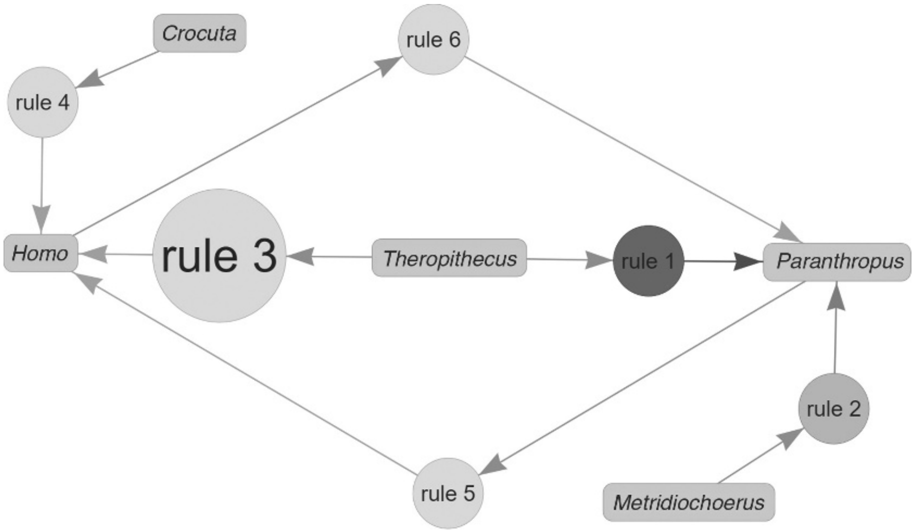

Figure 26.13 Faunal associations in the Koobi Fora Formation upper Burgi, KBS, and Okote members with abundance data at the genus level. Main taxa associated with *Homo* and *Paranthropus*, with a central role of *Theropithecus*, and with *Crocuta* and *Metridiochoerus* as the respective satellite associations in this reduced graph model. Parameters: minimum support = 0.4; minimum confidence = 0.5; minimum lift = 1; maximum length = 2; RHS = c("*Paranthropus*," "*Homo*").

was part of the larger ecosystem of the Omo-Turkana Basin (Figure 26.1), and that an ecosystem perspective is the best way to understand the evolution of hominins and their landscapes as documented in the Omo Group deposits (Figure 26.2) (Feibel, 1999a). The East Turkana region is central to our understanding of hominin evolution during the Pliocene and early Pleistocene, and here we provide a new map drafted by Frank Brown of the Koobi Fora Fm Paleontological Collection Areas (Figure 26.3). During the time documented by the Koobi Fora Fm hominins underwent profound changes in anatomy, behavior, and diversity. The vegetation and paleogeography of the region also changed significantly during this time (Feibel et al., 1991), as did ecological relationships among species.

The earliest intervals of the Koobi Fora Fm, between 4.3 and 3.6 Ma, have small samples of fossils, except for Locality 261–1 in Allia Bay (Figure 26.4). However, fossils from the Kanapoi and Nachukui Fms provide a rich picture of hominins and their environments during the early Pliocene of the Omo-Turkana Basin. The earliest record of *Australopithecus anamensis* is from Kanapoi at 4.2 Ma (Ward et al., 2020), and important collections of this species also derive from Allia Bay Locality 261–1 dated to 3.97 Ma (Leakey et al., 1995). The species *A. anamensis* is also found at the site of Asa Issie in the Afar region of Ethiopia (White et al., 2006), indicating that the geographic range of this species extended at least from the southern Turkana Basin to the middle Awash River in the Afar. It is noteworthy that the earliest records of both *Australopithecus* and *Theropithecus* occur at the same time and in the same place, Kanapoi at 4.2 Ma (Frost et al., 2020; Ward et al., 2020), establishing a long-lasting association between hominins and *Theropithecus* what would persist for millions of years. Both genera were also present at Allia Bay preserved within basal deposits of a massive volcanic eruption, the Moiti Tuff (Figure 26.5). It was only in these early intervals that *Parapapio* was more abundant than *Theropithecus* among the primates. In later periods, *Theropithecus* far outnumbered *Parapapio* and other primates. At Kanapoi, *Australopithecus* inhabited an ecosystem dominated by megaherbivores, with 10 species of mammals weighing 1000 kg or more (Bobe et al., 2020a). These megaherbivores included five species of proboscideans (Sanders, 2020), which undoubtedly had a profound impact on the local ecology, e.g., clearing paths for terrestrial animals, dispersing seeds, providing food for hunting and scavenging carnivores. These were proboscidean-dominated landscapes. The basin at this time was dominated by woodlands, although grasslands were an important element of the ecosystem (Figure 26.6). Hominins were feeding mostly on C_3 resources (Figure 26.7) even though C_4 resources were clearly available in the landscape. Fresh water in rivers, streams, and lakes was a persistent feature of the ecosystem.

