Review

Late Quaternary Proboscidean Sites in Africa and Eurasia with Possible or Probable Evidence for Hominin Involvement

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Abstract: This paper presents a list of >100 publicly known late Quaternary proboscidean sites that have certain or possible traces of hominin utilization in Africa, Europe, and Asia, along with a sample of references, chronometric or estimated ages, and brief descriptions of the associated materials and bone modifications. Summary discussions of important sites are also presented. Lower Palaeolithic/Early Stone Age hominins created far fewer proboscidean site assemblages than hominins in later Palaeolithic phases, in spite of the time span being many times longer. Middle Palaeolithic/Middle Stone Age hominins created assemblages at eight times the earlier hominin rate. Upper Palaeolithic/Later Stone Age hominins created site assemblages at >90 times the rate of Lower Palaeolithic hominins. *Palaeoloxodon* spp. occur in nearly one third of the sites with an identified or probable proboscidean taxon and *Mammuthus* species are in nearly one half of the sites with identified or probable taxon. Other identified proboscidean genera, such as *Elephas*, *Loxodonta*, and *Stegodon*, occur in few sites. The sites show variability in the intensity of carcass utilization, the quantity of lithics bedded with bones, the extent of bone surface modifications, such as cut marks, the diversity of associated fauna, and mortality profiles.

Keywords: late Quaternary; proboscideans; *Palaeoloxodon*; *Mammuthus*; Palaeolithic; butchering

1. Introduction

This paper begins by listing 116 proboscidean sites, mostly from the late Quaternary (Table 1), compiled from refereed and unrefereed publications and personal communications from colleagues. Only sites with possible or probable evidence for killing, scavenging, and/or butchering are included. Most of the searched publications and correspondence were written in English. Sites that were described only in languages other than English may have been overlooked. This list of sites and references is not claimed to be complete; new sites are announced often and the references are a sampling. Some sites in Table 1 were interpreted decades ago when interpretive standards were different or data were incomplete; the claims now may be questioned. A few of the unproven or ambiguous examples are included here because they have a history of appearing in published lists of proboscidean sites; not included are claims judged to be clearly fraudulent. The goals of this compilation are first to present the basic data in one place and second to highlight issues that become apparent from the compendium, such as changing frequencies of hunting large and dangerous prey and apparent differences in the intensity of carcass utilization.

Different proboscidean taxa are represented in the sites, including *Palaeoloxodon* spp. (incorporating *P. recki*, which was originally assigned to the genus *Elephas* but has been shown to be genetically closer to *Loxodonta* [1]), *Loxodonta* spp., *Elephas* spp., *Stegodon* spp., and *Mammuthus* spp. Only two sites contain possibly killed/scavenged/butchered cf. *Deinotherium* sp. bones. Two sites have indeterminate proboscidean taxa. In cases where either of two possible genera are identified, each is counted as an occurrence.

Species-specific differences in anatomy could account for some variability in the fossil sites. Major behavioral differences among the taxa are not well known, but the taxa were all elephant-like and probably had comparable dietary needs and life histories. Some might

have been more vigilant or effective in defending themselves against predators and escaping hominin attacks, or perhaps were more inclined to avoid ranges where hominins or other potential predators were present.

Table 1 is arranged by world landmasses. The chronometric ages were taken from published sources, noted as *Ma* (= million calendar years ago), *ka* or *ka BP* (= thousand calendar years ago or thousand calendar years before 1950 CE) or *k rcy BP* (= (uncalibrated) thousand radiocarbon years before 1950 CE). Some ages were calibrated using Calib 7.1 online [2] and cited as approximate midpoint estimates of the calibrated ranges. Isotope stages are cited directly from published sources as either OIS or MIS; in some cases, I have estimated chronometric ages for the materials assigned to the isotope stages.

Table 1. Proboscidean sites interpreted as killed/butchered or scavenged by hominins; the references are only samples. The list is arranged by world area, roughly from oldest to youngest in each area. Published citations that refer to *Elephas antiquus* have been changed to *Palaeoloxodon antiquus*, following on from [1]. Unless otherwise noted, skeletal elements were often fragmentary, incomplete or collected in multiple localities; MNIs are not always reported.

Name, Location	Age (Measured or Estimated)	MNI (Minimum Number of Individuals) of Proboscidean Taxon and Evidence for Human Association	Setting or Enclosing Sediments
AFRICA			
Olduvai FLK North Upper Bed I Level 6 (Tanzania) [3,4]	1.8–1.7 Ma	1 *Palaeoloxodon* (formerly *Elephas*) *recki*, Oldowan lithics, cut marked bones (re-interpreted as trample marked)	Streamside
Olduvai HWK EE (Tanzania) [5,6]	(?~1.7–1.5 Ma)	1 *Deinotherium* sp., 1 *P. recki*, astragalus from Proboscidea indet. with cut marks, Oldowan lithics	Low-energy fluvial sediments
Olduvai FLK North Lower Bed II (Tanzania) [3]	1.7–1.2 Ma	1 *Deinotherium bozasi*, Oldowan lithics	Fossil swamp?
Barogali (Djibouti) [7–10]	1.6–1.3 Ma	1 *P. recki*, Oldowan lithics	Paleomarsh
Olorgesailie Member I, Site 15 (Kenya) [11–13]	992–974 ka	1 *P. recki*, Acheulean lithics, cut rib	Abandoned paleochannel swale
Nadung'a 4 (Kenya) [14]	~700 ka	1 *P. recki*, 6700 lithics (mainly debitage)	Streamside
Mwanganda's Village (Malawi) [15–17]	Orig.1.2–0.6 Ma, bone re-dated 282 ka, lithics probably younger	1 cf. *Elephas/Loxodonta*, lithics	Paleoriver bank, channel lag deposits
Namib IV (Namibia) [18,19]	~350 ka	1 *P. recki*, other taxa, 394 lithics (Acheulean)	Eroded out of calcrete
Zoo Park (Namibia) [15,20]	5.2 ka [§]	1 *Loxodonta* sp., Later Stone Age lithics	Spring-fed marsh, fossil stream
EUROPE and *ASIA*			
Fuente Nueva-3 (Spain) [21]	1.3 or 1.5 Ma	1 *Mammuthus meridionalis*, abundant remains of other large mammals, Oldowan flakes and lithic debris	Lacustrine, swamp deposits
Indonesian sites on Flores (Mata Menge, Tangi Talo (also spelled Tallo), Boa Lesa (also spelled Leza), Kobatuwa) and Java (Ngebung 2) [22–27]	>0.9 Ma, 134–118 ka at Ngandong	35 *Stegodon florensis* (Mata Menge) and 12 smaller *Stegodon sondaari* (Tangi Talo), reptiles, other fauna, Acheulean lithic flakes and cores, hominin remains (possibly ancestral to *Homo floresiensis*) at Mata Menge	Volcanic and fluvio–lacustrine sediments, paleoriver bank at Ngebung and Ngandong
Xinglong Cave and other sites in China and SE Asia [28]	~2 Ma–0.13 Ma	(Multiple localities with varying MNIs) *Stegodon* spp., *Elephas namadicus*, often unclear associations with lithics, hominin remains, possible cut marks, engraved tusk at Xinglong Cave	Cave, other settings
Barranc de la Boella (Spain) [29,30]	Between 0.99 and 0.78 Ma	1 *M.meridionalis*, cervid, equid, Acheulean lithic cutting tools with use-wear, possible cut marks and doubtful green bone breakage	Fluvio-deltaic (stream channel and pool deposits)
Perdikas (Greece) [31]	<800 ka	1 *Palaeoloxodon antiquus*, unresolved association of bones, lithics (mostly non-local quartz), and possible bone tools	Alluvium, coarse sand
Sites (possible or proven) in Peninsular India (Kashmir, Mula Dam, Hagargundgi, Kalpi) [32]	Lower to Middle/Late Palaeolithic (? 780–45 ka)	(Multiple localities, low MNIs) *Elephas*? (ID uncertain at Hagargundgi), other large mammals, Lower and Middle Palaeolithic lithics, "associations" based on stratigraphic contexts	Various contexts, river valleys
Gesher Benot Ya'aqov (Israel) [33,34]	780 ka	1 *Palaeoloxodon antiquus* (or *P. recki*?), Acheulean lithics, broken and repositioned bones, cut marked bones	Paleolake shore
Kalinga (Luzon, Philippines) [35]	709 ka	Few remains of *Stegodon* sp., 57 lithics, bones of other fauna, including possibly butchered extinct rhinoceros	Clay-rich mudflow
Notarchirico (Italy) [36–39]	670–610 ka	1 *P. antiquus*, lithics	Stream/lake deposits

Table 1. *Cont.*

Name, Location	Age (Measured or Estimated)	MNI (Minimum Number of Individuals) of Proboscidean Taxon and Evidence for Human Association	Setting or Enclosing Sediments
Ti's al Ghadah Unit 5 [40,41]	~500–300 ka	6 *P.* cf. *P. recki* (two assemblages), birds, reptiles, mammals, Middle Palaeolithic lithics (mostly flakes), cut marked rib	Paleolake deposit
Revadim Quarry Area B (Israel) [42]	500–300 ka	3 (?) *P. antiquus*, Acheulean lithics, cut marked bones	Fluvial, paleoponds
Áridos 1 (Spain) [43]	500–300 ka	1 *P. antiquus*, Acheulean lithics	Fluvial sediments around bone lag deposits
Áridos 2 (Spain) [44]	500–300 ka	1 *P. antiquus*, Acheulean lithics, cut marks	Fluvial sediments around bone lag deposits
Marathousa 1 (Greece) [45–50]	500–400 ka	2 *P. antiquus*, small Lower Palaeolithic lithics, cut marked, peeled and flaked bones	Lacustrine, mudflat on lake shore
Fontana Ranuccio (Italy) [51–53]	~450 ka	? MNI *P. antiquus*, fragmented/flaked bone	Fluvial–lacustrine sediments, stream terrace
Ficoncella (Italy) [54,55]	450 ka or older	1 *P. antiquus*, 4 flakes	Fluvial–lacustrine sediments, stream terrace
Ebbsfleet (UK) [56,57]	425–375 ka	1 *P. antiquus*, Clactonian (presumed) lithics	Lacustrine
Bilzingsleben (Germany) [58–69]	MIS 11 or 9	23 *P. antiquus*, bones possibly from natural deaths, possible bone tools, possible cut marks, thousands of lithics (most are disputed [67]), *Homo erectus* cranial fragments	Fluvial sediments, mass flow
Kärlich-Seeufer (Germany) [70]	MIS 11 or 9 (~396 ka)	8 *P. antiquus*, 6 other mammalian spp., 12,000 pieces of wood, Acheulean lithics, probably reworked palimpsest deposit with uncertain association of artifacts with wood and bones	Lacustrine, debris flow
Ambrona (Spain) [71–81]	>350 ka	47 *P. antiquus*, Acheulean lithics, few cut marked bones	Fluvial–lacustrine
Terra Amata (France) [82–85]	Possibly MIS 11 (or ~400–300 ka)	13 *P. antiquus*, >68,000 lithics, incl. Acheulean (probably mixed [85])	Originally on ocean beach
Panxian Dadong (Big Cave) (China) [86–89]	MIS 8–6 (330–130 ka)	12 *Stegodon orientalis* and diverse fauna, incl. *Rhinoceros*, *Megatapirus*, primates, cervids, bovids, rare carnivores, hominin teeth, possible Levallois artifacts, juvenile-dominated *Stegodon* mortality profile interpreted as created partly by hominin hunting/scavenging	Cave sediment (clay)
Bełchatów (Poland) [90,91]	MIS 11 or 9 (? 500 ka)	2 *Mammuthus* cf. *M. trogontherii* (*M. primigenius* also present at the locality), possible "slice" marks on a rib fragment, marks interpreted as cuts on a tusk with red ochre spots	Fluvial system
Schöningen (Germany) [92,93]	300 ka	10 *P. antiquus* (natural death?), 30 small lithic flakes, 2 long bone pressure flakers with embedded microflakes	Lacustrine
Roman Basin and Sacco–Liri valley, multiple sites (Italy): e.g., La Polledrara di Cecanibbio [94–99], Rebibbia Casal de' Pazzi [70,100,101], Castel di Guido [102–111], Isoletta [52]	~360–250 ka	25 (?) *P. antiquus* (multiple sites), carnivores, bone and stone tools (including Acheulean bifaces at some sites), piled and broken bones, percussion marked bones, hominins might have scavenged trapped proboscideans, uncertain associations of artifacts and proboscidean bones in some sites [70] (p. 333)	Fluvial and fluvio-palustrine deposits
PRERESA (Spain) [112–114]	~270–169 ka	1 indeterminate taxon (*Palaeoloxodon/Mammuthus*), other large ungulates, carnivores, lithics, cut bone shafts, bone breakage (for marrow?)	Fluvial
Stanton-Harcourt (U.K.) [115–117]	245–190 ka	>20 *M.* cf. *M. trogontherii* and *P. antiquus*, other large ungulates, carnivores, nine lithics, incl. handaxes (may not be contemporaneous with elephant)	Fluvial, lag deposit (secondary mixing?)
La Cotte de St. Brelade, Levels 3 and 6 (Jersey) [118–126]	238–40 ka	26 *M.* cf. *M. primigenius*, other large ungulates, carnivores, lithics, burnt bone frags., cut marks on tusk, scapula, femur, a rib inserted into a cranium	Ravines on steep coastal cliff
Latton/Swindon Quarry (U.K.) [127,128]	220–210 ka (MIS 7)	5 *M. trogontherii*, giant elk, plant fossils, lithic hand axe and scrapers, possible "butchery marks" [127]	Alluvium? Paleomarsh?
Ranville (France) [129]	230–205 ka	1 *P. antiquus*, other large ungulates, wolf, elephant bones missing (interpreted as transported), >300 lithics, Levallois	Redeposited by collapse into karstic fissure
Torralba (Spain) [74–76,80,130–135]	~200 ka	6 (or more) *P. antiquus*, Acheulean lithics, few cut marked bones	Fluvial
Bucine (also known as the Campitello Quarry) (Italy) [136]	Before 200 ka	1 *P. antiquus*, 3 lithic items	Fluvial

