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ORIGINAL PAPER

Late Middle Pleistocene Elephants from Natodomeri, Kenya and the Disappearance of *Elephas* (Proboscidea, Mammalia) in Africa

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Abstract

Comparative morphometric study of recently recovered fossil elephant molars from Natodomeri, Kenya identifies them as belonging to *Elephas jolensis* and confirms the presence of this species in Members I and II of the Kibish Formation. Improved datation of these geological units constrains them between 205 and 130 ka. *Elephas jolensis* is also reported from localities in northern, northwestern, eastern, and southern Africa. Thus, including its Natodomeri occurrence, *E. jolensis* appears to have been pan-African in distribution. Despite the wide geographic distribution of the species, molars of *E. jolensis* are remarkably uniform morphometrically. They are characterized by their extreme hypsodonty, high amplitude of enamel folding, high lamellar frequency, and plates that are anteroposteriorly thick relative to transverse valley interval spacing. In addition, they exhibit only a modest number of plates (<20 in M3/m3). *Elephas jolensis* either evolved from or represents the last stage of *Elephas recki*, the dominant elephant species in East Africa during the late Pliocene-Pleistocene. The dental morphology and isotopic composition of *E. jolensis* indicates that, like *E. recki*, it was a dedicated grazer. In the Kibish Formation, *E. jolensis* is succeeded by *Loxodonta africana* at 130 ka, coincident with an intensely cool, dry interval marked by episodes of extreme drought. This marked the extirpation of *Elephas* on the continent. The intensity and increased rate of climate fluctuation may have played an important role in the demise of the specialist, grazing *E. recki*-*E. jolensis* lineage in favor of a generalist, mixed feeder such as *L. africana*.

Keywords Natodomeri, Kenya · Kibish Formation · Elephantidae · *Elephas jolensis* · Late middle Pleistocene

Introduction

After persisting though most of the late Pliocene-Pleistocene as the dominant or lone proboscidean taxon in the eastern and central regions of the continent, the cause and timing of the disappearance of *Elephas* in Africa remain to be established and calibrated more precisely. Analysis of dental isotopic composition indicates that these elephants preferred to eat C_4 plants (Cerling et al. 1999), and the fossil record of African representatives of the genus correspondingly provides abundant evidence for strong directional selection for increasingly effective morphological adaptations to grazing (Maglio 1973; Beden 1980, 1983; Sanders et al. 2010; Sanders and Haile-Selassie 2012). Sudden replacement of *Elephas* in Africa toward the end of the Pleistocene by the extant savanna elephant *Loxodonta africana* is an enduring mystery (Sanders et al. 2010). Recovery of new elephant specimens from the Kibish Formation site of Natodomeri, Kenya provides fresh impetus to investigate the morphological homogeneity of the last species of *Elephas* present in Africa, *E. jolensis*, its relationship to the Plio-Pleistocene Afro-Arabian species *Elephas recki*, which was the dominant elephant on the East African landscape for much of its existence (Beden 1980; Sanders et al. 2010), the timing of the replacement of *E. jolensis* by *L. africana*, and factors that may have played a role in its demise.

The Kibish Formation exposed along the Omo River near Kibish in southwestern Ethiopia has produced important

Francis H. Brown is deceased. This paper is dedicated to his memory.

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mammalian assemblages that include some of the earliest fossils of anatomically modern humans (Assefa et al. 2008; Fleagle et al. 2008). Member I is the oldest of four geological units that comprise the formation (Butzer et al. 1969; Butzer and Thurber 1969) and has produced a hominin-bearing fauna that has been dated by stratigraphy and $^{40}Ar/^{39}Ar$ analysis of the Nakaa'kire Tuff to between 205 and 195 ka (McDougall et al. 2005; Brown and Fuller 2008; Brown et al. 2012), revised from an initial Th/U calculation of 130 ka for the unit (Butzer et al. 1969, 1972). Radiometric dating of tuffs in Members II and III, and on molluscs in Member IV indicates that the faunas of Members III and IV are 130–74 ka and early Holocene in age (<10 ka), respectively (Butzer et al. 1972; Assefa et al. 2008; Brown et al. 2012). Thus, the Kibish Formation spans the late middle Pleistocene to Holocene. Notably, remains of the extant species of African savanna elephant, *Loxodonta africana,* have been documented in Members III and IV (Assefa et al. 2008). These specimens are among the very few fossil occurrences of the species (Sanders et al. 2010).

Outcrops of Kibish Formation sediments are also exposed at the site of Natodomeri in the Ilemi Triangle, adjoining the southeasternmost corner of South Sudan, which has been administered by Kenya since at least the 1950s. This site is located about 35 km southwest of the type area of the Kibish Formation in Ethiopia. Natodomeri was first noted as fossiliferous by Karl Butzer (International Omo Research Expedition), who in 1968 very briefly investigated the localities of Natodomeri I and II on the Natodomeri floodplain along watercourses tributary to the Kibish River. Correspondence between Member I at Natodomeri and in the type area of the Kibish Formation is based on sequence stratigraphy and recognition of the KHS tuff in lower Member II at both sites (Manthi et al. 2017). Members I-III of the Kibish Formation are composed of delta-plain, delta-fringe, and prodeltaic sediments, expressed as sandstones, siltstones, and mudstones at Natodomeri, deposited during intervals when Lake Turkana was considerably higher and its shoreline extended far more northerly than at present (Butzer and Thurber 1969; Butzer et al. 1969, 1972). During his brief visit to Natodomeri, Butzer made a small collection of vertebrate fossils from Member I, including testudinids, hippopotamids, bovids, rhinocerotids, and elephantids (KW Butzer and VJ Maglio, unpublished manuscript, undated; Maglio 1973).

Butzer's elephant fossils from Member I of the Kibish Formation at Natodomeri I and II include two partial upper molars and an incomplete tusk. These fossils were initially identified as "*Elephas transvaalensis*" in the unpublished account (see Maglio 1973). The nomenclature appears to be a variant of Dart's (1927) "*Archidiskodon transvaalensis*," applied to a very hypsodont elephant molar from younger gravels of the lower Vaal River Basin in South Africa, later synonymized with the late middle Pleistocene-late Pleistocene species *Elephas "iolensis*" in Maglio's (1973) comprehensive taxonomic revision of the Elephantidae. Maglio (1973), following on earlier erroneous usage of the species nomen for this taxon (e.g., Boule 1900; de Lamothe 1904; Deperet and Mayet 1923; Arambourg 1938, 1952, 1960, 1970), referred to it as "*Elephas iolensis*," despite the unambiguous employment of "*jolensis*" and explanation of its etymology in the type paper (Pomel 1895: 32 and 39). Although broken, dimensions of Butzer's Natodomeri specimens, such as crown height, enamel thickness, and lamellar frequency (Table 1), are indeed suggestive of affiliation with *E. jolensis*. If the identification is correct, together with the elephant fossils from Members III and IV of the Kibish Formation they constitute valuable evidence for determining the timing of the disappearance of the *Elephas* lineage and successive geographic re-emergence of representatives of the genus *Loxodonta* in East Africa.