By 3.4 Ma, hominins had diversified into at least two species, with evidence of *Australopithecus afarensis* and *Kenyanthropus platyops* in the basin (Kimbel and Delezene, 2009; Spoor et al., 2010). The vegetation in the basin remained a mosaic of woodlands and grasslands but with a greater proportion of grasslands than before (Figure 26.6). By this time hominins had shifted from a largely C_3 diet to a mixed diet of C_3 and C_4 resources (Cerling et al., 2013a; Figure 26.7). The reasons for this shift in hominin diets remain to be fully explored, because C_4 resources were clearly present and available to early *Australopithecus* at Kanapoi and Allia Bay, but apparently not exploited. The earliest archeological site, with lithic artifacts that emphasize percussive activities, dates to 3.3 Ma (Harmand et al., 2015), and signals the deep roots of hominin use of technology.

After 3 Ma there is evidence of further hominin diversification, with the earliest records of *Homo* and *Paranthropus*. Earliest *Homo* derives from the Afar site of Ledi-Geraru (~2.8 Ma) and from the upper Tulu Bor Mb at East Turkana (~2.7 Ma; Villmoare et al., 2015), while the earliest record of *Paranthropus* is from Shungura Mb C (~2.7 Ma; Bobe and Carvalho, 2019). In the Shungura Fm there is evidence of important faunal changes at about 2.9–2.8 Ma (Bobe and Eck, 2001; Bobe et al., 2007b; Bibi et al., 2013), but the overall composition of the vegetation in the basin seems to have remained relatively stable (Figure 26.6). *Homo* and *Paranthropus* coexisted in the Omo-Turkana Basin for about 1.5 million years (Bobe and Carvalho, 2019). Further faunal changes are documented in the Omo during the interval from 2.5 to 2.3 Ma, with an increase in the abundance and diversity of grazing bovids (Bobe and Eck, 2001) and frequent deposition of volcanic ash (Figure 26.5).

The richest and most continuous record of fossil vertebrates in the Koobi Fora Fm comes from the upper Burgi, KBS, and Okote Mbs, from about 2 Ma to 1.4 Ma (Figure 26.4). Beginning at about 2 Ma there were major paleogeographic and environmental changes in the basin, with more extensive wooded grasslands, although gallery forests likely played a key ecological role as relatively stable habitats associated with river corridors (Figure 26.6). The center of the basin was dominated by the Lorenyang Lake, the longest-lived of the paleo-lakes documented in the Omo Group deposits (Figure 26.2; Feibel, 2011). Relative to earlier hominins, *Homo* and especially *Paranthropus* consumed greater proportions of C_4 resources after 2 Ma (Figure 26.7). *Theropithecus* shifted from a mixed diet to a C_4-dominated diet during this time (Figure 26.8). After 2 Ma, hominins had diversified into three or four species (depending on taxonomic attributions): *Homo habilis*, *H. rudolfensis*, *H. erectus*, and *Paranthropus boisei* (Figure 26.10). Thus, there may have been four hominin species coexisting in the highly variable and dynamic environments of the Omo-Turkana Basin (Bobe and Carvalho, 2019).