Table 1. *Cont.*

Name, Location	Age (Measured or Estimated)	MNI (Minimum Number of Individuals) of Proboscidean Taxon and Evidence for Human Association	Setting or Enclosing Sediments
Liang Bua Cave, Flores (Indonesia) [137–141]	~190–50 ka	47 *Stegodon* sp. fragmentary remains, other fauna, thousands of lithics, hominin remains (the small *Homo floresiensis*), possibly cut marked *Stegodon* pelvis and rib	Cave deposits
Bollschweil (Germany) [142]	Possibly MIS 6 (198–131 ka)	6 *M. primigenius*, other large ungulates, bear, 12 lithics, incl. a handaxe, association of lithics and fauna uncertain due to reworking of deposits	Loess
Poggetti Vecchi (Italy) [143]	~171 ka	7 *P. antiquus* (no evidence of butchering), aurochs, deer, bear, rodents, possibly knapped bones, lithic cores, flakes, retouched tools, choppers, 34 shaped boxwood digging sticks	Lacustrine
Ariendorf 2 [144]	MIS 8 or 6	1 *Mammuthus* sp., wolf, 37 lithics	Loess
Neumark Nord 1 and 2 (Germany) [145–154]	~126 ka	Up to 70 *P. antiquus* [149], butchery marks and bone breakage at Neumark Nord 2	Incremental silts deposited in shallow basin
Ust'-Izhul' (Russia) [155]	125 ka[e]	12 *M. primigenius*, long bones and scapulae with "vigorous hammerstone indentations marks" [155] (p. 516), bipolarly flaked ivory core	River terrace eroded alluvia
Arriaga Iia [156,157]	MIS 6-5 (133 ka)	2 *P. antiquus*, other large ungulates, 43 (Acheulean?) lithics associated with elephant, possibly cut marked rib	Fluvial
Mealhada (Portugal) [158,159]	MIS 5 ("Riss Interstadial")	1 *P. antiquus* bone fragments, Upper Acheulian and Mousterian lithics	Stream terrace deposits
EDAR Culebro 1 (Spain) [160]	~130–100 ka	1 *Mammuthus* cf. *M. intermedius* or *M. primigenius*, other large ungulates, percussion fractured elephant humerus, lithics	Sandy/gravelly channel fills in low flow streamway
Kůlna Cave (Czech Republic) [161,162]	MIS 6–3 (98–29 ka)	? MNI *M. primigenius*, cut bones, small lithics	Cave, possibly with a small stream in it
Gröbern (Germany) [150,163–167]	120 ka	1 *P. antiquus*, other large ungulates, Middle Palaeolithic lithics	Lacustrine
Lehringen (Germany) [74,168–170]	120 ka	1 *P. antiquus*, other large ungulates, carnivores, wooden spear, lithics	Lacustrine
Ngandong (Java, Indonesia) [171]	117–108 ka	1 *Elephas hysudrinducus* with articulated elements, bones of 14 *Stegodon trigonocephalus ngandongensis*, contemporaneous/associated *Homo erectus* bones (mostly skull frags.), nearby lithics, numerous remains of other fauna, no direct signs that hominins butchered the proboscideans	Fluvial sediments from flood event/debris jam
Les Fieux (France) [172]	[Mousterian layer M1]	1 (?) *M. primigenius*, lithics, cut rib and femur	Multi-layer cave
São (or Santo) Antão do Tojal (Portugal) [158,159]	[first Würm interglacial; U-Th date 81.9 ka +4000, −3800]	1 *P. antiquus*, Mousterian (?) lithics, including 2 flakes in a femur	Fluvial deposits
Foz do Enxarrique (Portugal) [158,159]	MIS 3/2 transition (~30–40 ka)	1 *P. antiquus*, Mousterian lithics, bone fragments	Fluvial deposits
Molodova I (Russia) [173]	>44 ka [§]	15 *M. primigenius*, Mousterian lithics, dwelling structure of mammoth bone, cut and broken bones	Loess
Salzgitter-Lebenstedt (Germany) [174–177]	49–45 ka [§]	17 *Mammuthus* sp., late Middle Palaeolithic lithics, 5 bones from 2 Neanderthals, mammoth bone tools, other fauna	Mainly fluviatile sediments
Spy (Belgium) [178]	~41.5 ka, ~46 ka [§]	10–15 (?) *M. primigenius* (mainly juvenile molars), woolly rhino, bovids, hyena, other mammals, Neanderthal bones, Mousterian lithics	Terrace layer, clay with limestone blocks, above river in front of cave
Lake Nojiri [Tategehana site] (Japan) [179–186]	39–33 ka [§]	~46 *P. naumanni*, cut (?) bone, possible bone tools, lithics	Lakeshore
Byzovaya (Russia) [187,188]	~35–32 ka [§]	21 *M. primigenius*, Middle Palaeolithic (Mousterian) lithics, cut marked mammoth ribs	Debris flow sediments in a paleogully
Yana Mass Accumulation of Mammoths (YMAM), YANA site complex, near YANA RHS (Russia) [189–195]	~34–32 ka [§]	>26 *M. primigenius*, Upper Palaeolithic lithcs, lithic fragments embedded in bones, weapon-damaged bones, cut marks	Alluvium (stream side)
Gruta da Figueira Brava (Portugal) [158,159]	~34 ka	1 *M. primigenius* (tooth fragment), Neanderthal tooth and bone, upper Mousterian lithics	Sandy cave sediments
Skaratki (Poland) [196,197]	32–29 ka [§]	1 *M. primigenius*, 1 lithic flake, small charcoal crumbs separated from bones, claimed cut marks (actually tooth marks)	Bog or marsh

Table 1. *Cont.*

Name, Location	Age (Measured or Estimated)	MNI (Minimum Number of Individuals) of Proboscidean Taxon and Evidence for Human Association	Setting or Enclosing Sediments
Nowa Huta (Poland) [197,198]	27,750 rcy BP (~33 ka [§])	1 *M. primigenius*, Upper Palaeolithic lithics, possible cut/planing marks	Loess
Multiple sites in the Middle Danube and adjoining region: Willendorf, Langmannersdorf, Krems-Hundssteig, Krems-Wachtberg, Grub-Kranawetberg, Ruppersthal (Austria: [199–202]); complex of Dolní Věstonice-Pavlov-Milovice sites around the Pavlov Hills (Czech Republic [203–213]	~33–20 ka [§]	Different MNIs (8–51) at each site with >1000 estimated for one site (Předmosti, Czech Republic), *M. primigenius*, Upper Palaeolithic lithics, most with varying amounts of cut marks or other marks on bones, burning, bone breakage	Loess, also more complex sedimentary sequences (fluvial, colluvial, aeolian)
Kotelny Island (Taba-Yuriakh) Mammoth (Russia) [214]	26,244 ± 224 BP	1 *M. primigenius*, marks on bones thought to be made by tools, worked tusk fragments, lithic projectile tip embedded in a scapula	Thermokarst (alas) depressions in permafrost
Kraków Spadzista B + B1 (Poland) [215–221]	~27.9–27.6 ka [§]	>100 *M. primigenius*, Upper Palaeolithic lithics, 2 mammoth ribs with embedded lithic point tips, few cut marks, broken bones	Soliflucted loess/colluvium collected around bone midden(s) on a hill
Valea Morilor and Climăuţi II (Moldova) [222–225])	~25–20 ka	6 *M. primigenius* at Valea Morilor, 17 at Climăuţi II, other large fauna, many flint implements (Epi-Aurignacian at Climăuţi II), pebble hammerstones, possible windbreak, marked bones, bone points, one ulna with a hole (pierced by a spear point?) at Valea Morilor, ivory implements, mammoth bones burned as fuel, uncertainty if mammoth included in diet	Fluvial sands, slope wash, loessic loam
Krasnoyarskaya Kurya (Russia) [226]	~24 ka [§]	3 *M. primigenius* in middle level, 4 in lower level, older level apparently visited by hominins to remove some bones	Alluvial sediments in middle bone-bearing level, alluvial–lacustrine sediments in older (lower) bone-bearing level
Halich (also Halych or Galich) (Ukraine) [227–229]	24–14 ka [§]	2 *M. primigenius*, Upper Palaeolithic lithics, bone breakage	Loess
Soyons Mammoth, Rhône valley (France) [230]	Gravettian (34–24 ka) or Solutrean (22–17 ka)	1 *M. primigenius*, few lithics, cut marks on 2 ribs	Loess on paleoterrace
Kostenki-Borshevo sites (Russia) [231,232]	~35?–15 ka BP	(Multiple sites with varying MNIs) *M. primigenius*, Upper Palaeolithic lithics, worked bones and ivory, hearths, pits, bone structures, weapon-damaged bones	Complex polygenetic sediments
Khotylevo 2 (also Chotylevo 2) (Russia) [233,234]	27.9–26.6 ka [§]	~50 *M. primigenius*, Upper Palaeolithic lithics, worked bones and ivory, hearths, pits, bone structures	Subaerial sediments
Shestakovo (Russia) [235–237]	29.8–21.8 ka [§]	18 *M. primigenius* (multiple sites near Shestakova village), worked bones, lithics	Subaerial sediments in topographic depression
Mal'ta (Russia) [238,239]	Multi-layered (43–12 ka), 27–24 ka [§] in Gravettian-like layer	? MNI *M. primigenius*, Upper Palaeolithic lithics, worked bone and ivory (including female and zoomorphic figurines), hearths, pits, other features	Alluvial and subaerial sediments
Gari I and II, Evalga, Rychkovo, and others in the Trans-Ural (Sosva River) region (Russia) [240]	27–15 ka [§] for main assemblages	(Multiple sites with 11 MNI at Gari) *M. primigenius*; other fauna (98% mammoth), Upper Palaeolithic lithics, cut marks, flaked bones and tusks	Alluvial and subaerial sediments
Mogochino 1 (Russia) [241,242]	Maybe ~24 ka [§] but probably younger	? MNI *M. primigenius*, other fauna, Upper Palaeolithic lithics	Alluvium
Achinskaya (also Achinsk) (Russia) [237,242]	LGM (Early Sartan)	2 *M. primigenius*, other fauna, Upper Palaeolithic lithics, hearths, coal fragments, worked, broken, and cut bone	Subaerial sediments
Tomsk (Russia) [242–244]	~20–12 ka [§] (charcoal under/around the bones = 18,300 ± 1000 rcy BP or ~23–20 calBP, but its applicability to the bones is unclear)	1 *M. primigenius*, Upper Palaeolithic lithics, broken bones, burned bones and charcoal (hearth?)	Loess-like sediments (loam)
Epigravettian (Upper Pleniglacial or late to post-LGM) sites in East European Plain (Ukraine and Russia) dominated by mammoth bones (*n* = 20 or more): e.g., Mezyn (also Mezin), Mezhyrich, Yudinovo, Eliseevichi (alsoYeliseevichi), Gontsy, Pushkari [245–256]	~20–14/12 ka	(Multiple sites with varying MNIs) *M. primigenius*, abundant Upper Palaeolithic lithics, worked bones and ivory, bone and ivory artwork, hearths, pits, dwelling structures made of bones	River terraces
Svobodné Dvory (Czech Republic) [257,258]	>17 ka (Gravettian lithics)	1 *M. primigenius*, lithic point, blades, flake, assumed kill site	Brickyard clay (Loess)

Table 1. *Cont.*

Name, Location	Age (Measured or Estimated)	MNI (Minimum Number of Individuals) of Proboscidean Taxon and Evidence for Human Association	Setting or Enclosing Sediments
Shikaevka II (Russia) [259–262]	~21.5 ka and 12.9 ka [§](18,050 + 95 rcy BP [237])	2 *M. primigenius*, Upper Palaeolithic blade-like flakes	Marsh (weak streamflow on terrace above floodplain) [259]
Algar de João Ramos (Portugal) [159,263,264]	~17.2 ka [§]	? 1 *M. primigenius*, femur fragment with cut(s) (?)	Cave sediments
Volchia (also Volch'ya and Volchya) Griva (Russia) [265,266]	~20.0–16.0 (to 13?) k rcy BP for human occupation	>70 *M. primigenius*, bison, horse, wolf, Upper Palaeolithic lithics	Loess, alluvium, colluvium, mineral lick
Berelyokh (also Berelëkh) (Russia) [192,267–271]	In dispute: ~16.5–14.7 ka [§], mammoths might have mostly died in the earlier time range	>100 *M. primigenius*, osseous materials possibly scavenged by Upper Palaeolithic people at a nearby site	Alluvial–lacustrine (oxbow lake) accumulation of bones
Sevsk (Russia) [272–274]	~16.9–16.5 ka [§]	33 *M. primigenius*, 16 "worked flint pieces" at base of main bone layer, no cut marked bones, no hearths, no killing implements, no burned bones	Alluvial sediments
Urez-22 (Russia) ("human habitation…next to the accumulation of mammoth bones" [194])	14.9–13.9 ka (or later?)	11 *M. primigenius*, lithic flakes and microblade fragments, ivory fragments	Colluvium, redeposited stream lake/bog sediments, disturbed by modern ivory miners
Lugovskoye (also Lugovskoe) (Russia) [275–279]	~14.0–13.0 k rcy BP, older and younger materials	1 *M. primigenius* with microliths (insets) embedded in a vertebra	Swampy ravine on floodplain
Nikita Lake (Russia) [194]	~13.9–13.6 ka	≥ 10 *M. primigenius*, lithic fragment embedded in a rib	Alluvium (low-energy stream)

? Question marks indicate either an unclear number of proboscideans or a characteristic, such as cut marking, that should be further tested/proven. [§] Unless otherwise noted, age estimates younger than ~50,000 years are calendar years before the present, either taken from publications or roughly calibrated from reported radiocarbon dates [2]: differences between ages estimated using this and the other available calibration programs are not significant for the purposes of this table.