More recent collecting at Natodomeri starting in 2016 by the Kenyan-led West Turkana Palaeo Project (headed by one of us, FKM) recovered additional vertebrate fossils, featuring a lion cranium considerably more immense than those of any living relative (Manthi et al. 2017). Among these fossils are a small number of elephant partial molars from Member I preserving morphological details suitable for taxonomic evaluation. Comparative morphometric study and identification of these specimens confirms the presence of *E. jolensis* in Member I at Natodomeri that was suggested by the smaller elephant molar collection of Butzer. The combined Natodomeri *E. jolensis* fossil sample constitutes the only precisely dated evidence of the species, between 205 and 195 ka in Member I and no younger than 130 ka in Member II. Earlier, Maglio (1973) and Coppens et al. (1978) had reported a now discounted age of 35,000 years B.P. generated by U-Th analysis for Butzer's *E. jolensis* assemblage. Comparative study of the sample with material assigned to *E. jolensis* from elsewhere in Africa suggests that it is a valid species with widespread occurrence. Chronological succession, shared biogeography, general morphological similarity, and continued increase in molar hypsodonty and enamel folding support the hypothesis that *E. jolensis* evolved from or is the last stage of *E. recki recki* in the late middle Pleistocene, though *E. jolensis* does not exhibit closer plate spacing, thinner enamel, or a greater number of plates than its presumed predecessor. Fossil occurrences and radiometric dating of the Kibish Formation suggest that *L. africana* replaced *E. jolensis* at the end of the middle Pleistocene, coincident with an intensely dry, cool interval marked by episodes of extreme drought that may have favored generalist mixed-feeding elephants over grazing specialists (see Cerling et al. 1999; Saarinen et al. 2015), bringing an end to the dominance of *Elephas* in Africa.

Table 1 Comparative dimensions and indices of *Elephas jolensis* and *Elephas recki recki* teeth, including new specimens from Natodomeri, Kenya (in bold text)

Accession or Field#/Site.	Specimen	Plate Formula	LF	L	W	H	HI	ET
KNM-ND 68505, Natodomeri, Kenya	**Partial upper molar,? M3**	**+8x**	**5.75**	**+176.1**	**93.5 (VIII), (77.8 near apex, VIII), 90.9 (VI)**	**worn, 192.0+ (VIII), tallest plate 220.8 (VI)**	**205+ 243**	**3.5**
KNM-ND 68136, Natodomeri, Kenya	**l. M3**	**+8x**	**5.5**	**+161.2**	**90.9 (V)**	**worn**	**–**	**3.0–3.5**
KNM-ND 68511, Natodomeri, Kenya	**r. m3**	**+6x**	**6.0**	**+147.5+**	**88.5 (6)**	**+164.5 (6)**	**186+**	**2.8–3.0**
KI-1, Natodomeri I, Kenya[m]	r. M3	+5x	6.3	–	89.0 (I)	+ 148.0 (II) (original height of crown estimated between 200 and 220 mm)	e. 215–220	2.3–2.7
KI-11, Natodomeri II, Kenya[m]	r. upper molar? (M2?)	2+	5.6	–	69.0	worn	–	2.2–2.7
	Partial I2			+600–700+	75.0			
Carrière Sidi Abder Rahmane (Casablanca), Morocco[e, i]	dp3	5+	8.0	40.0+	31.0	–	–	–
Carrière Sidi Abder Rahmane (Casablanca), Morocco[e, i]	dp4	x10x	8.0	135.0	45.0	70.0	170	–
Carrière Sidi Abder Rahmane (Casablanca), Morocco[e, i]	M3	14	5.5–6.0	245.0	91.0	155.0	200	3.5
Carrière Sidi Abder Rahmane (Casablanca), Morocco[e, i]	M3	13x	6.0	245.0	98.9	175.0	216	3.0
Carrière Sidi Abder Rahmane (Casablanca), Morocco[e, i]	M3	+10 (e. 13)	5.5	+187.0 (e. 257.0)	79.5	169.0	210	2.5–3.0
Carrière Sidi Abder Rahmane (Casablanca), Morocco[e, i]	M3	11+	5.0	204.7+	84.0	170.1	201	2.9
n° 1974, 5–1, El Douira, Tunisia[i]	dentary fragment with r. m3	13	5.2–5.3	249.0	80.0 (12)	e. 170.0 (4)	>212	1.5–2.5
Beauséjour Farm, Algeria (type)[e, i]	m2	x11x	6.0	210.0	64.0	127.0	200	–
Port de Mostaganem, Algeria[e, i]	m2	+11x (e. 12–13)	5.5	+225.0 (e. 240.0–260.0)	68.0	114.0	170	–
Port de Mostaganem, Algeria[e, i]	m3	11+	4.4	234.5+	73.9	125.0+	200+	2.5
Gué de Constantine?[d] (?*Loxodonta atlantica*?)[h]	m2 or m3	12+	5.5–6.0	250.0+ (e. 270.0–280.0)	70.0	120.0	180	3.0
Gué de Constantine[e, i]	dP4	8.0	5.0	136.0 (e. 156.0)	54.0	64.0	120	2.5
Gué de Constantine[e, i]	M3	13	5.5	+255.0	88.0	169.0	220	–
M 26628, Behanga I, Democratic Republic of Congo[g]	M2 or M3	5+	5.5	92.0+	81.0	220.0	272	2.5–3.5
Fragment A, left bank Zambezi River, Victoria Falls, Zimbabwe[c]	m3	+8 ½	3.9–4.2	+212.0	95.0	160.0	168	4.0
Fragment B, left bank Zambezi River, Victoria Falls, Zimbabwe[c]	m3	+3+	5.0	+67.0+	–	–	–	4.0
Fragment C, left bank Zambezi River, Victoria Falls, Zimbabwe[c]	M3	+3+	5.0	+60.0+	93.0	209.0	225	4.0
Fragment D, left bank Zambezi River, Victoria Falls, Zimbabwe[c]	M3	12+	4.9–5.5	234.0	94.0	219	232	3.5–4.0
SA Mb555, Vaal River, South Africa[h]	m3	9+	3.7	276.5+	96.0	177.0	186	3.0–3.5
MMK 10624, Vaal River, South Africa[h]	m3	5+	4.7	163.0+	104.0	206.0	198	2.5