The abundance and distribution of archeological sites changed dramatically from a few Oldowan sites before 1.9 Ma (Braun et al., 2010) to a large number of sites with thousands of artifacts and bones across multiple landscapes by 1.5 Ma (Figure 26.11; Isaac and Harris, 1978; Rogers et al., 1994; Presnyakova et al., 2018). The earliest Acheulean technologies appeared by 1.76 Ma at Kokoselei 4 on the west side of Lake Turkana (Lepre et al., 2011), and possibly the earliest indications of hominins using fire appear at 1.5 Ma at the FxJj 20 site complex (Hlubik et al., 2017, 2019). Analyses of the fauna from archeological sites indicate that hominins accessed alcelaphin bovids in higher proportion than their overall representation in the paleo-communities (Patterson et al., 2017b). This happened as *Homo* underwent a significant shift toward greater reliance on C_4 resources (Patterson et al., 2019) and *H. erectus* was becoming the dominant species of the genus. It is likely that hominins accessed animal resources in grassland habitats at this time.

In our analyses of Koobi Fora faunal associations between 2 Ma and 1.4 Ma, some significant patterns emerged. We found *Theropithecus* to be a key taxon in predicting the occurrence of both *Homo* and *Paranthropus* (Figure 26.12 and Figure 26.13). The combined association of *Theropithecus* and the suid *Metridiochoerus* proved to be a particularly strong predictor of *Paranthropus*, while *Tragelaphus* and *Crocuta* also associated with *Homo*. It is noteworthy that some of these associations were also found for earlier periods in the Omo Shugura Fm. At around 2.3 Ma (a time "missing" from the Koobi Fora Fm because of the Burgi Unconformity), *Theropithecus* was significantly associated with *Paranthropus*, while *Parapapio* and *Tragelaphus* were significantly associated with *Homo* (Bobe and Behrensmeyer, 2004). These associations provide an indication of the ecological communities in which these hominins lived during the early Pleistocene, with monkeys like *Theropithecus* and *Parapapio* likely sharing the hominin landscapes. We can speculate that the association of *Homo* with *Crocuta* may indicate a shared interest in animal carcasses, but further work is needed to test these ideas.

In sum, the Koobi Fora Fm preserves a record of hominin evolution spanning nearly 3 million years, from the earliest species of *Australopithecus* prior to 4 Ma to a time of high hominin diversity between 2 Ma and 1.4 Ma with *Homo habilis*, *Homo rudolfensis*, *Homo erectus*, and *Paranthropus boisei* occupying the Omo-Turkana ecosystem. This time also saw the rise of *Theropithecus* from a rare taxon around 4 Ma to the most common primate in the landscape by 1.5 Ma, as well as a decline in the diversity of carnivorans and megaherbivores. During the time span from *Australopithecus anamensis* to *Homo erectus* the environments in the Omo-Turkana Basin shifted from extensive woodlands and wooded grasslands to diverse and dynamic habitats that included a greater proportion of grasslands. The archeological record underwent a dramatic transformation from a few Oldowan sites before 1.9 Ma to numerous Developed Oldowan and Acheulean sites at about 1.5 Ma, a transformation associated with the increasingly prevalent species *Homo erectus*.

Acknowledgments

This work is dedicated to the memory of Frank Brown (1943–2017), a generous colleague who spent his lifetime dedicated to studying the geology, paleontology, vegetation, and cultures of northern Kenya and southern Ethiopia. Frank drafted the map presented here as Figure 26.3, and wrote the notes accompanying the map of paleontological collection areas (Appendix). Richard Leakey passed away as this chapter went to press. We are immensely grateful for his enormous contribution to the development of vertebrate paleontology and paleoanthropology in the Lake Turkana region, and for the support and encouragement that he provided to so many colleagues and students of human evolution in Africa. We are very thankful to David Patterson, Sally Reynolds, and Anna K. Behrensmeyer for thoughtful comments and corrections that greatly improved this chapter.