2. Exploring Meaning in the Proboscidean Bone Sites

The listed finds are only a small fraction of all proboscidean discoveries made worldwide. Cuvier [280] (p. 4) admitted that "wanting to report…all the places where there were fossil bones of elephant would be an infinite enterprise" (translated from the original French). The total number of recorded discoveries going back to the days of ancient Greece and earlier must be huge, but perhaps even more notable is the possibility that "more than 99 percent" of global proboscidean kill/scavenge sites may still be undiscovered [281] (p. 296).

2.1. Summaries and Perspectives

This section includes short summaries about important sites that have been interpreted as places where proboscideans were killed/scavenged/butchered or as camps where proboscidean bones (often presumed to be from kills) were transported. Not all of the sites can be described or evaluated because of limits on this paper's length. The references cited are selected and are not meant to be complete. The list starts with African sites, including many that were originally classed as butchery locales [282–284], some of which also may have been "central places" where smaller carcasses were transported by hominins who were camped at proboscidean carcass sites. It is not debatable that Lower and early Middle Pleistocene hominins "exploited pachyderms" in Africa, the Near East, and Europe, according to Delagnes et al. [14] (p. 463).

2.1.1. Sites in Africa

This discussion begins with the oldest sites that have claims for butchery, although several examples may no longer meet all generally acceptable standards for such claims.

The Olduvai FLK (Frieda Leakey Korongo) North Upper Bed I Level 6 (FLK N 6) (Tanzania) *Palaeoloxodon* (formerly *Elephas*) *recki* [3] is a mostly complete skeleton of one elephant plus a few bones of another individual in a silty clay, found in a cluster about 37 m^2 in area that also included 123 lithics and ~400 bones and teeth of around three dozen

other animals. The age is >1.7 Ma. Most of the elephant's left side bones were beneath the right-side bones, possibly because the animal had died on its left side. Leakey [3] (p. 64) thought this was a "butchering site where an elephant was cut up by early man, who may have come upon it accidentally, or deliberately driven it into a swamp to be slaughtered." The displacement of the bones was considered "similar to that which takes place when scavengers tug at a carcass" [3] (p. 64). Most limb epiphyses were unfused, except for those of the humeri and the distal tibiae, indicating a possible ontogenetic age at death of >20 years. Bunn [285] thought there were possible cut marks on some bones, but Domínguez-Rodrigo et al. [4] re-interpreted the marks as probable results of trampling.

Bones from smaller taxa are often interpreted as natural or "background" accumulations at elephant butchery sites [3,284–286], although not always. Binford [72] thought that the lithics at the *Elephas* area at FLK N 6 were associated with the smaller animal bones and not with the elephant bones. Some of the smaller animal bones with possible cut marks might have been transported by hominins to a central place associated with the elephant carcass or its bones. A re-examination of materials in other excavated levels at FLK N [4] concluded that hominins did not contribute any faunal elements and that the bones of different types of animals had accumulated due to different processes. In other words, the lithics are not behaviorally associated with the animal bones, which were deposited at different times and mostly before the lithics were discarded. Hyenas and felids might have transported some bones to the site. Domínguez-Rodrigo et al. [4] interpreted the assemblage as a time-averaged palimpsest created in a savanna at a streamside location.

The Olduvai HWK EE (Henrietta Wilfreda Korongo East East) Bed II assemblage (Tanzania) contains bones of *Palaeoloxodon* (formerly *Elephas*) *recki* and *Deinotherium* sp., plus a large Oldowan lithic assemblage of mostly cores and flakes and a taxonomically rich faunal assemblage of bones "covered in the feeding traces of both hominins and carnivores" [5] (p. 137). Pante and de la Torre [5] speculated that hominins (*Homo habilis*) shared access to carcass flesh with carnivores but were able to access most or all of the bone marrow from those carcasses. A proboscidean astragalus (indeterminate taxon) had been cut marked on the dorsal surface, possibly when hominins separated a rear elephant foot to retrieve the fat pad.

The Olduvai FLK North Lower Bed II (Tanzania) *Deinotherium* sp. is a partial skeleton [3] (pp. 85–86) associated with seven lithic artifacts, nine utilized stone materials, seven pieces of debitage, and sixteen manuports in a clay sedimentary matrix. The age is 1.7–1.5 Ma. The tusks were well preserved but the rest of the bones were friable. The limb bones were partly articulated but one scapula was 8 ft (~2.4 m) away from the humerus. Foot bones were found "considerably below the rest of the skeleton" [3] (p. 85), leading to the suggestion that the animal had been immovably stuck in wet deposits. Bed II also yielded an assortment of other elephant bones with modifications, which have been interpreted as battering, flaking, and abrasion from use [3] (pp. 239–244). Near the *Deinotherium* skeleton, a crushed hyena skull was found along with part of a suid jaw, a *Damaliscus* sp. skull and horn cores, and "sundry" bovid remains [3] (p. 254). Leakey [3] (p. 262) suggested that the *Deinotherium* had been driven into a swamp by hominins, although she also conceded that it could have been accidentally stuck. The *Deinotherium* might have been butchered with the lithics of inferred Oldowan type, but Domínguez-Rodrigo et al. [4] thought evidence for hominin butchering was lacking.

The Barogali (Gobaad Basin, Djibouti) *Palaeoloxodon* (formerly *Elephas*) *recki* [7–10] is dated 1.6–1.3 Ma. It was apparently lying on its left side when it died in a paleomarsh and was then butchered by hominins. Additionally, 569 stone tools were found (mostly debitage that was knapped on-site, probably Oldowan) that were made from poor quality local lava. Few artifacts were retouched; many were broken. The tusks were in place but the top of the cranium was separated from the rest of the skull, which has been interpreted as the result of hominins trying to access the brain. The breakage of the mandible has been interpreted as performed by hominins to extract the tongue [9], which is a post hoc accommodative argument that overlooks the fact that breaking the dense bone of a proboscidean mandible

would be unnecessary for accessing the tongue when the skin under the chin could be cut open. Another possible reason for breaking the mandible could be to gain access to the edible marrow fat inside.

Upper Bed II in the two gullies of the BK (Bell's Korongo) site in Olduvai Gorge (Tanzania) contained >1700 "Developed Oldowan B" lithic tools, >600 utilized stone materials, and >11,000 pieces of lithic debitage [3] (pp. 199–221). Multiple examples of cut marked and green broken bones of small, medium, and large mammals were also found, including one elephant [287]. The faunal assemblage has been interpreted as resulting from multiple butchery events by hominins predominantly using quartzite tools ~1.35 Ma in a riverine setting [288]. Domínguez-Rodrigo et al. [287] and Yravedra et al. [157] considered this site to be the oldest reliably documented case of elephant butchery, as evidenced by long bone breakage, which implies that the claims about hominin butchering of the older FLK and Barogali elephants are not supported by the taphonomic evidence.

The Olorgesailie Basin Member 1 Site 15 (Kenya) *Palaeoloxodon* (formerly *Elephas*) *recki* [11,12] is dated 992–974 ka. The site has been interpreted as the place where "an elephant died and butchery took place" [13] (p. 763). Cut marks were identified on one rib. Over 2000 ESA stone artifacts from 17 different toolstone sources were found, mostly consisting of sharp-edged lava flakes along with cores and two bifaces, "within and around the confines of the carcass in the central excavation area of 23 m^2" [13] (p. 768) in a sediment thickness of about 40 cm. The elephant's bones were separated from "five or six small remains" of other animals [12] (p. 480) and the "virtually exclusive association between the elephant skeleton and stone artifacts is an exceptional find that may prove to be an important example of hominin utilization of a large mammal carcass." The animal "died and was butchered in an abandoned channel swale" [13] (p. 769), which is thought to be a spot to which hominins had no other reason to be attracted.

Nadung'a 4, Lake Turkana (Kenya) [14], contains bones of a single (?) *Palaeoloxodon* (formerly *Elephas*) *recki*, dated ~700 ka. The elephant bones occur vertically dispersed through 150 cm of a vertisol that has been subject to wet–dry cycles of cracking and swelling, along with "rare, isolated [bone] fragments attributed to bovids and fish" which have been interpreted as background fauna [14] (p. 460) and over 6700 associated stone artifacts. The elephant bones are weathered and the surfaces are too poorly preserved to show cut marking. The lithic artifacts are mainly debitage and do not fit into a classical Acheulean category. Flintknapping was carried out on this spot, but many of the tools were apparently not used for butchering the animal. Some tools might have been used to manufacture meat-carrying vessels made from wood or plant fibers.

The site of the Mwanganda's Village (Malawi) elephant (indeterminate taxon) was originally described in Clark and Haynes [15] (also see [16,17]) as containing a mix of animal bones, including parts of elephant, and about 300 lithics classified as possibly Sangoan. Its age was first estimated as Middle to early Upper Pleistocene (~400 ka?), but the elephant bones and the lithic materials (mostly late Middle Stone Age) have more recently been interpreted as having disparate ages. Three concentrations of bones were described by Clark and Haynes [15], mostly from a single elephant but also including hippopotamus tooth, bone, and tusk fragments as well as a giraffe tooth, along with 314 mostly light duty or small artifacts (i.e., smaller than handaxes and choppers) "scattered around and under the bones" [15] (p. 393, and plate 3). Nearby were other bones, parts of a turtle carapace, an *Equus* tooth, and another "light scatter of artifacts" [15] (p. 393). The bones were said to "provide clear evidence of intentional bone breaking by man" and were to leave no doubt "that this is a site where an elephant was butchered" using tools made on the spot [15] (p. 394). Kaufulu [16] (pp. 24–25) later interpreted the site as having been created on a paleoriver bank, about 1 m from the water course. In his view, the bones and artifacts lay on the ground surface for "long periods" before final burial. Although the stream itself did not deposit the bones and the artifacts, its relatively weak overbank flow did re-distribute the materials. Clark and Haynes [15] had interpreted the three clusters of artifacts and bones as signs that three individuals or groups of hunters butchered the

elephant, but Kaufulu's work [16] suggested that moving water partly moved the materials into clusters. Wright et al. [17] re-investigated what remained of the site and observed that lithics from the site's main find level were very abraded, probably part of a channel lag deposit, and proposed that the site was not a single elephant butchery locale, but instead was a place where recurring human occupations took place late in the Pleistocene, 42–21 ka. The oldest faunal material, including the elephant bones, were buried in a channel lag deposit, as were the oldest lithics.

The Namib IV (Namibia) *Palaeoloxodon* (formerly *Elephas*) *recki* [18,19] is a partial skeleton dated ~350 ka that was found eroded out of a calcrete deposit. A random surface collection of 394 stone artifacts included mostly small flake tools and a high proportion of cleavers and handaxes, which were made from many different raw materials. The scattered bones of the elephant, an alcelaphine antelope, and another medium size antelope were interpreted as the remains of a butchery site that was revisited several times by hominins.

The Zoo Park elephants (either *Loxodonta* or *Elephas*) (Namibia) [15,20] were radiocarbon-dated as 5200 ± 140 BP, a date doubted by Clark and Haynes [15] (p. 407), who thought that the site's diatoms instead indicated a late Pleistocene or early Holocene age. The scattered bones of two disarticulated elephants were found atop sand deposited by a fossil stream in a spring-fed marsh, along with an unspecified number of mostly unretouched flakes and some choppers and hammerstones. The site was interpreted by MacCalman [20] as a kill site where humans either drove elephants into the marsh or found them mired and then "presumably pelted [them] to death with stones or attacked [them] with wooden spears" before taking away the missing parts of the skeleton [20] (p. 103). The "pelting" to death may be less than likely, since stones massive enough to injure a proboscidean would probably have been too heavy for humans to lift and throw. Another suggested possibility is that the bones were dispersed partly by trampling animals or stream action.