Table 1 (continued)

Accession or Field#/Site.	Specimen	Plate Formula	LF	L	W	H	HI	ET
MMK 3682 "*Archidiskodon broomi*" (type)[b], Vaal River, South Africa[h]	m3	6+	3.4	165.0+	114.0	175.0	153	3.8
MMK 4157, Vaal River, South Africa[h]	M3	13	5.0	290.0	113.0	210.0	228	3.0–4.0
MMK 2930 "*Archidiskodon hanekoni*" (type)[b], Vaal River, South Africa[b, h]	M3	x14x	4.8	304.0	102.0	259.0	254	2.0
MMK 4523, Vaal River, South Africa[h]	M3	5+	4.5	99.0+	96.0	247.0	257	2.0
MMK 4439, Vaal River, South Africa[h]	M3	8+	5.6	130.5+	83.0	186.0	224	1.5–2.5
"*Archidiskodon transvaalensis*" (type), Vaal River, South Africa[a]	M3	+16? (figures of the specimen do not appear to show that many plates)	–	246.0	110.0	247.0	225	–
"*Archidiskodon sheppardi*" (type), Vaal River, South Africa[a]	M3	13	–	246.0	100.0	202.0	202	–
Mb 555, "'*Archidiskodon*' cf. *transvaalensis,*" Melkbosstrand, South Africa [f]	M3	+8 ½+	–	+246.0+	95.0	175.0	184	4.0
Elephas recki recki (early to middle Pleistocene)[j, k, l]	m3	14x-18x	5.5–6.0	285.0–362.0	68.0–90.0	123.0–160.0	161–190	2.3–3.0
	M3	x13x-x19	4.6–6.5	330.0–350.0	82.0–104.0	148.0–190.0	177–200	1.8–3.2
	m2	x12	5.5–6.0	218.0	68.0–83.0	89.0–130.0	129–175	1.9–2.3
	M2	x10	5.0–5.2	250.0	68.0–80.0	130.0–147.0	198–205	1.8–2.6

All linear dimensions are in mm. Abbreviations: e., estimated; ET, enamel thickness; H, height; HI, hypsodonty index, H × 100/W; L, length; LF, lamellar (plate) formula, calculated as number of plates per 100 mm; W, width; x, indicates a pre- or postcingulum(id); 1, 2, 3. .., plates counted from anterior end of crown, in parentheses indicates plate of greatest width or height; I, II, III,. .., plates counted from posterior end of crown, in parentheses indicates plate of greatest width or height; +, indicates broken segment of tooth.

[a] Dart 1927

[b] Dart 1929

[c] Cooke and Clark 1939

[d] Arambourg 1952

[e] Arambourg 1960

[f] Hendey 1967

[g] Cooke and Coryndon 1970

[h] Maglio 1973

[i] Coppens and Gaudant 1976

[j] Beden 1980

[k] Beden 1983

[l] Beden 1987

[m] F. Brown personal communication

Dental Abbreviations

ET, enamel thickness; H, crown height; HI, hypsodonty index, H/W × 100; L, crown length; LF, lamellar frequency, number of plates or loph(id)s per 100 mm; M/m, upper or lower molar (e.g., M1 is an upper first molar and m1 a lower first molar); mm, millimeter; W, width; x, anterior or posterior cingulum (upper case "X" represents a large cingular ridge that could be considered an incipient plate); +, indicates a missing portion of a tooth, and that the original dimension was greater.

Dental Definitions

Accessory conules, enamel pillars associated anteriorly or posteriorly with molar plates, that may become incorporated into enamel wear figures on the occlusal surface of the crown; apical digitations, the small projections or minor subdivisions of conelets at the occlusal surface of molar plates; lamellar frequency, number of plates per 100 mm, measured normal to the long axis of molar crowns; molar crown height, in elephants, brachyodonty and hypsodonty are arbitrarily defined as HI <100 and ≥ 100, respectively, calculated as height × 100/width.

Institutional Abbreviations

KI, Natodomeri; KNM-, National Museums of Kenya; M followed by a series of numbers, Natural History Museum, London; ND, Natodomeri.

Systematic Paleontology

Proboscidea Illiger, 1811
Elephantidae Gray, 1821
Elephantinae Gray, 1821
***Elephas* Linnaeus, 1758**
***Elephas jolensis* Pomel, 1895**

Synonymy *Elephas iolensis* Boule, 1900; *Elephas iolensis* de Lamothe, 1904; *Elephas iolensis* Depéret and Mayet, 1923; *Archidiskodon transvaalensis* Dart, 1927, 1929; *Archidiskodon sheppardi* Dart, 1927, 1929; *Archidiskodon broomi* Osborn, 1928; *Archidiskodon hanekomi* Dart, 1929; *Palaeoloxodon kuhni* Dart, 1929; *Pilgrimia wilmani* Dart, 1929; *Archidiskodon yorki* Dart, 1929; *Pilgrimia yorki* Dart, 1929; *Pilgrimia archidiskodontoides* Haughton, 1932; *Pilgrimia subantiqua* Haughton, 1932; *Palaeoloxodon transvaalensis* Osborn, 1934, 1942; *Elephas iolensis* Arambourg, 1938; *Loxodonta (Palaeoloxodon) darti* Cooke, 1939; *Palaeoloxodon darti* Cooke and Clark, 1939; *Archidiskodon yorki* Osborn, 1942; *Palaeoloxodon hanekomi* Osborn, 1942; *Palaeoloxodon jolensis* Osborn, 1942; *Loxodonta* (*Palaeoloxodon*) *transvaalensis* Cooke, 1947, 1949; *Loxodonta* (*Palaeoloxodon*) *darti* Cooke, 1947; *Loxodonta* (*Palaeoloxodon*) *hanekomi* Cooke 1947, 1949; *Elephas recki* (in part) Biberson and Ennouchi 1952; *Elephas pomeli* Arambourg, 1952 (in part); *Elephas iolensis* Arambourg, 1952 (in part); *Loxodonta jolensis* Hopwood and Hollyfield, 1954; *Elephas jolensis* Cooke, 1960; *Elephas iolensis* Arambourg, 1960; *Archidiskodon tranvaalensis* Cooke, 1960; *Archidiskodon* cf. *transvaalensis* Hendey, 1967; *Elephas iolensis iolensis* Arambourg, 1970; cf. *Mammuthus* (*Archidiskodon*) *transvaalensis* Cooke and Coryndon, 1970; *Elephas iolensis* Maglio, 1973; *Elephas iolensis*, Coppens and Gaudant, 1976; *Elephas iolensis* Coppens et al., 1978; *Elephas iolensis* Geraads, 1980; *Elephas iolensis* Sanders et al., 2010; *Elephas iolensis* Marinheiro et al., 2014.

Revised Diagnosis (Based on Pomel 1895; Arambourg 1960; Maglio 1973; Coppens and Gaudant 1976; Coppens et al. 1978) Medium- to large-sized species of elephant characterized by extremely hypsodont molars (HI usually ≥200 in unworn third molars); thick molar plates separated by very thin intervals of abundant cementum, yielding high lamellar frequencies; modest number of plates in third molars (<20); enamel thin (typically ET = 2.0–3.5 mm) and strongly folded, occasionally irregularly and usually more in the central part of enamel loops; plates anteroposteriorly parallel-sided, and transversely widest around mid-height.

Occurrences (Fig. 1) Beauséjour Farm, Algeria (type site); Gué de Constantine, Algeria; Port de Mostaganem, Algeria; Gouraya, Algeria; El Kantara near Cherchell, Algeria; Carrière Sidi Abder Rahmane (Casablanca), Morocco; Thomas (Casablanca), Morocco;? Anchrif Quarry, Taghrout, Morocco; El Douira, Tunisia; Zouerate, Mauritania; Vaal River younger terraces and gravels, Transvaal, South Africa; Melkbosstrand, South Africa; Victoria Falls, Zimbabwe; Behanga I and Kaiso Village, Uganda; Natodomeri Members I and II, Kibish Formation, Kenya (Dart 1927, 1929; Cooke and Clark 1939; Arambourg 1952, 1960; Hendey 1967; Cooke and Coryndon 1970; Maglio 1973; Coppens and Gaudant 1976; Coppens et al. 1978; Geraads 1980; Marinheiro et al. 2014).

Description *Elephas jolensis* is a "dental species," represented only by isolated molars, many of them fragmentary. As the new molar specimens recovered by the West Turkana Palaeontology Project conserve abundant diagnostic morphological details, they constitute valuable additions to the species sample.

KNM-ND 68136 (Fig. 2a, b) The most informative of the fragments of two molars that comprise this specimen is a very worn distal portion of a left M3. The root pattern and occlusal longitudinal convexity of the crown indicate that it is an upper molar and its size is consistent with its identification as a last molar. It preserves eight full plates and a postcingulum composed of a single large conelet. Lamellar frequency is moderately high and enamel thickness is modest (Table 1). Traces of cementum remain, but in occlusal view, the transverse valleys are nearly obliterated by the anteroposterior crowding of the worn plates on one another. In the central three-quarters of each plate, enamel is tightly and regularly folded with a frequency of approximately three to four folds per cm at low amplitude. The enamel loops do not exhibit loxodont sinuses ("<>"), but in occlusal view they are either anteriorly convex and transversely straight or slightly concave along their posterior margins. Dentine is excavated into smooth concavities within each enamel loop that are slightly lower than the level of the enamel rims. Ridging of enamel on vertical plate faces corresponds with enamel folding observed on the occlusal surfaces of the crown.

The second molar fragment is broken at both ends and has three full plates and part of a fourth plate worn into enamel loops. Although the occlusal surface is more abraded than in the larger partial molar of this specimen, it is possible to observe that the plates are transversely straight and that there is no midline expansion of the enamel loops (no loxodont sinuses), that enamel folding is more pronounced in the anteriormost, more worn plates, and that abundant cementum fills the transverse valleys between the plates.

KNM-ND 68511 (Fig. 2c) This specimen is a partial right m3 broken at both ends and preserving six full plates. The longitudinal concavity of its occlusal surface and strong anterior tilt of its plates indicate that it is a lower molar. It size is consistent with its identification as a last molar. It is impressively hypsodont (Table 1) despite all plates having been worn to enamel loops on their occlusal aspect. The crown is longitudinally curved so that the buccal margin is concave. Abundant cementum is in evidence, filling the anteroposteriorly narrow, U-shaped transverse valleys. On the occlusal surface of each plate, the dentine is not much recessed below the level of the enamel rims. Lamellar frequency is high and enamel is modestly thick (Table 1). In lateral view, plates are anteroposteriorly parallel-sided, and slightly curved anteriorly at their apices. Enamel is tightly folded throughout most of the central three-quarters of each plate. In occlusal view, the plates are primarily transversely straight or exhibit slight midline expansions, but do not form loxodont sinuses. A few folds in the middle third of the enamel loops are more prominent (higher amplitude), a condition reminiscent of *Elephas jolensis* molars from other sites (e.g., Behanga I, Uganda, El Douira, Tunisia, Vaal River, South Africa). In cross-section, plates appear as tall rectangles, and are widest well above their bases, at approximately the one-third to one-half point of the crown.

KNM-ND 68505 (Fig. 2d) This specimen is an upper molar, probably an M3. The longitudinal convexity of the occlusal surface of the crown suggests it is an upper tooth and its size indicates that it is a last molar. It is broken anteriorly and