In addition to the sites summarized above, many others yielded proboscidean bones that have been interpreted as cut marked and/or spatially associated with stone tools or the cut bones of other species. Starting with oldest through progressively younger sites, examples that are not in Table 1 include: Bouri, Hata Member (Ethiopia); Lower Omo, Shungura Formation (Ethiopia); Kanjera South, Homa Peninsula (Kenya); Melka-Kontouré, Awash (Ethiopia); Gadeb (several sites) (Ethiopia); Konso-Gardula, Ethiopian Rift (Ethiopia); Buia, Danakil Formation (Eritrea); Tighénif (Ternifine) (Algeria); Olduvai Lower Bed IV HEB (containing a possible elephant bone biface) (Tanzania); and Sidi Zin, Le Kef (Tunisia). The last named site is Upper Acheulean. Of the dozens of younger MSA and LSA sites in Africa, proboscidean bones that have been interpreted as derived from killed or scavenged proboscideans are claimed only for Mwanganda's Village, Namib IV, and Zoo Park, as described above. An interesting question is why the very earliest sites (Early Stone Age) contain most of the possibly butchered elephant remains in Africa. Klein [289] pointed out that Acheulean people in southern Africa co-existed with the extinct elephants, hippos, and other animals during much wetter conditions than recorded in the Holocene and if so, preservational factors could account for the disproportionate number of elephant sites created, rather than pre-modern hominins having a special talent for elephant-hunting. Acheulean-associated faunas in southern Africa mainly come from open-air sites where different causes of death and post-mortem processes affecting the carcasses have been scrambled together, thereby obscuring hominin hunting tactics. Klein [289] suggested that Acheulean hominins rarely or never killed elephants. More recently, Byers and Ugan [290] and Lupo and Schmitt [291] applied foraging theory to data about the costs and benefits of hunting animals as large as proboscideans and proposed that elephants are too expensive to efficiently pursue or attempt to kill now, and so by implication would also have been too expensive in prehistory. Regardless of the reluctance by some archeologists to view proboscidean hunting as productive in the Palaeolithic, it can hardly be doubted that these giant animals were actively hunted from the earliest times.

2.1.2. Sites in Europe, the near East, and Asia

A contested European claim in Table 1 is Perdikas (Greece). It was originally claimed that *Mammuthus meridionalis* bones were found there with osseous and lithic tools [31] (p. 288) and dated > 3.3 MA. The proboscidean has since been identified as *Palaeoloxodon antiquus* and the age is now known to be <800 ka. The material has not been systematically studied and functional associations should be verified.

Fuente Nueva-3 layer c.III.1 (Spain) yielded a scapula, mandible, and anatomically ordered vertebral column, pelvis, and ribs of a female *M. meridionalis* dating to 1.3 Ma, which were closely associated with about 36 hyena coprolites and 17 lithic flakes. The mammoth was probably about 60 years old [21]. The remains of many other mammals were also found; some were spirally fractured and some had cut marks, hammerstone marks, and carnivore tooth marks [292]. The mammoth bones did not have any identified cut marks or tooth marks, but the surfaces were not well preserved. Espigares et al. [21] hypothesized that hominins butchered the freshly dead carcass, transported limb elements somewhere else, and then hyenas (*Pachycrocuta brevirostris*) scavenged the remaining soft tissue of the carcass.

Level 2 of Pit 1 at the Barranc de la Boella site (Spain) [29,30] contained 485 bone fragments of a midlife adult *M. meridionalis* in one level, along with the bones of cervid, equid, and other unidentified taxa. Two fragments of mammoth rib diaphysis may be cut marked. Associated with the faunal assemblage were 125 lithics that were considered to be Acheulean, including retouched and refittable flakes, flakes with use-wear, and a pick, dating between 0.78 and 0.99 Ma. The material was interpreted as a single use butchering site [30] (p. 11), following on from Isaac's [282] classification scheme, located in a resource-rich locale where competition for prey and carcass utilization was sometimes high between carnivores and hominins.

The Gesher Benot Ya'aqov (Israel) site contained *Palaeoloxodon antiquus* remains, including a part of a skull, teeth and tusk fragments, and a limb bone fragment among other bits, as well as an Acheulean lithic handaxe and bifaces [33,34], all of which had been deposited in anaerobic lacustrine sediments on the beach of a paleolake [293] dated ~780 ka. Cut marks and marks made by percussion were reported on a number of the large bones. The site is located in the northern sector of the African Rift Valley in a corridor connecting Africa to Eurasia, and the stone tool technology is very similar to what has been found in Africa. Repeated hominin occupations at seven loci within the site occurred over a time span of 100,000–150,000 years. Thousands of lithic artifacts were found, including Acheulean handaxes, cleavers, and biface production flakes made from three different raw materials. Micromammal remains, thousands of pieces of wood and seeds, including some that were burned, nuts and nut cracking stones, fruits, bark, and pollen were also recovered from numerous layers and all were well preserved in waterlogged sediments. An elephant skull was found upside down (ventral aspect upward) and lay atop a stone core, a boulder, and one end of an oak log, which has been interpreted as a lever possibly used to invert the skull. The finds were interpreted as the remains of a female or young male adult elephant driven to the lakeshore to be killed and butchered by a relatively small group of hominins. The cranium was broken, which has been interpreted as the result of an effort to extract the brain. Skull breakage occurs at modern non-anthropic elephant bone sites [294], especially around resource-rich sites, such as water sources and along well-used game trails where elephants and other large ungulates walk through the bones. The recently observed non-anthropogenic breakage affects dry bones after the soft tissue has naturally decayed or been eaten by scavengers and, therefore, the fracture characteristics could be identifiably distinct from hominin attempts to extract proboscidean brain.

Revadim Quarry is another Acheulean site in Israel with over 27,000 lithics and thousands of animal bones, including 155 bones of 3–6 *P. antiquus* [34]. An elephant rib that has been interpreted as cut marked and carnivore scratched was found alongside lithic tools, including a handaxe [295]. A scapula with flint artifacts around it was also reported as cut marked. The cuts were interpreted as resulting from meat removal. The lithics are

late Acheulean and the dating of the finds is between 300 ka and 780 ka. Several different parts of the site contain elephant bones. Some specimens of elephant bone fragments were interpreted as hominin-shaped tools and flakes. Use-wear was found on a lithic biface and scraper and both tools also had animal fat residues, supporting the possibility that the Acheulean tools had been used to process an elephant carcass.

The Notarchirico (Italy) *P. antiquus* [36–39] was uncovered on one of the site's 11 paleosurfaces dated 640–740 ka. An elephant skull with tusks in place, a displaced mandible, and 42 lithics, including bifaces, choppers, and scrapers, were found within an area of 6 × 4 m. The materials had been buried by stream and lake deposits. According to Piperno and Tagliacozzo [39], the elephant's head and trunk might have been meat-stripped and the bones broken to recover the brain and tongue. No cut marks were identified on the bone surfaces.

The following sites in Europe are dated after 500 ka or MIS 11–12 and later and, therefore, some might have been created by Neanderthals. Yravedra et al. [157] list 60 Middle and Lower Palaeolithic sites in central Spain with proboscideans (*Palaeoloxodon*, *Mammuthus*, and indeterminate taxon). Some are not discussed here because of the ambiguous associations of lithics and bones or the possible mixing of materials from more than one event.

The Tafesa site in central Spain [157,296], dated to MIS 11–12, contained the bones of two adult *P. antiquus* and over 600 Acheulean lithic pieces in four levels. Cut marks were noted on long bone shafts and axial fragments, along with trampling marks on some elements. Many proboscidean bone surfaces had been abraded and polished, which could have obscured or removed marks made by hominin cutting [157].

At Áridos 1 (Spain) a subadult female *P. antiquus* [43] was found disarticulated and lacking limb bones in floodplain deposits. The estimated age is ~500–300 ka (MIS 11–9). Closely associated, but somewhat scattered, were 331 stone artifacts, partly "intermingled" [43] (p. 66) with the skull fragments and other elements. Some lithics were flaked on-site and separate pieces were conjoinable. No cut marks were reported, but the site was interpreted as an elephant butchering site even though the elephant's cause of death was left open. The bones of other animals lying just above the elephant bones were interpreted as possibly resulting from either human and carnivore predation or from carcasses that had floated and clustered around the elephant bone obstacles.

Áridos 2 is located about 200 m from Áridos 1 and has a similar age. It contained the anatomically connected remains of an old male *P. antiquus* deposited in floodplain and low-energy channel sediments. Associated with it were 34 stone artifacts, none of which could be conjoined. Yravedra et al. [44] identified clusters of cut marks on bones, some of which might have been made by handaxes. Yravedra et al. [44] supported Villa's [297] conclusion that Áridos 2 and Áridos 1 were death sites where hominin butchering was performed before other carnivores reached the carcasses.

The Marathousa 1 *P. antiquus* site [45–50] may be the oldest stratified site in Greece [298]. Hominin activity at the site is dated to MIS 12, from ~0.5 to 0.4 Ma. The site is located in an opencast lignite mine in the once shallow water nearshore part of a Middle Pleistocene lake, where the finds had been reworked post-deposition [50]. Both areas A and B contained elephant bones. Area A yielded the associated, but disarticulated bones, of a single old male elephant and the bones of hippopotamus, beaver, deer, and mustelid, along with small lithic flakes, cores, retouched tools, and chunks, which are the kinds of Lower Palaeolithic lithics that were apparently typical of non-handaxe assemblages associated with elephant bones. Possible cut marks and percussion damage are visible on two elephant bones from Area A (an astragalus and a tibia) and one from Area B (a rib fragment) and on the bones of other large mammals. Some bones had also been gnawed by carnivores [47]. The cuts on the Area A astragalus were interpreted as made when hominins disarticulated the tarsals to gain access to the rear foot fat pad. The mark on the Area A tibia is thought to have been inflicted during the stripping of meat. The marks on the Area B rib are thought to be evidence of early hominin access to a fresh carcass [48] (p. 78).

The archeological layer at the Fontana Ranuccio site in central Italy, dated 458 ka but possibly younger [52,53], yielded fragmentary bones of *P. antiquus*, other possibly background fauna, and a modest lithic assemblage, including small flakes and five handaxes. Many smoothed and scratched bone fragments were interpreted as utilized, including bifaces made from flaked elephant bone. The materials were enclosed in a paleosol with lacustrine, fluvial, and volcanic origins. One or two hominin teeth were also found. No cut marks were identified on the elephant bones.

The site of La Ficoncella (Italy) [54] contained fragments of the tusks, cranium, vertebrae, scapula, and pelvis of a single *P. antiquus* and >400 lithic pieces, including very small flakes. The bones were in floodplain deposits, probably dating back to before 441 ka. Two concentrations of lithics occurred around the elephant skull and the vertebrae. A few fragmentary remains of a very large bovid (*Bos primigenius*) and a caballine horse (*Equus* sp.) were also found buried in the fluvial sediments. Carnivore tooth marks were identified on the vertebrae and the pelvic girdle. No cut marks could be identified [55], but the closeness of the lithics to the elephant bones was interpreted as implying the human utilization of the carcass, perhaps alternated with carnivore scavenging.

The Ebbsfleet (also known as Southfleet Road) (U.K.) *P. antiquus* [56,57] is dated to ~420 ka. Along with the incomplete skeleton of an adult male elephant and ~100 flint artifacts in lacustrine sediments, the jaw and skull of an extinct rhino (*Stephanorhinus hemitoechus*) and the bones of numerous other mammalian species, such as red deer and a large bovid, were also found along with small mammals, fish, mollusks, and amphibians. No surface marks could be identified on the elephant bones because they were in poor shape from crushing and excavation damage, but cut marks were found on contemporaneous red deer bones. The elephant bones were in a 4 × 6 m cluster with ~80 sharp flint artifacts, presumed to be of Clactonian industry but without handaxe technology. Two flint pieces could be fitted together. Several of the lithic pieces weighed about 1 lb (0.4536 kg) each. Almost 2000 more flint artifacts were ~30 m away. A younger deposit over the Clactonian level was rich in handaxes and other tools. According to Wenban-Smith et al. [57] (p. 480), "the site appears to reflect on-the-spot production of large sharp-edged flakes and simple flake-tools for butchery of meat or other soft tissue from the elephant carcass." Another conclusion was that the "exploitation of elephant carcasses was an element of human adaptations at this time" [57] (p. 481). The animal was probably not mired when it died. Hominins might or might not have killed it with wooden spears.

At Bilzingsleben (Germany), the bones, teeth, and tusks of multiple *P. antiquus* were found on a paleolake shore, deposited near a paleospring. The site, dating to either the MIS 11 or MIS 9 interglacial [62] (which could range from ~424 ka–374 ka or ~337 ka–300 ka), contained several tons of fossil bones from dozens of animal species, plant impressions in travertine from many species, the fragmentary remains of three hominins (*Homo erectus*), and thousands of lithic specimens, including chopping tools (but no handaxes), wooden artifacts, and a number of tools made from bone, antler, and ivory [58–61,66–69]. The minimum number of individual elephants was initially estimated as 60–70 [63], but Brasser [68] later tallied 23, which is < 10% of the total MNI of all large mammals. Most of the proboscidean remains were teeth. The remains of *Stephanorhinus* sp. and *Ursus* sp. contributed almost 80% of the total large mammal MNI [68]. A low proportion of bones had traces that were possibly made by human actions. Several elephant long bone fragments had multiple flake scars and notches that have been interpreted as the result of human actions [68]. There was also a cut marked tusk [68] along with probable sedimentary scratches on many specimens and a tibia fragment with sets of parallel etched lines, which were interpreted as either simple artwork or a counting aid [59]. Once thought to be a locality where mid-Pleistocene hominins hunted and camped, the site assemblage has more recently been re-interpreted as mostly accumulated through many different natural processes, such as stream action and debris flow [299] (p. 65), [66] (p. 44), [67]. Brasser [68] has demonstrated that the fluvial sorting and redistribution of the bone assemblage was only minor and localized, while carnivore activity was apparently a large factor in modifying and moving the large

mammal bones. The original claims are not universally accepted that the thousands of lithics were human-made and that the several hundred elephant bone fragments were tools or had been flaked or marked by hominins [66] (pp. 40–41 and references therein).