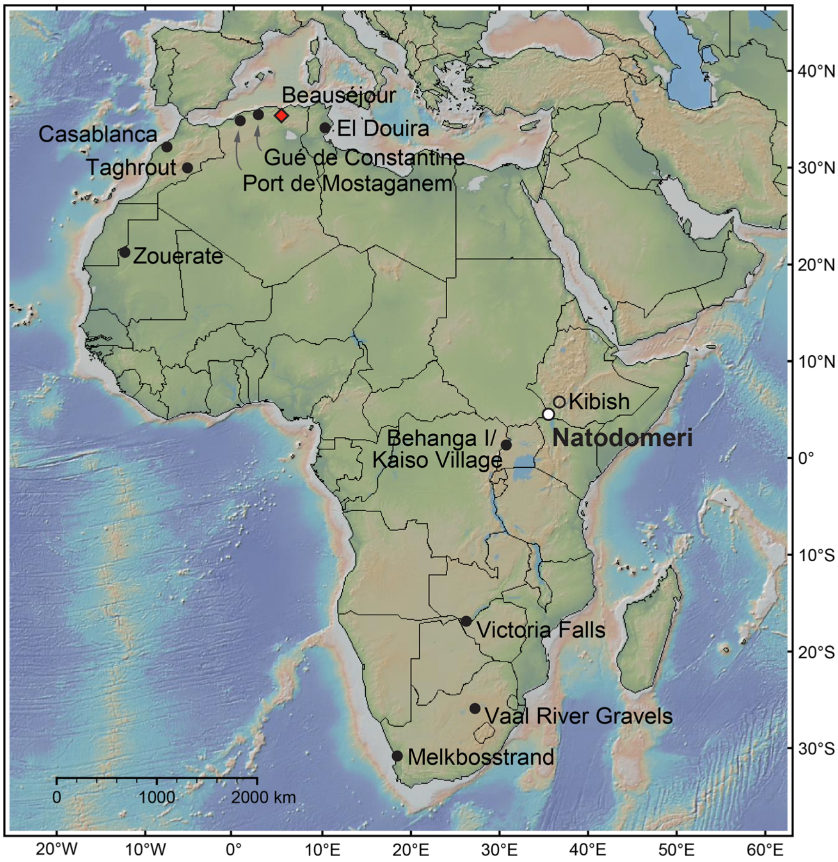

Fig. 1 Map of Africa showing distribution of major *Elephas jolensis* sites. Symbols: diamond, type site; black circle, *E. jolensis* occurrence; white circle, *E. jolensis* occurrence in Natodomeri Members I and II, Kibish Formation; open circle, Kibish Formation section and occurrence of *Loxodonta africana* in Members III and IV

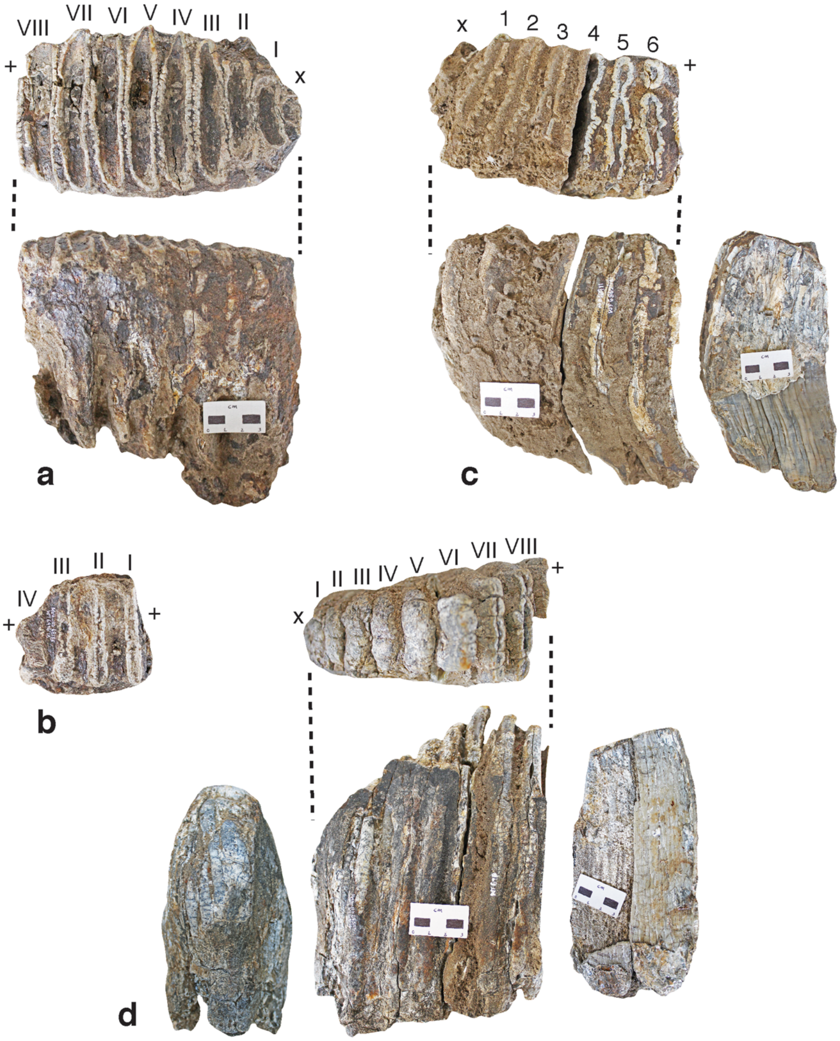

Fig. 2 Recently collected molar specimens of *Elephas jolensis* from Natodomeri, Kenya. Abbreviations: I, II, III, . . ., plates counted from the posterior end of the crown; 1, 2, 3, . . ., plates counted from the anterior end of the crown; x, anterior or posterior cingulum(id); +, denotes missing section of morphology. All specimens are to the same scale. **a** Occlusal and lateral views, KNM-ND 68136a, left M3, anterior to the left. **b** Occlusal view, KNM-ND 68136b, molar fragment, anterior to the left. **c** Occlusal, lateral, and transverse views, KNM-ND 68511, right m3, anterior to the left in occlusal and lateral views. **d** Transverse, occlusal, and lateral views, KNM-ND 68505, upper molar (?M3), anterior to the right in occlusal and lateral views

preserves eight plates formed of as many as seven apical digitations, along with a low postcingulum composed of five apical digitations. Enamel thickness is modest and lamellar frequency is high (Table 1). There is abundant cementum filling the U-shaped transverse valleys that narrowly separate the plates. The plates are anteroposteriorly parallel-sided and extremely hypsodont (Table 1). The apex of each plate curves anteriorly. Bilaterally, the plates gently converge towards the apex, and are widest well above the base, about at the half-way point of the crown. In cross-sectional view, the plates generally have a tall, rectangular outline. In the worn plates, enamel folding is restricted to the central moiety of the occlusal surface and is insignificant; however, vertical surfaces of broken plates reveal that their enamel is ridged, suggesting that folding would be more extensive with greater wear of plates. This corresponds to what is observed in more worn M3 specimen KNM-ND 68136.

Remarks Morphological and metrical similarities of new molar specimens from Natodomeri indicate that they probably represent a single taxon. Based on the extreme hypsodonty of KNM-ND 68505 and KNM–ND 68511, despite occlusal wear of their crowns, these specimens are referred to the late middle Pleistocene-late Pleistocene species *Elephas jolensis*. The degree of hypsodonty, amplitude and frequency of enamel folding, and absence of true loxodont sinuses in enamel wear figures confirms that these specimens belong in the genus *Elephas*. Although there is some overlap in dimensions between molars of *E. jolensis* and early to middle Pleistocene *E. recki recki*, KNM-ND 68505 exceeds hypsodonty of the latter taxon and undoubtedly KNM-ND 68511 also would have exceeded its range of hypsodonty (Table 1).