Kärlich-Seeufer (Germany) contains an interglacial lakeside assemblage of Acheulean lithics, thousands of pieces of wood, other plant remains, and a fauna dominated by *P. antiquus*, mostly in the form of teeth and cranial fragments (MNI = 8) [70]. Other mammalian remains included lion, equid, suid, red deer, cf. reindeer, and *Bos/Bison*. The materials were probably time-averaged via debris flows. The age of the assemblage is either MIS 11 or 9. No cut marks or any other evidence has been found that hominins killed or butchered the elephants, although an early interpretation was that the site was an elephant hunting camp [70] (p. 332).

At Ambrona (Spain), multiple individuals of *P. antiquus* were recovered ([76,81] and see also [71–75,79,300]). The deposits date to either OIS 9 or the end of OIS 11 [80]. Some elephant and deer bones were in partial articulation or closely clustered within a fluvial mud deposit, but bones in other sediments were isolated and dispersed. Elephant bones and ivory objects from the site and a sister site at Torralba (described below) were interpreted as shaped by humans who deliberately broke and flaked them ([71,301]). Biberson and Aguirre [302] suggested that the broken elephant bones were used in the place of stone tools because lithic raw material was not locally available. Villa and d'Errico [303] demonstrated that the tusk fragments were probably broken by elephants during intraspecific shoving and fighting.

A few traces of hominin butchering have been documented on the elephant bones, such as cut marks and green bone breaks that have been interpreted as caused by hominins [79]. Re-excavations uncovered the clustered bones of one older male elephant that had not been exposed long enough to weather measurably before burial but that had been on the surface long enough for some elements to be trampled and displaced by gravity or disturbance by other elephants. A lithic biface and 13 other artifacts were associated with it. Other elephant bones had accumulated in the same sediments over time. Acheulean stone artifacts were spatially associated with the elephant bones and some were abraded. The bones and lithic artifacts at Ambrona were episodically mixed within the deposits from butchering events and non-anthropogenic deaths that were untouched by hominins [79], so the evidence is ambiguous about hominin killing versus possible scavenging [79].

The Torralba site (Spain), located near Ambrona, contained animal bones dominated by *P. antiquus* [76]. The site is younger than Ambrona, probably dating to 300–200 ka [76,80]. As with Ambrona, the site had a low spatial density of several hundred artifacts of probable Middle Acheulean affiliation [43]. Pineda and Saladié [135] briefly reviewed the history of the site's interpretations, discussing how scientific thoughts have changed through recent times. Howell [74] and Freeman [130,131] interpreted Torralba as a frequently revisited locality where the hominin killing and butchering of elephants and other animals occurred as single events. Freeman [132] (p. 57) used multivariate analyses to define the "covariations of artifacts", which indicated to him that elephant skull fragments, scapulae, pelvis, and vertebrae were statistically grouped with lithic perforators and scraper-edged implements. He thought that the groupings suggested hominins did complete the butchering of the elephants. Later studies (e.g., [75,133]) concluded that the site is a palimpsest of mixed materials rather than a series of discrete occupations and has little evidence for the human killing of elephants. Shipman and Rose [304] found that marks fitting their definition of cuts were rare on the bones from Torralba and Ambrona, while the effects of sedimentary abrasion were abundant. Haynes [305,306] suggested that the elephant bones had accumulated from natural deaths. Villa [297] (p. 307) stated that the "Torralba evidence has been overinterpreted" and ruled out Torralba as an elephant hunting site. Freeman [73] disagreed with the conclusions of Shipman and Rose [304] and Klein [75], proposing that those researchers did not see all of the original bone surfaces, with some being in plaster jackets or obscured under thick varnish, or they failed to recognize the marks that Freeman considered to be made by hominin tools. Freeman [73] illustrated what

he termed scraping marks on an elephant innominate, hacking/chopping marks on an elephant skull and mandible, and slicing and battering marks on other (non-proboscidean) bones. Domínguez-Rodrigo [307] and Yravedra et al. [113] could not identify any cut marks or other evidence of hominin modifications on the elephant bones. Pineda and Saladié [135] examined bones from excavations that were made the early 1900s and 1961–1963 and found "an elephant remain with cut marks", but this represented only 0.1% of all elephant bones seen and has been interpreted to mean that hominins had no leading role in the bone accumulation; although at least one elephant had apparently been butchered, perhaps after it was killed. As with Ambrona, Torralba's evidence remains ambiguous.

At the Bełchatów opencast coal mine in Poland, bones were found from an adult steppe mammoth (*M. trogontherii*) [90,91] along with other fauna dating tentatively from either the MIS 11 or MIS 9 interglacial. Bones of *M. primigenius* were also found in the locality [308]. A secondarily deposited rib of the steppe mammoth was "slightly shiny" and marked by "elongated scratches and small rounded indentations" and "slicing fileting marks" [91] (p. 454). Twenty marks were interpreted as cuts made by stone tools during meat removal, possibly by *Homo heidelbergensis*, and fifteen other marks were considered to be only scratches [91]. No lithic items were found in association with the bones.

La Polledrara di Cecanibbio (Italy) [94,99,309], dated to ~360–300 ka, yielded over 20,000 bones and fragments from large and small animal taxa (including a juvenile *Homo heidelbergensis*), which were mainly from straight-tusked elephant (*P. antiquus*) and aurochs (*Bos primigenius*). Bone tools, including possible bifaces, associated with lithics in numbers variously reported as from 61 to 500 were also found. The lithics included denticulate tools, notches, scrapers, and multi-use tools, made from mostly small and non-local pebbles as well as manuports. The materials were within sandy fluvial and fluvio-palustrine deposits. The behavioral contemporaneity of the bones and tools is not solidly established [97] because the materials had been transported by a low-energy streamflow, leaving some bones smoothed from sediment abrasion. Some bones had probably piled up behind the large elephant bones during the streamflow. About 1% of the identified elephant bone specimens had surface marks that were interpreted as created by percussion. A few of the elephant bones were interpreted as having features that indicated green bone fracturing [97,99]. The remains of one *Palaeoloxodon* have been interpreted as being from an animal aged ~40 years old that had been mired in mud and then scavenged by hominins who made their butchering tools at the site [99]. About 600 spatially associated lithic items were made from small pebbles with some pieces being refittable to cores. An analysis of 24 flakes and fragments showed wear that suggested use in scraping and cutting soft material, such as meat and fat. Some marks could have been butchering cuts but were not firmly identified. The distal ends of both femora had helical fracture morphology. The right femur also had a flake that was still attached, which was possibly made by hard hammer percussion. Near the elephant skeleton were the fragments of other elephant long bones with green bone fractures, some of which were serially created, which were interpreted as being carried out to shape fragments or make usable flakes and not just to break the element for marrow extraction.

Castel di Guido (Italy), thought to date from ~327–260 ka or earlier [102–109,111], yielded the bones of 11 *P. antiquus* and dozens of individuals of other mammalian taxa of different body sizes. Not all of the bones were well preserved and many surfaces showed signs of abrasion and polishing. Two ribs had possible cut marks, as did a long bone diaphysis fragment, and a few carnivore marks were identified. Green bone fractures were abundant. The materials were recovered in the lacustrine and fluvial sediments of former marshy ground along with ~1100 lithics, including handaxes. Radmilli and Boschian [107] (pp. 146–163) classified hundreds of bone fragments and flakes as tools, including nearly 100 bifaces that were made from elephant bone [107] (p. 151); for a more recent re-analysis see Villa et al. [110]. Multiple agencies created or affected the Castel di Guido faunal deposit, including hominins, carnivores, and stream re-transportation. One interpretation [109] is that hominins scavenged naturally deceased proboscideans or carnivore kills, with one aim

being to procure bone material for making tools, such as bifaces, some of which had been reused/recycled from earlier occupations.

At Stanton-Harcourt (U.K.) [115–117], bones were found from multiple *Mammuthus* cf. *M. trogontherii* individuals, along with smaller numbers of bones from equids, cervids, bison, and *P. antiquus*. The fossil material of interest dates from ~245–90 ka (OIS 7), during an interglacial interval. Mammoth bones and tusks, pieces of wood, mollusk shells, 5 handaxes, and at least 27 other stone artifacts occurred together in point bar and lag deposits along a paleoriver channel. Some lithics were damaged from waterborne transport. Parts of the mammoth skeletons were articulated or semi-articulated. The animals might have died from natural causes, such as starvation or exposure following miring in soft or waterlogged deposits, or they were perhaps killed by hominins. The possible spatial and behavioral association of the mammoth bones and the artifacts, including handaxes, is still under study [116] (p. 146).

At La Cotte de St. Brelade (Jersey, Channel Islands), Layers 3 and 6 contained bones of young and prime age *Mammuthus* cf. *M. primigenius* and other large mammals in loess [118–126], which is dated to ~240–38 ka, along with flint tools [310]. The bones were excavated from a collapsed cave-like setting in coastal headland ravines. Interpretations in earlier publications differ from those that emerged later. In Layer 3, which is the older of the two layers described here, the bones of seven mammoths and two woolly rhinos (*Coelodonta antiquitatis*) were found, while in Layer 6.1 (whose deposition was separated by a long span of time from Layer 3), bones were found from eleven mammoths and two woolly rhinos. Cranial fragments dominated the specimen counts in both layers. The number of flint tools in Layer 3 was reported as 129 ([119], (Table 26.17), which does not include debitage and cores. B. Scott et al. [120] (p. 25) reported an inclusive total of 786 artefacts from Layer 3 and that Layer 6 had "few artefacts…firmly assigned" to it. Originally the only unambiguous cut marks were identified on mammoth tusks from Layer 3 [311], which were possibly associated with attempted skinning or the removal of the tusks from their sockets. G. Smith [126] later identified cut marks and other modifications made by Neanderthals (presumably chop marks and signs of fracturing). Layer 3 contained numerous mammoth skulls, many ribs, and few limb bones, but Layer 6 had few skulls, few ribs, and many limb elements. Both layers were initially interpreted as the remains of kills made by hominins using a natural "trap" at the bottom of a steep cliff where butchering could then be carried out by the by the hominins, but little explanation could originally be provided for why the bone representation in Layers 3 and 6 were so different. K. Scott [123] suggested that the distinctions were caused by a spatial sampling bias and by carnivore destruction or post-depositional processes. The bones had been exposed long enough for some to disarticulate and become dispersed, but not long enough for all of the bones to weather or for all of the ligament attachments to disappear. Both Layer 3 and Layer 6 were thought to be the results of short-term single events [122,123]. Later research [118,312] has led to re-interpretations that cast doubt on the hypothesis that mammoths were driven over a cliff by Neandertal hunters [120,126,313]. Many more effects of hominin and carnivore actions have been identified on the bones of mammoths and other large mammals [126] (p. 188, Table 6). The later interpretations consider the bone heaps to be more likely the partial components of long-term debris from hominin occupations.

A sand and gravel quarry site near Bucine (Italy) contained several scattered bones of an 18–19 years old female *P. antiquus*. Above the level of the bones, numerous rodent remains were also found that were used to assign a date for the elephant bones to a cool stadial phase: before MIS 6, possibly ~200 ka. Three lithic artifacts were associated with the bones, two of which had birch bark "tar" on one end, suggesting that they had been attached to hafts [136]. There were no cut marks or evidence of bone breakage by Neanderthal hominins.

A small, steep valley at a limestone quarry in Bollschweil (Germany) contained abundant faunal remains and a few lithics, including the bones of six *M. primigenius* and a Middle Palaeolithic handaxe with estimated age of MIS 6 (penultimate glaciation) [142].

This was announced as "the only open-air archaeological site in southwestern Germany characterized by an abundance of mammoth remains" [142] (p. 199). It is unknown whether any of the fauna (mammoth, woolly rhino, large bovid, equid, red deer, bear) had been killed or butchered by Neanderthals. The mammoth bones were too poorly preserved to allow for the identification of marks made by humans or carnivores.

Sediments in a thermal spring-fed lake at Poggetti Vecchi (Italy) contained the mostly broken bones of seven *P. antiquus*, three aurochs, several deer (three species), a bear, and a few smaller animals, dated to sometime before ~171 ka [143]. The elephant bones were scattered and had been trampled when dry, but were thought to have not moved from their original depositional place, while the bones of aurochs and some deer might have been moved by streamflow. The site also contained possibly knapped large-mammal bones, lithic cores, flakes, retouched tools, choppers, and 34 boxwood sticks shaped as though for digging. Four of the seven *Palaeoloxodon* individuals (57%) are classified as subadult or juvenile, which is suggestive of a mortality profile resulting from intensive environmental stress, such as a short-term drought. "Early" Neanderthals who occupied the site might not have killed the elephants, but the use-wear traces on some of the lithics were interpreted to mean meat cutting was performed using tools that had been retouched at the site, suggesting that elephant carcasses were processed when the carcasses were found dead after a natural die-off.