Beden (1983) pointed out that in *E. recki recki*, enamel loop configuration and intensity of enamel folding in molars varied with wear, producing pseudo-loxodont sinuses with moderate occlusal wear in some individuals. This is also the case for *E. jolensis*, reflected by the variation observed in the small sample of new molar specimens from Natodomeri. A good example of intra-individual variation is present in MMK 4286, a right m2 from Vaal River, South Africa, which exhibits rounded conelets in little-worn posterior plates, pseudo-loxodont sinuses with some anteroposterior projections in the enamel loops of middle plates, representing accessory conules integrated into these plates, and transversely more rectilinear enamel loops with tight, uniform enamel folds along the breadth of the most worn, anterior plates.

A right m2 or m3 from Gué de Constantine was assigned to a junior synonym of *E. jolensis*, "*E. pomeli*," by Arambourg (1952), but later re-assigned by Maglio (1973) to *Loxodonta atlantica* (Table 1). There is little reason to accept this re-assignment, given the light wear on the crown and morphometric consistency of the specimen with other molars of *E. jolensis*, along with the undoubted presence of additional molars of *E. jolensis* at the site. However, a smaller, sectioned fragment of a left m2 from Gué de Constantine, illustrated by Arambourg (1952: fig. 8), has strong anterior and posterior central accessory conules incorporated into its enamel loops, forming the distinctive wear patterns of *L. atlantica* and greatly exceeding any midline enamel folds observed in *E. jolensis*. This indicates the presence of two elephant species at Gué de Constantine, and demonstrates that, even with variation in enamel loop patterns at different occlusal wear stages, molars of *E. jolensis* can be readily distinguished from those of contemporaneous specimens of *Loxodonta*.

Nine samples of tooth enamel from Natodomeri *E. jolensis* molar specimens were analyzed for stable isotopes using standard methods of pre-treatment to remove carbonate and isotope analysis (see Passey et al. 2002); one specimen was sampled multiple times and the average of its isotope values is reported here (Table 2). Previous isotope studies of fossil elephantids in East Africa show that in the past, *Elephas* and *Loxodonta* were both primarily grazers (Cerling et al. 1999, 2015). In contrast, *Elephas* is now extinct in Africa but modern *E. maximus* is a mixed feeder in India (Sukumar et al. 1987; Sukumar and Ramesh 1992) and extant African *Loxodonta africana* is primarily a browser (Cerling et al. 1999, 2007, 2015), although seasonal grazing can be very important for this species (Cerling et al. 2004, 2009).

The carbon isotopes results show that the *E. jolensis* individuals from Natodomeri had predominantly grazing diets with δ^{13}C values averaging +0.3 ± 0.5‰. Using the widely used isotope enrichment value of 14.1‰ for African ungulates (Cerling and Harris 1999) from diet to tooth enamel, a diet of ca. −14‰ is indicated for these individuals; such a value corresponds to a diet dominated by C_4 plants. Passey et al. (2005) suggested that the isotope enrichment for non-ruminants may be somewhat smaller than this value: an isotope enrichment of 12‰ would give a δ^{13}C value of ca. −12‰ for diet, which would indicate an even higher fraction of C_4 biomass comprising the diet. Using the mixing lines of Cerling et al. (2015), the average diet values of −12‰ to −14‰ provide estimates between 75 to 100% C_4 biomass contributing to diet. Tejada-Lara et al. (2018) suggested a larger isotope enrichment factor for elephants. Using an isotope enrichment of 15.7‰ as suggested by Tejada-Lara et al. (2018) would indicate a somewhat lower fraction of C_4 biomass contributing to the diet (ca. 60%). However, the isotope enrichment value in the model presented by Tejada-Lara et al. (2018) is much higher than the observed data for *Loxodonta* (14.0‰) used in their regression analysis. Further work on isotope enrichment measured directly in *Elephas* and *Loxodonta* may better resolve the exact proportion of C_4 biomass in the diets of extant and fossil elephants.

The δ^{18}O of tooth enamel from the nine specimens sampled have a wide range, from +1.7 to −6.3‰ (average − 3.5‰) relative to the isotope reference VPDB (Table 2). All but the most positive specimen strongly indicates high water dependency. This is not surprising given the strong reliance of extant African elephants on surface water (e.g., Hayward and Hayward 2012). Further discussion of the implications of the δ^{18}O values awaits comparison with other extant taxa.

Discussion

Elephas jolensis was first diagnosed at the turn of the previous century as a dwarfed species (Pomel 1895), due to misidentification of the type specimen as an undersized third molar (Arambourg 1960; Coppens et al. 1978; Geraads 1980). Subsequently, the specimen was recognized as a more anterior molar, and supported by additional evidence the species consequently was determined to be of medium-to-large size for an elephant (e.g., Arambourg 1960; Maglio 1973; Coppens and Gaudant 1976). The species has a robust presence in North Africa, as the type specimen and other molars attributed to it

Table 2 Stable isotope (δ^{13}C and δ^{18}O) values for *Elephas jolensis* specimens from Natodomeri, Kenya

KNM Number	Tooth	δ^{13}C	δ^{18}O
-ND 68136	M3	0.7	−3.2
-ND 68359	m3	0.3	−6.2
-ND 68478 average	molar	−0.1	−2.8
-ND 68505	?M3	0.7	−3.0
-ND 68508	m3	−0.6	−5.3
-ND 68510	M3	0.5	1.7
-ND 68511	m3	−0.2	−5.2
-ND 70615	molar	0.8	−3.3
-ND 70618	molar	0.4	−3.7
All	**avg**	**0.3**	**−3.5**
	st dev	**0.5**	**2.3**
	N	**9**	**9**
	max	**0.8**	**1.7**
	min	**−0.6**	**−6.2**

Abbreviations: avg., average; max, maximum; min, minimum; N, number of samples; st dev, standard deviation are from sites of reported Tyrrhenian Stage antiquity (latest middle Pleistocene to the end of the late Pleistocene) located in Algeria, Morocco, and Tunisia (Table 1 and Fig. 1; Arambourg 1952, 1960; Biberson 1952a, 1952b; Biberson and Ennouchi 1952; Coppens and Gaudant 1976; Geraads 1980; Marinheiro et al. 2014). Molar specimens deriving from younger gravels and terraces of the Vaal River in South Africa (Fig. 1; Table 1) also appear to belong in *E. jolensis*, though they have suffered through a reckless profligacy of nomenclatural indulgence comprising at least three genera and nine species (e.g., Dart 1927, 1929; Osborn 1928; Haughton 1932). Vaal River *E. jolensis* fossils are probably of late middle Pleistocene age (see Butzer et al. 1973). Molars attributable to *E. jolensis* also were recovered from the Older Falls gravels, calcareous sand, and ferricrete levels at excavations on the left bank of the Zambezi River near the Victoria Falls in Zimbabwe (Table 1; Fig. 1), broadly estimated to be middle or late Pleistocene in age (Cooke and Clark 1939). In addition, Maglio (1973) placed isolated molar specimens of uncertain stratigraphic provenience from Behanga I and Kaiso Village, Uganda in *E. jolensis* (Table 1; Fig. 1). Thus, including the Kibish Formation molars from Natodomeri, *E. jolensis* has a pan-African distribution (Fig. 1). The only absolute dates for *E. jolensis* are radiometric calculations of 205–195 ka for the Natodomeri specimens in Member I and 130 ka bracketing the top of Member II of the Kibish Formation, with the KHS tuff in Member II dated to 1.54 ± 7 ka (McDougall et al. 2005; Brown and Fuller 2008; Brown et al. 2012), validating the late middle Pleistocene age of the species estimated for its occurrences at other sites.

Despite the wide geographic distribution of sites at which *E. jolensis* occurs, the molar sample of the species is remarkably uniform morphometrically and provides a suite of consistent features supporting its identification as a valid paleontological species (Coppens and Gaudant 1976). The Natodomeri molars closely match the morphology of *E. jolensis* in all anatomical details and metrics. The most striking feature of the species is its very great molar crown hypsodonty, which reaches well above HI = 200 in M3/m3, comprising the most high-crowned molars of any elephant that occurred in Africa; in addition, *E. jolensis* is characterized by (1) strong folding of enamel in occlusal wear figures; (2) moderately thick enamel (generally 2.0–3.5 mm but as great as 4.0 mm in southern African specimens [Table 1]); (3) bilaterally parallel plate sides that are widest at about half the height of the crown; (4) tall, rectangular cross-sectional plate shape; (5) plates that are anteroposteriorly thicker than transverse valley intervals; (6) absence or very diminished expression of accessory conules that are incorporated into plates when present; (7) moderate to high lamellar frequency (which may reach 6.3 in third molars); (8) moderate number of plates, < 20 in third molars (up to 14 in M3 and estimated to reach 16–17 in m3); and (9) transverse valleys between plates filled with abundant cementum (Dart 1927; Arambourg 1960; Maglio 1973; Coppens et al. 1978). In addition, plates appear to be composed of no more than four-seven conelets. Compared with the final stage of *E. recki*, *E. jolensis* is distinguished by attainment of greater hypsodonty, anteroposteriorly thicker plates, greater enamel folding, lower range of third molar length, and third molar plate formulae at the low end of the range documented for the former (Table 1; Arambourg 1960). The greater thickness of plates, similar thickness of enamel, and generally fewer number of plates in third molars is unexpected for a taxon that has been described as the direct descendant of *E. recki* and as the terminal constituent of the *E. ekorensis*-*E. recki* lineage (Arambourg 1970; Maglio 1973; Coppens et al. 1978). Nonetheless, the general morphological similarity, increase in hypsodonty, overlapping geographic distribution, and chronological succession all indicate a derivation of *E. jolensis* from *E. recki*.

The earliest candidate for the first appearance of the genus *Elephas* is *E. nawataensis* from the late Miocene Upper Nawata Formation and early Pliocene Apak Member of the Nachukui Formation at Lothagam, Kenya (Tassy and Debruyne 2001; Tassy 2003). This species is known from a small sample of gnathodental specimens that lack obvious synapomorphies of the genus. For this reason, its generic attribution is not universally accepted and the species hypodigm has been alternatively referred to as an advanced morph of *Primelephas korotorensis* (Sanders et al. 2010). Nonetheless, molecular evidence indicates that the *Mammuthus* + *Elephas* and *Loxodonta* clades diverged about 7.8–7.6 myr ago (Rohland et al. 2007; Murata et al. 2009), and as the first appearance of *Mammuthus* is dated to the late Miocene of Africa (Cooke and Coryndon 1970; Maglio and Hendey 1970; Maglio 1973; Kalb and Mebrate 1993; Haile-Selassie 2001; Sanders 2006, 2007; Sanders et al. 2010), it is reasonable to expect that *Elephas* had a late Miocene African origin, as well.

Credible paleontological evidence for *Elephas* first appears in early Pliocene deposits, initially in the form of *E. ekorensis*, diagnosed by Maglio (1970a, 1973) as belonging to the genus based on cranial features such as nascent bossing and midsagittal depression of the parietals, parallel configuration of tusk alveoli, and sharp edges of parietofrontal flanges separating the forehead from the temporal fossae. The type site of the species, Ekora, Kenya, is dated to slightly less than 4.0 Ma (Behrensmeyer 1976), and other site horizons where it is present, most notably at Kanapoi, Lothagam, and Allia Bay, Kenya, are of similar age (Coffing et al. 1994; Feibel 2003; Harris et al. 2003; McDougall and Feibel 2003; Tassy 2003; McDougall and Brown 2008; Bobe 2011; Brown and McDougall 2011). It is the first elephant species to commonly have hypsodont molars (crown height > width; HI = 100–125), and exhibits a greater number of plates (M3/m3 with 11–12 plates) than contemporaneous or older confamilials (Maglio 1970a, 1973; Sanders et al. 2010).

The latter part of the early Pliocene marked the oldest occurrences of the species that became the dominant, and for a time, the only elephant taxon in eastern Africa, *E. recki* (Kullmer et al. 2008; Sanders et al. 2010; Sanders and Haile-Selassie 2012). There is convincing evidence for continual, anagenetic evolution of this species, demonstrated as an impressive serial increase over time in molar plate number, crown height, lamellar frequency, and enamel folding, with concomitant decrease in enamel thickness (Maglio 1973; Beden 1980; Sanders and Haile-Selassie 2012). The temporal expression of morphological change in the lineage led to the erection of several schemes to subdivide it into time-successive stages (Maglio 1973; Coppens et al. 1978) or subspecies (Beden 1980) that are segmented arbitrarily largely by chronostratigraphic unit boundaries of the Omo Shungura Formation (Beden 1980, 1987). These lineage segments have proven useful for biochronological correlation of site horizons within a span of over three million years (e.g., Maglio 1970b, 1973; Cooke and Maglio 1972).

Alternatively, it has been suggested that the lineage should be partitioned into a number of species (Todd 2005). The arbitrary subdivision of the lineage, sample size disparities between lineage segments, large degree of variation, and typological rigidity of definition of subspecies or stages has led to the suggestion that subspecies overlap temporally and to the rejection of anagenesis as its mode of evolution (Todd 2001, 2005; see also Lister 2004). However, if names and stages are ignored, the emergent pattern of morphological change is "of a continuously, directionally evolving lineage with robust variation and substantial morphometric overlap between successive generations" (Sanders et al. 2010: 234). These generations of *E. recki* are analogous to a ring species rolled out over time (Sanders and Haile-Selassie 2012), with following generations very similar to preceding ones but with end members (in this case, *E. recki brumpti* beginning in the early Pliocene and *E. recki recki* ending in the middle Pleistocene) substantially different, so much so that if they were found in the same horizon they would not be recognized as belonging to the same species.