Neumark Nord (Germany) yielded ~120,000 faunal remains of mostly from large mammals, including a relatively low frequency of *P. antiquus* bones, although the MNI is estimated at 70 [314], as well as ~20,000 Middle Palaeolithic cores, flakes, and tools, which were all excavated from an open-cast lignite mine and buried within calcareous silt loams that had been deposited incrementally in a shallow basin during the Eemian interglacial (~130–114 ka) [145–148,151–153]. The well-preserved bones of large mammals at Neumark Nord 2 apparently showed "abundant traces of butchery and marrow extraction" [148] (p. 170). An analysis of the ontogenetic ages of 18 out of the 54 or 55 individual elephants [149] from one stratigraphic level and of different body size found a very low number of young animals but abundant adult and old individuals, including males. The mortality profile is not similar to the characteristic social structure of modern African elephants. The cause of the unusual population structure of the assemblage was possibly "prolonged phases of reduced rainfall" [149] (p. 215), which had killed off younger animals, leading to a seriously declining living population. Taphonomic and zooarchaeological analyses are ongoing by researchers at the Monrepos Archäologisches Forschungszentrum und Museum für menschliche Verhaltensevolution, Germany.

EDAR Culebro 1 (Spain) contained 35 fragments of bones from *M. intermedius/primigenius* in interglacial sand and gravel sediments, dated to MIS 5, along with 243 Middle Palaeolithic lithic pieces in the same stratigraphic unit [160]. No cut marks, marks of hammerstone impact or carnivore tooth marks were found, but a fractured humerus was interpreted as having been broken by Neanderthals to obtain the bone marrow when the element was still green. Trample marks on the fracture surface of the broken humerus led Yravedra et al. [160] to propose that the trampling occurred after the breakage and thus, did not cause the break. The lack of cut marks could be explained by humans recovering the bones from a decaying carcass whose muscle masses had started to rot and, therefore, could be removed from the bones without heavy cutting against bone surfaces.

Gröbern (Germany) contained almost 200 bones of at least two adult *P. antiquus* [150,163–167], a male and a female, dated to the Eemian interglacial, ~120 ka. This site, in a lignite mine, contained a ~20 m^2 scatter of bones from a 35–40 years old, possibly ailing, male elephant lying on a paleolake shore. Some of the bones of the feet and spine were articulated. Carnivores had gnawed on some long bone epiphyses. In the early excavations, 27 lithic artifacts (mostly flakes) were found under the bones [167] (p. 177). They were made from about half a dozen different raw materials. Several more lithic flakes were found in later excavations. None were refittable, but all lacked signs of transport or sedimentary abrasion; hence, they were interpreted as having been produced on-site. The site has been interpreted

as a Middle Palaeolithic kill and butchering locus, based on the use-wear traces on some of the stone tools [167]. Carnivore scavenging is suggested to have followed the human use of the carcass.

The Lehringen IV (Germany) site contained the bones of an adult *P. antiquus*, including ribs, tusk, and mandible [74,165,167–170], which were recovered in paleopond deposits dated to ~120 ka, and associated with a wooden spear that was broken into 11 pieces by sediment pressure. When the wooden spear was first exposed, it apparently lay "between the ribs of the elephant", although it was never photographed in situ; later on, a broomstick was placed among the bones to represent the spear when a photograph was taken of the find [170] (p. 23, plate 3) [167] (p. 182). The spear was a stem from a yew tree whose bark and smaller branches had been removed and the shaft smoothed before use [170] (pp. 45, 47–49, plates 16–19). The ontogenetic age of the elephant was ~45 years old at death. Some bones might have been taken away by visitors [74] (p. 185). About two dozen flint flakes were also found, some of which were refittable and some had been retouched. The associated lithic technology is assumed to be Upper Acheulean and included two different raw materials. Technologically, the lithic materials were similar to those from Gröbern [165]. The spear in the skeleton, apparently behaviorally associated, argues for a killing event rather than the scavenging of an already deceased animal.

The sand quarry site in Spain that is known as Preresa (also written in uppercase letters) [112–114] is located in floodplain deposits in a fluvial terrace, dated to ~84 ka (MIS 5a, near the end of the last interglacial). Dozens of bone fragments were found from an individual elephant of indeterminate genus, likely either *Palaeoloxodon* or *Mammuthus*, along with hundreds of lithic pieces and the remains of reptiles, mollusks, birds, and small and large mammals. The proboscidean remains might have been preserved in an area where accumulating animal carcasses were seldom scavenged by carnivores [113] (p. 1066). There were no identified carnivore tooth marks on the proboscidean bone fragments. Tooth marks have been identified on less than 1% of the total NISP of all of the animal bones. The large mammal bone fragments are "relatively small diaphysis fragments and flakes" [113] (p. 1064), but cut marks and notches on fracture edges that are suggestive of hard hammer impact have been identified on a few of the proboscidean bone fragments [112]. The breakage caused by humans was interpreted as a sign of marrow extraction rather than the first steps of bone tool production. Panera et al. [156] (Table 1) list 18 other sand quarries near Preresa with *Palaeoloxodon* or *Mammuthus* remains and abundant lithics dated to the Middle and Late Pleistocene.

The Asolo site (Italy) contained the partial skeleton of an adult female *M. primigenius* in stream-laid sandy gravels with an estimated age of ~50 ka. Associated with the remains were two Levallois lithic points and three flakes, including one with an impact fracture on the tip that has been interpreted as damage from use as a spear point [315]. No bones had cut marks, but the undisturbed spatial association of the lithics with the bones plus the impact damage on the flake led Mussi and Villa [315] (p. 2611) to conclude that Neanderthal hunters had killed the mammoth and utilized the carcass.

Portuguese proboscidean sites [158,263,316] (also see [317] for a study of Acheulean stratigraphy) are not especially well known in English language literature. Evidence is slim but does exist for hominin associations with straight-tusked elephants and woolly mammoths. An example is the find at São Antão do Tojal, containing a *P. antiquus* femur, a tibia, part of a vertebra, and a phalanx, along with an equid tooth and a hyena coprolite, discovered on a stream bank and associated with lithic flakes that could be Middle Palaeolithic (Mousterian) implements. Two small flint flakes were described as being stuck in the femur. An estimated geological age is the first Würm interglacial, MIS 3. Another much younger site is Algar de João Ramos, a cave with materials dated to ~17.2 ka that included a possibly cut femur fragment, presumably of *M. primigenius* [158] (p. 612). Other sites with lithics and fragments of proboscidean teeth and bones are listed in Table 1.

At Tategahana, Lake Nojiri (Japan), the remains of more than 40 *P. naumanni* have been found in 8 different stratigraphic units during >20 excavation seasons. The sediments

containing bones are dated as 60–38 ka. The depositional rate is low per stratigraphic unit. A total of 10 mammalian taxa have been recovered, but most of the identified specimens by far were from *P. naumanni*. The assemblage is dominated by adult animals whose dental features are similar to those of African elephants >25 years of age. Juveniles comprise a minor part of the assemblage [184]. The mortality profile and the vertical dispersal of individuals appear to reflect the attritional deaths of mainly adults, which might suggest to some archeologists that selective ambush hunting by humans occurred. Three dispersed bone clusters occurred in one stratigraphic unit, along with bone and lithic flakes and tools. The bones in the clusters could be from a single individual. Some of the lithic materials were not local. A "spear-form wooden tool" was found near an elephant skull [181] (pp. 257, 266). This locus has been interpreted as a "kill–butchering site" ([185] (pp. 286, 288) and [179–183]). A small quartz flake was found embedded in an elephant rib [186] (p. 119, Figure 4). Suggested interpretations range from this being a piece that was broken off a spearpoint or hammerstone or being part of a lithic tool that broke during butchering to it being a flake fortuitously embedded when the rib was trampled by animals against a substrate containing the flake. There were also possible cut marks on one elephant rib and a giant deer's bones, although these marks were "shallower and more irregular" than cut marks on bones from other Pleistocene sites in Japan [186] (p. 117) and thus, could be trample marks, carnivore tooth marks or even excavator marks. Proboscidean long bone fragments have been interpreted as a sidescraper, a cleaver, a knife-like tool, and retouched flakes [318]. No other archeological evidence exists in the Japanese Islands for a human presence before 40 ka, so any earlier presence must rest on unambiguous proof that the broken and marked bones were affected by human actions.

The open-air site Salzgitter-Lebenstedt (Germany) contained >4000 late Middle Palaeolithic lithic artifacts and five bones from two Neanderthals, along with the bone remains of 86 reindeer, 17 *M. primigenius*, 3 bison, 8 equids, 1 woolly rhinoceros, and 1 wolf [174,175]. Different preservational qualities and variable percentages of marks from carnivore gnawing on the bones possibly indicate that some of the assemblage is natural (i.e., background) and some is anthropogenic [174–177]. Attempts at dating produced unclear results because of the incomplete provenance data, probable selective bone recovery, and evidence of stratigraphic mixing. Direct dates on the mammoth bones are ~13,500 and ~38,000 rcy BP. Other dates on reindeer bones and peat suggest that the archaeological material is ~46–42,000 rc years old (OIS 3) [177]. Several mammoth ribs and fibulae were modified into tools [174]. Eleven mammoths are less than ~13 years old and nine are ~24–60 years old; no animals were found in the ~12–24 year old age group.

A number of central and eastern European *M. primigenius* bone deposits from the late Middle Palaeolithic and Upper Palaeolithic are listed in Table 1. A notable Middle Palaeolithic site is Molodova I (Ukraine) [173,319]. Its Layer 4, dated > 44 ka, contained a rich assemblage of Mousterian lithics (40,000 specimens) and 3000 bones of mammals, including 15 male and female mammoths of various ages. The mammoth remains are thought to have come from kills made by Neanderthals and from scavenged carcasses. Some of the bones were apparently used to make a structure that housed multiple hearths and flint workshops, although the interpretations of the origins of the bone accumulation have widely varied [173,319]. Some of the mammoth bones might have been broken for access to the interior grease and marrow [173]. Marks on several mammoth bones were interpreted as cuts and scrapes made by lithic edges with some possibly resulting from the de-fleshing and disarticulating of scavenged carcasses. Markings on other bones in Layer 4 had been interpreted as being deliberately engraved by Neanderthals into symbolic shapes [319]. A study of a sample of marked items by Nowell and d'Errico [319] made it plain that natural processes, such as recent trampling or excavation tools, created the marks that were once thought to be Neanderthal symbols.

Skaratki (Poland), dating from the Middle Palaeolithic or Early Upper Palaeolithic, was originally reported [196] to have mammoth bones that were cut marked and broken by hominins, charcoal, and a small flake found near the bones; however, the marks were made

by carnivore teeth and the scarcity of lithics bedded with the bones led Wojtal [197] (p. 119) to doubt that the site was a human-made kill, although the Neanderthal scavenging of a mammoth carcass is a possibility.

Most mammoth sites with lithics in central Europe contain Upper Palaeolithic artifacts, with ages ranging from ~33 ka to ~21 ka. An unusual early Upper Palaeolithic assemblage was found in the multicomponent site of the Vogelherd Cave in Germany [320,321]. The rich Aurignacian levels (~36 ka) were dominated by mammoth (MNI = 28), along with >20 other species of mammals and some bird species. The site also had thousands of lithic implements, 10 figurines carved from mammoth ivory, and 10 ivory tools. The deposition was mostly during a cold period, but with significant oscillations in temperature in the later phases. What makes the site so uncommon is that its cave setting contained far more mammoth teeth and crania than any other parts of the skeleton. Humans selected these mammoth elements to carry to the cave for use, possibly as barriers against carnivores, cache protectors or raw materials, but there is no clear evidence that humans killed, or even butchered, most of the mammoths [321] (p. 222).

Other Upper Palaeolithic sites in central and western Europe that have evidence of the human butchering of proboscideans are Soyons in the Rhone Valley of France [230], Langmannersdorf, Krems-Hundssteig, Krems-Wachtberg, and Grub-Kranawetberg in Austria [199–202], Předmostí, Dolní Věstonice I and II, Milovice I, and Pavlov I and II in the Czech Republic [203–213], and Kraków-Nowa Huta [197,198] and Kraków-Spadzista in Poland [197,215–221,322–324]. The sites date from ~33–20 ka. Multiple animal taxa were represented besides mammoth. At Kraków-Nowa Huta [198], 12 flint specimens were found near 8 bones and skull fragments and 4 teeth from an adult female mammoth. Wojtal [197] (p. 121) classed the site as a butchery locale and possibly a kill. The Kraków Spadzista site has three zones of different activities. Thousands of lithics were found along with tens of thousands of animal bones that were dominated by the remains of >100 *M. primigenius*. The mammoth bone dump is dated ~29 ka [325]. Two mammoth ribs were found with embedded lithic fragments that were probably broken off from stone-tipped spears.

The Gravettian and Epigravettian phases of the Upper Palaeolithic are known for impressive archeological characteristics, including large accumulations of animal bones, especially those of multiple woolly mammoths. The Gravettian culture emerged after ~37 ka in central Europe, around the end of MIS 3. During MIS 2, mammoths were more than just a source of meat. People used their bones and ivory to make decorative and functional artifacts, burned the bones for fuel, and built dwellings and shelters from them. The human tendency to focus on mammoth resources might have begun even earlier than the Gravettian in central Europe, as suggested by the mammoth-dominated Aurignacian levels at the Vogelherd Cave site (Germany) [321] (p. 222). The Epigravettian followed the Gravettian after ~21 ka, although some archeologists consider it a post-LGM continuation of the Gravettian.