A number of authors assign *Palaeoloxodon* as either the genus (e.g., Osborn 1942; Lister 2013; Lister et al. 2013) or subgenus (e.g., Beden 1980, 1983, 1987; Saegusa and Gilbert 2008) for some or all of the *E. recki*-*E. jolensis* lineage. Those who treat *Palaeoloxodon* as a subgenus view *Elephas* as monophyletic (e.g., Saegusa and Gilbert 2008). Presumed nascent or full development of synapomorphic cranial features in specimens of *E. recki* (there are no crania known for *E. jolensis*) that are common among Eurasian species of *Palaeoloxodon* have been invoked to justify the use of "*Palaeoloxodon*" in connection with the *E. recki*-*E. jolensis* lineage. These features of various specimens of *E. recki* include occurrence of a central parietofrontal swelling, formation of a post-temporal crest, wide divergence of tusk alveoli coupled with a shallow premaxillary fossa, and vertical, rectangular extension of the temporal fossa to give the upper cranium a box-like shape (Saegusa and Gilbert 2008). A scenario has been presented in which a trend occurred within the *E. recki* lineage for greater acquisition of *Palaeoloxodon*-like features over time, with greatest similarity between Eurasian *Palaeoloxodon* crania and specimens from the latest early Pleistocene Daka Member of the Bouri Formation, Ethiopia, just slightly older than the first records of *Palaeoloxodon* in Eurasia (Saegusa and Gilbert 2008). However, the full morphological pattern of Eurasian *Palaeoloxodon*, including development of a distinct parietofrontal crest, appears to have evolved subsequent to the migration of *E. recki* out of Africa at the end of the early Pleistocene. For this reason, it is possible to treat the Eurasian radiation of palaeoloxodonts as a separate, clearly definable clade. Presumably, the lineage that led to the evolution of the clade that includes the extant Asian elephant was separately derived from African *Elephas*. The issue is clouded by the recent paleogenomic work of Meyer and colleagues (Meyer et al. 2017) yielding the unexpected result that *Palaeoloxodon antiquus* is the sister taxon to the African forest elephant, *Loxodonta cyclotis* rather than *Elephas*.

In East Africa, the final named segment of *E. recki*, *E. recki recki*, extended well into the middle Pleistocene at site horizons such as the Masek Beds at Olduvai Gorge, Tanzania and Olorgesailie, Kenya (Beden 1985; Potts and Deino 1995; Tamrat et al. 1995). Investigations of southern African archeological sites such as Kathu Pan, Power's Site, and Namib IV show that *E. recki* does not occur in levels above those yielding Acheulean stone tools (Klein 1988; Porat et al. 2010). Klein (2000) felt that *E. recki*-bearing stratigraphic levels at Kathu Pan and Power's Site could be bracketed within the interval 1 myr-500 kyr. Earlier work by Klein (1984) did not distinguish between *E. recki* and *E. jolensis* in associating the genus with younger, Middle Stone Age (MSA) horizons. A transitional industry between the Acheulean and MSA, the Fauresmith, characterized by prepared cores, blades, Levallois points, and bifaces (including handaxes) has had its latest phase dated to around 286–276 kyr in southern Africa (Beaumont and Vogel 2006), and the shift to the MSA in eastern Africa also appears to occurred around this time (Porat et al. 2010) or a little earlier. Potts et al. (2018) recorded the transition to the MSA at Olorgesailie between 320 and 305 kyr; however, the occurrence of *E. recki* at the site is documented from older, pre-MSA horizons (O'Regan et al. 2005). This shift was marked by an abrupt transformation in artifact technology and composition, associated with a radical change in human anatomy and behavioral capabilities that coalesced with the emergence of modern humans throughout the continent (Klein 2000; Beaumont and Vogel 2006). Stratigraphic horizons with Fauresmith and MSA tool kits have not yielded evidence of *E. recki*; thus, the species (as presently composed) reached its termination before the end of the middle Pleistocene. However, the stone tool industry from horizons of the Vaal River sequence that produced *E. jolensis* resembles the transitional aspect of the Fauresmith and features Levallois points and bifaces (Cooke and Clark 1939), suggesting evolution of the *E. recki* lineage into *E. jolensis* during the time of transition of the Acheulean into the MSA. If *E. jolensis* is the last stage of *E. recki*, the species nomen "*jolensis*" would have priority for the entire lineage, as *E. jolensis* was named twenty years before *E. recki* (Coppens and Gaudant 1976). As shown by the precise dating at Natodomeri, *E. jolensis* subsequently persisted at least until the close of the middle Pleistocene.

The fossil record of *L. africana* is poorly documented (Sanders et al. 2010), and there are no records of its co-occurrence with *Elephas* except possibly in the Apoko Formation at the middle Pleistocene site of Kanjera, Kenya, around 500 ka (Plummer and Potts 1989; Behrensmeyer et al. 1995). *Loxodonta atlantica* co-occurred with *E. jolensis* at Gué de Constantine (see above). Results of molecular analyses indicate a substantial expansion of the *L. africana* population between 500 and 100 ka, nearly synchronous with the disappearance of *E. recki* (Murata et al. 2009; Brandt et al. 2012). Replacement of *E. jolensis* by *L. africana* in the northern Turkana Basin is documented as occurring at the middle to late Pleistocene boundary (Assefa et al. 2008). There is no credible evidence to support human hunting as the main agency for this replacement or the terminal occurrence of *E. recki* (Klein 1988), but there are some indications that intensity and increased rate of fluctuation of climate change could have played a role in the demise of *Elephas* and its replacement by *L. africana* in Africa. Isotope and mesowear analyses indicate that the *Elephas* lineage existed as dedicated grazers (Table 2; Cerling et al. 1999; Saarinen et al. 2015), in warm, moist conditions during the middle Pleistocene (Klein 2000), but onset of a severe dry, cold climate interval marked by intense episodes of drought that occurred just prior to the start of the late Pleistocene (Cohen et al. 2007; Scholz et al. 2007; Tierney et al. 2017) may have impacted negatively on these specialized grazing elephants and favored generalist mixed feeders such as *L. africana* (see Cerling et al. 1999; Saarinen et al. 2015).

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