Associations between humans and mammoths were also fairly abundant in eastern Europe. One example is Halich (also spelled Halych) in Ukraine, which has been interpreted as a kill and butchering locus [227–229], with 105 flint artifacts, charcoal concentrations thought to be hearths, and 151 poorly preserved and disarticulated mammoth bones from at least two individuals buried in loess dated to 29–14 ka. Root etching obscured any possible cut marking, but at least one limb element (a femur) was fractured when still green.

Mammoth sites in European Russia include Byzovaya with cut marked bones and Middle Palaeolithic lithics [187] dating from ~35–32 ka, Spytihněv-Dochonce with cut marked bones and Upper Palaeolithic lithics [326], and Yudinovo with cut marked and broken bones and late Upper Palaeolithic lithics dating from 19–15 ka [248], among others. Pidoplichko [245] and Soffer [246] described the Middle and Upper Palaeolithic sites on the Russian Plain that contained enormous numbers of bones from dozens of *M. primigenius*, along with the bones of other fauna (equid, wolf, reindeer, etc.), abundant stone artifacts, osseous adornments and artwork, fire features, and sometimes traces of dwellings that were

partly made from mammoth bones. For such sites to have been created by human actions, mammoths might have been killed individually on-site or their bones were frequently collected from natural carcasses. Mortality profiles are variable; some sites have a preponderance of younger animals but some have old animals, possibly reflecting combinations of selective human predation and non-selective and non-cultural death events. Some sites, or different levels within them, have been interpreted as mammoth butchering loci that were perhaps seasonally revisited, although others appear to be living sites where dry bones were transported from death sites elsewhere.

The frozen almost whole or partial carcasses of *M. primigenius* are well known from northern Siberia [327], beginning with the first one that was reported in 1692. A more recent example is the single well-preserved and nearly complete young male mammoth skeleton with a little frozen soft tissue, dated ~45 ka, which was found north of 70° latitude at the mouth of the Yenisey River in the Taimyr Peninsula of Arctic Siberia [328]. The discovery was formally named the Sopochnaya Karga (SK) mammoth and nicknamed Zhenya. No lithics were associated with the find, but a tusk tip is said to have been flaked by humans while still in place in the cranium and hunting lesions and cuts are claimed to be present on skyward side bones. If the marks were inflicted by humans in prehistory, they are then evidence for an unexpectedly early human presence in the high Arctic [329]. However, arguments have been put forward [330] that the marks were in fact made by recent excavators using metal tools and shovels, including the original discoverers and the team that then recovered the carcass.

The well-preserved and nearly complete mammoth mummies in Arctic Siberia may number in the dozens or far more and, along with the abundant scattered bones from hundreds of other mammoths, are generally considered to be from non-cultural deaths. However, some sites with clustered bones could include remains from serial scavenging or killing by humans [331,332]. Possible examples are Shikaevka [259–262], Shestakova [235,260], and Volchia (also spelled Volch'ya and Volchya) Griva [259,262,265,266,333]. Three Siberian sites have shown evidence for the human killing of mammoths. The oldest is the Yana site complex [189,190,193–195,334], which yielded fragments of composite ivory and lithic projectiles and holes in *M. primigenius* bones, which were presumed to be made by projectile points. The large accumulation of mammoth bones is partly attributed to humans collecting from both the natural deaths and human-made kills of mammoths with relatively small tusks that could be efficiently made into ivory tools. The Lugovskoye site (also spelled Lugovskoe) in western Siberia [275–279] contained thousands of mammal bones preserved in permafrost that had a "high water content" [277] (p. 42). The faunal assemblages include the remains of multiple woolly mammoths whose bones were osteoporotic or otherwise dystrophic [279]. One mammoth thoracic vertebra contained the embedded fragments of microliths that had been inserted by a bone or antler point that was no longer inside the bone. A direct date on the vertebra is 16.2 ka BP. A few hundred Upper Palaeolithic stone artifacts were found about 60 m away from the vertebra, including bladelets. Nikita Lake, dated 13.8–13.6 ka, was originally described as containing "several mammoth ribs . . . [with] clear hunting lesions (embedded lithic tool fragments)" [335] (p. 155), although a later paper stated that only "one of the ribs contains a preserved fragment of a stone tool" [194] (pp. 205, 207, Figure 3). Lithic items were associated with the bones, including points similar to the Chindadn type found in Alaska and the Berelyekh site in Siberia.

A possible example of a single animal kill is the Tomsk *M. primigenius* [243,244]. Most of the bones of a "young mammoth" (translated from the Russian [244], (p. 75)) were present and a thin layer of charcoal underlay them in an 8 × 4 m area, along with ~200 lithic blades, flakes, and cores but no microblades, perhaps suggesting a pre-LGM age [336] (p. 314). A radiocarbon date of 18,300 ± 1000 BP is on charcoal possibly taken from below the mammoth bones. Some bones might have been cut and scraped and a number of the elements, such as the cranium, both femora and a humerus, were fragmented as though impacted with hard hammers; however, the damage could be attributable to the shovels, picks, and digging bars that were used to uncover the bones from the frozen

ground. The spatial association of the bones with the burned area and the stone tools is not closely documented, although a behavioral association is a possibility.

3. Discussion: Variability in the Assemblages

Clark and Haynes [15] thought that the oldest proboscidean sites were of three types:

(1) The clustered but sometimes cut/broken bones and less than a dozen to barely >100 stone artifacts. These sites could be interpreted as having had human involvement on a limited scale, such as small hominin group butchering a killed or scavenged proboscidean;

(2) The well-dispersed bones of one or more proboscideans, often with a variable number of artifacts. These sites could suggest human butchering and perhaps other activities occurring more than once in the same spot, perhaps after killing or after a planned encounter with dead proboscideans in predictable locations, such as along streamways or at the edges of marshes;

(3) The broken and dispersed bones of multiple proboscideans along with large numbers of light and heavy duty stone artifacts. These cases could represent recurring episodes of human butchering after either killing or finding the animals dead at predictable spots. Gamble [337] (p. 71) called such revisited sites "enduring locales", where hominins gathered at carcasses for short-lived events, such as butchering.

Clark and Haynes [15] (p. 409) proposed that "human butchering practices generally resulted in the disarticulation, dispersal and differential fracture of the bones of large food animals," and that large animals "were butchered at the place where they were killed or where the carcase [sic] was found." In their view, this commonality did not change very much throughout the Early and Middle Pleistocene, although Upper Palaeolithic sites later appeared with heaps of mammoth bones that could be examples of large-scale transport away from original skeletal loci mixed with the remains of in situ carcass processing. Cave sites such as Vogelherd (Germany) [321] and Spy (Belgium) [178] also have been found to contain proboscidean bones and teeth, although often in smaller quantities than in open-air Upper Paleolithic sites, again indicating probable transport of remains away from original skeletal loci. Clark and Haynes [15] speculated that the signs of variability in butchery would increase as more sites were discovered and analyzed. Indeed, in recent decades, more variability has been discovered in proboscidean sites. For example, Delagnes et al. [14]) added to the observed variability in single skeleton sites by reporting several thousand flakes and other stone tools that appeared to be more numerous than necessary to butcher one elephant carcass.

3.1. Taxon Associations

Overall, the available evidence that elephantids contributed non-negligibly to hominin subsistence throughout human evolution may seem scarce when the huge span of ages for these sites is considered. It is also apparent that the different proboscidean species varied in their importance for human subsistence over time and space. *Palaeoloxodon* bones have been found in Lower and Middle Palaeolithic archeological sites in Europe and the Near East and Early and Middle Stone Age sites in Africa. *Mammuthus* remains have been present in more than half of the important Upper Palaeolithic sites on the Russian Plain and more than half of Siberia's Upper Palaeolithic sites [338]. Although not discussed here, some Americanist archeologists think that up to half of the sites that were left by the continent's earliest human colonizers contain proboscidean bones [339–341].

3.2. Temporally Varying Rates of Human–Proboscidean Associations

The occurrence of hominin associations with proboscideans varies over time (Table 2). I emphasize that these numbers are, at best, tentative and subject to correction.

Table 2. The percentages of Table 1 sites that can be tentatively assigned to lithic phases (*n* = 85).

Phase	N (Rounded%)
ESA/Lower Palaeolithic	20 (23.5)
MSA/Middle Palaeolithic	32 (37.6)
LSA/Upper Palaeolithic	32 (37.6)
(Post-Pleistocene)	1 (0.1)

The rough temporal rates of proboscidean killing/scavenging/butchering could provide perspective on the frequency of assemblages created by hominins. The ESA/Lower Palaeolithic sites in Africa, Europe, and Asia that were ostensibly made by hominins are chronometrically distributed from 1.8 Ma to ~400 ka. A roughly estimated rate of assemblage creation for this span of time is one assemblage per ~88,000 years. The MSA/Middle Palaeolithic is here estimated to have spanned from ~400 ka to 40 ka; therefore, a very rough temporal rate of assemblage creation for this length of time is one assemblage per 11,250 years. A rough temporal rate for the creation of LSA/Upper Palaeolithic assemblages is one assemblage created per 938 years. These estimated rates may signal major differences in terms of human behavior during the three phases of hominin evolution or they may be no more than the reflections of discovery trends. The differences may also be due to taphonomic factors, i.e., the younger Pleistocene sites greatly outnumber the older ones because subtractive agents such as diagenesis would have affected bones more and more over time. Some differences could also be attributable to varying abundances or vulnerabilities of proboscideans affected by environmental perturbations.

Table 3 shows the rounded percentages of sites in Table 1 for which different proboscidean taxa were identified. As with Table 2, these numbers should not be considered as the final say; they are approximations derived from published source materials and reflect the fuzziness of the boundaries between Palaeolithic technocomplexes and hominin evolutionary transitions. I especially note that the totals for *Mammuthus* spp. and *Stegodon* spp. are undercounts because sites in localities or regions with multiple named assemblages, such as the Kostenki–Borshevo series (Russia) and Chinese/SE Asian sites, have been lumped together. More detailed study is needed on the non-English literature and corrections should be made to this preliminary table. New discoveries are expected to change the percentages as well.

Table 3. The percentages of sites in Table 1 for which proboscidean genera were identified (*n* = 104).

Taxon	N (Rounded%)
Palaeoloxodon	38 (36.5)
Mammuthus	50 (48.1)
Stegodon	8 (7.7)
Elephas/Loxodonta	7 (6.7)
Deinotherium	2 (0.2)

3.3. Can Killing Be Distinguished from Scavenging by Palaeolithic Hominins?

Many archeological assemblages have been interpreted as procurement by killing, but scavenging also might have been responsible for the associations of bones and lithic artifacts or bone surface modifications that are suggestive of butchering actions. The simple presence of sharp-edged artifacts or cut marked bones in proboscidean assemblages could indicate either killing or scavenging. Palaeolithic foragers likely would have extracted resources from dead proboscideans that they had not killed. Proboscidean carcasses that were scavenged after being found dead might have been utilized differently from the carcasses of kills, but the specific features in bone assemblages that could distinguish between the butchering of found and killed large mammals have been disputed [342].

Domínguez-Rodrigo et al. [343] analyzed Early Pleistocene faunal assemblages and concluded that cut marking indicates hominins were not habitual scavengers; thus, ho-

minins generally had first access to fleshed carcasses, which implies an active role in procuring animal resources, although opportunistic scavenging might have been more frequent with megafauna [287]. Konidaris and Tourloukis [344] (p. 84) concluded that while "the archeological evidence does not support the case for regular, systematic hunting [of proboscideans] in the Early Pleistocene", there was later a "remarkable increase of sites with proboscidean exploitation after ~500 ka" [344] (p. 85) due, at least partly, to "an overall increase of archaeological sites in western Eurasia, signaling a more continuous hominin occupation," among other possible reasons, which does not necessarily equate to a new focus on proboscideans as primary prey. Based on a review of archeological sites, such as those in Table 1, and a survey of ethnographic and ethnohistorical literature, Agam and Barkai [345] proposed that Palaeolithic people "possessed the necessary abilities to actively and regularly hunt elephants" and they "performed this unique and challenging task at will" [345] (p. 20).

Not every archeologist thinks that proboscideans could have been so regularly killed by people [290,291] because of the perceived high handling costs and relatively low post-encounter returns. However, it has been demonstrated that elephants would have a much higher return rate than previously modeled [346], that prey body size does correlate with foraging efficiency [347], that large prey are efficient to acquire [348], and that even when the hunting of large game animals has a low success rate, it can be a major source of calories and essential nutrients and create significant social advantages from sharing meat and fat [349].

Explicit and clear guidelines are not available for distinguishing hominin killing from the scavenging of proboscideans. Archeologists have ambiguous evidence at best; they must rely on the patterns of bone modifications, the presence of potential killing implements such as projectile points, and associations with specialized (and utilized) butchering tools. Yet those kinds of features are not solid evidence for killing, since projectile points and butchering tools would also be useful for scavenging carcasses that were found dead. The determination of a killed versus a scavenged carcass is even more difficult or impossible in the modern field studies of large mammal mortality. One modern day wildlife biologist wrote that predation could only be distinguished from carnivore scavenging of elk calves in Yellowstone National Park by "signs of struggle at the scene, a trail of blood, evidence of a chase, and the pattern of flesh wounds." Bone consumption patterns alone were not adequate to make the distinction [350] (p. 399). Mortality profiles dominated by prime age animals are often interpreted as the result of selective hunting by hominins, but the variability in the mortality profiles of the proboscidean assemblages in Table 1 strongly suggests that mortality profiles are not so simple to interpret.

Humans might have killed or scavenged proboscideans as much for the tusks and bones as for the meat and fat, or sometimes possibly even more for the osseous materials than for the edible resources. The remains of proboscideans that were killed primarily to harvest ivory or bones to use as raw materials or to acquire within-bone nutrients probably would be cut marked from the disarticulating of limb elements and the cleaning of meat and periosteum in preparation for the breaking of the bones. That is to say, the bones might be marked in the same way as bones from animals killed mainly for meat. If the main use of proboscidean carcasses was to extract hard tissues rather than meat and fat, the cumulative mortality profiles might be dominated by larger animals because the bones from adults would have provided far more raw material and within-bone nutrients.

Models have been applied to Lower Palaeolithic/Early Stone Age fossil assemblages in attempts to distinguish whether hominins had first access to the large mammal carcasses, presumably after killing them, or whether their access was secondary after finding the animals already dead. The models are based on characteristics such as the placement and frequency of carnivore tooth marks and lithic tool marks. Different models have been disputed in the literature about African and Eurasian prehistory. Specific information is lacking about carcass utilization by hominin killers or scavengers of proboscideans.

3.4. What Evidence Would Support Killing Rather Than Scavenging in the Palaeolithic?

Probably the most commonly imagined killing method in the Palaeolithic is the use of thrown, thrust or atlatl-propelled spears. The oldest examples of sharpened weapons that could be thrown or thrust are the wooden lance tip from Clacton-on-Sea (U.K.) and the wood javelins from Schöningen (Germany). Both finds date to the early Neanderthal phase of hominin evolution (i.e., between MIS 9 and MIS 6, when technocomplexes evolved from Lower Palaeolithic to Middle Palaeolithic) [351]. Other evidence for the use of thrown or thrust hunting weapons in the Middle Stone Age/Middle Palaeolithic includes impact damage to lithic projectiles (see [352]). Even though it is probable that Lower Palaeolithic hominins could kill large game animals and did not always scavenge from carnivore kills, unambiguous evidence is hard to find for the possible killing methods, such as trapping in pits or fire drives, or for how weaponry was employed, such as by throwing or thrusting hafted implements (see [136] for evidence of hafting as early as the mid-Pleistocene).

Robust archeological evidence for the use of lithic- or osseous-tipped spears as weapons against live prey would be lithic fragments embedded in bone [353], projectile lesions such as bone punctures that show no signs of healing (i.e., bone regeneration/repair) or infection, plus cut marks from the de-fleshing of elements that already would have been stripped by carnivores which killed the animal or found it dead before the humans discovered it. Punctures, lesions, and embedded lithics have been recorded in the bones of many different non-proboscidean species in Africa, the Near East, and Europe, from Mousterian through to Late Aeneolithic times (a list of non-proboscideans is in the Appendix of [354]).

Projectile lesions on proboscidean bones such as embedded lithics [353,355] or nick marks do not necessarily indicate a fatal wounding. Studies have shown that various weapon delivery systems would have different effectiveness [356,357]. Bone lesions show that weapons injured only the animal's outer soft tissue and bone. Elephants can survive the complete break of a rib, as proven by several fully healed examples found in African fieldwork [358]), so bone lesions might have been survivable injuries for healthy animals, unless the weapons were poisoned, of which there is no evidence in Palaeolithic assemblages.

Even so, and importantly, if there is no trace of infection, sclerotic lesions, or new bone repair on the injured bones, the wounded animals must have died soon after the injury, i.e., the injury was perimortem. The time needed for proboscidean bone to begin regeneration is not known for certain. Visible healing-related changes in cortical bone and on the margins of injury lesions occur after 4–7 days in humans [359], which may be close to the post-traumatic interval for proboscideans. If this time estimate is correct, it means that projectile lesions in proboscidean bones with no sign of tissue repair were inflicted from just moments to no more than several days before the animal died.

No Lower or Middle Palaeolithic assemblages contain proboscidean bones with lesions that have been interpreted as weapon injuries. Only Upper Palaeolithic assemblages in eastern and central Europe and northern Asia contain proboscidean bones (all from *Mammuthus primigenius)* with projectile lesions or weapon fragments embedded in them, which are presumed to be signs of perimortem wounds inflicted just before the animals died from human attacks. The oldest site is the Sopochnaya Karga (SK) mammoth (>40 ka) with slashed ribs [325]. Other sites are Yana [190] in Arctic Siberia (~34–32 ka) with two lithic fragments and a small piece of ivory embedded in the mammoth scapulae, the Taba-Yuryakh mammoth indirectly dated ~30 ka on Kotelny Island [214] with a small lithic fragment embedded in a mammoth scapula with no signs of bone healing, Ilin-Syalakh-34 (~26.5 ka) with nicked split rib fragments [325], the Mamontovaya River mammoth from Wrangel Island (~26 ka) with a hole in a scapula [325], Lugovskoye [276,277] with lithic fragments embedded in a mammoth vertebra directly dated ~16 ka and showing no signs of bone healing, and Nikita Lake with a small lithic fragment embedded in a rib [194].

Two possible examples of projectiles embedded in mammoth bones in eastern Europe are Kostenki (also Kostyonki) 1 (Russia), where a relatively large fragment of a lithic projectile tip was found stuck in cancellous bone at the broken end of a mammoth rib [351], and at Kostenki (also Kostyonki) 14 (Russia), where a tapered ivory object was also stuck

in cancellous bone in the broken end of a woolly mammoth rib [232]. The published photographs and drawings of the lithic point fragment from Kostenki 1 do not show the serious damage at the tip that would be expected from an impact with the rib's cortical surface; the tip is still quite sharp. The cortical bone where the point would have entered the rib was also not preserved, so it is not clear whether there had been any regeneration/healing, thereby making it uncertain as to whether the lithic point had entered the bone antemortem, perimortem or postmortem. The embedded ivory point from Kostenki 14 had a beveled (bending) break on its tip similar to those recorded by experimental antler points propelled by a spear thrower into animal carcasses [353], which is possibly indicative of impact; however, as with the Kostenki 1 find, this important discovery also does not have the preserved entry through the cortical bone that would indicate whether the wound was perimortem or postmortem.

Elsewhere in eastern Europe, a woolly mammoth ulna at the Valea Morilor site (Moldova, ~25 ka) had an oval hole that could have been made by a trapezoidal point [222], but the bone has also been affected by a "modern metal tool" [223] (p. 10). The only known central European examples of embedded projectiles in mammoth bones are at Kraków Spadzista (Poland) [355], where three rib fragments have the tips of lithic points embedded in them and the bones' cortical surfaces show no early trace of bone regeneration or healing (P. Wojtal 2022 pers. comm.). This kind of breakage upon impact resulted from forceful penetration into fresh cortical bone after passing through skin and soft tissue. Such breakage did not occur with the Kostenki 1 lithic specimen mentioned above. Several lithic points that were found in the Gravettian level at Kraków Spadzista have been identified as being damaged from impact, which implies that other mammoth bones besides the two ribs were struck by thrust or thrown weapons.

The hunting lesions on bones in some Eurasian archeological assemblages suggest that weapons were thrust at mammoths from "a rather close distance" [277] (p. 50), estimated at 2–8 m for Lugovskoye. The angles of entry and postulated nearness of the weapon delivery may indicate that hunters were stabbing mammoths that had fallen. Whether thrust or thrown, the points embedded in mammoth bones indicate tactical mammoth hunting with weaponry that was aimed at mammoth torsos, a probability that is also supported by the results of ballistic experiments on non-proboscideans [356,358,360].

If hunting lesions such as bone surfaces marked by weapon points or the embedding of weapons themselves are present in Palaeolithic proboscidean assemblages, the case would be further strengthened that humans killed the animals for meat if there were also tool marks on the external (lateral) surfaces of ribs [361] The rib meat from fresh elephant carcasses is usually quickly scavenged by carnivores and some ribs are broken midshaft by the larger feeding carnivores, so lithic tool cuts on ribs could indicate that humans butchered a carcass before large carnivores had access. Not so expected are cut marks inflicted by humans during the stripping of muscle masses from diaphyses of rear limb bones of fresh carcasses. As with rib meat, the large muscles on the rear legs are very quickly eaten by carnivores when they feed on a carcass before humans strip the meat. Without these kinds of bone surface modifications, proboscidean bone assemblages with spatially associated pointed or sharp artifacts that do not have bone lesions or embedded weapons must be cautiously interpreted as kills.

3.5. What Evidence Would Support Scavenging Rather Than Killing in the Palaeolithic?

A case for scavenging instead of killing would be supported by a different set of characteristics. Lupo [362] discussed the butchering cuts that were made when humans process large mammal carcasses hours after the killing in east Africa. "Frozen, rigored [as in rigor mortis] and/or desiccated carcasses all require similar types of dismemberment techniques" [362] (p. 835). Bones from the carcasses of non-proboscideans in rigor mortis were recorded as cut marked in locations and frequencies similar to those expected on frozen carcasses or on carcasses that humans found and scavenged days after the animal died. Alternatively, proboscidean carcasses from natural deaths that had been found by

chance could have almost no cuts on long bone diaphyses and ribs when the carcasses were not frozen because the soft tissue was either readily strippable following carcass ripening [361] or was missing due to decay and scavenging by carnivores. Some cut marks might be present on post-rigor proboscidean bones at joints that might have been made when disarticulating the bones meant for breaking. Broken bones would have marks from impact by percussors or supports (anvils).

An actualistic study of the placement of cut marks on stiffened elephant carcasses would be a useful line of future inquiry for neo-taphonomists with access to elephant carcasses in rigor mortis that have not been ravaged by large carnivores.

3.6. Intensity of Carcass Processing

The material evidence from archeological sites has shown that hominins differed in how intensively they processed proboscidean carcasses. The extent of carcass utilization may not be clear in many assemblages due to post-depositional processes, for example, but quantitative measurements, such as the numbers of broken bones or cut marks, can provide clues. The characteristics of the different intensities of carcass utilization are discussed by Haynes and Krasinski [361]. An apparently light degree of carcass utilization could be interpreted to mean that people did not need as much food or other resources that were available from the carcasses. The abandonment of a carcass before most of the available resources were collected could be a form of optimizing behavior, when the costs of further butchering had been considered too high. The evidence of light carcass utilization could reflect "gourmet" butchering, defined as the recovery of only the highest utility resources [363] or, alternatively, it may reflect "piece-butchering", referring to incomplete processing for one reason or another, such as the avoidance of bad weather [363] (p. 61). A common form of incomplete utilization is here termed satisficing, a blend of the words satisfy and suffice [364] (p. 9). This degree of utilization may appear as gourmet butchering when the high-utility body parts were rapidly or partially stripped of meat, leaving the bones with limited or even no evidence of cut marking.

Satisficing behaviors might have been selected by Palaeolithic hominins under certain conditions, such as: (1) when proboscideans were abundant and easily found in specific ranges and a sustained rate of harvest was expected to continue in the future; (2) when competition from carnivores or other hominin groups was very low; (3) when conditions were unusually stressful for proboscidean populations, making prey more vulnerable and easier to procure, such as during climate-related crowding of animals at resource refugia or last remaining water points; or (4) during periods of extreme mobility among human groups.

In contrast, hominins who completely utilized proboscidean carcasses would have removed almost all edible tissue while sectioning the body parts to strip meat. A hominin signature of this behavior would include relatively abundant surface marks from the meat removal and the disarticulating of joints and a scattering of disarticulated elements. However, even relatively abundant surface marks may be meager in number compared to marks on the remains of smaller mammals. Meat stripped proboscidean bones might have been broken by impactors, such as heavy stones, especially the long limb bones, to access the within-bone resource of yellow marrow. This degree of utilization would reflect rational behavior to harvest the most resources, or what can be termed maximizing behavior, perhaps to be expected in: (1) periods of real or expected food shortages when the extra costs of fuller carcass processing had to be absorbed; (2) when competition from carnivores or other hominin groups was high; or (3) during periods of reduced mobility.

The signs of maximizing behavior are possibly present in prehistory, such as bones that were broken when fresh, although there should be continuing debate about whether some breakage resulted from non-anthropic causes. When the maximized use of a carcass did occur, the responsible hominins accepted the costs and benefits of extending the time and work needed to harvest more carcass resources. Maximizing behavior might have been adaptive during exploratory dispersals into new ranges, when live prey or

scavengeable carcasses were not predictable or easily located or when prey vulnerability was unpredictable. Hominins also may have maximized carcass utilization not because they wanted to fill immediate needs or avoid feeding competition, but to store resources for anticipated future shortages or to share between different groups. Maximized carcass use could imply an ability to preserve meat, such as with smoke or by sun drying.

3.7. Other Possibly Significant Variables in the Assemblages

Other aspects of late Quaternary proboscidean sites vary greatly. For example, the measurable sizes of bone scatters differ in major ways in all Palaeolithic phases. The differences could be attributable to the varying intensities of carnivore scavenging, hominin dispersal of elements, strength of local streamflow, dispersal by animal trampling, or other processes. These factors could be brought to light through standard zooarchaeological and taphonomic analyses [365,366], but some differences might be trickier to explain, such as the different numbers of lithic artifacts in fossil proboscidean bone sites. At one extreme is a scarcity (or complete lack) of lithic artifacts in sites whose bones are thought to be marked or broken by human actions, such as Asolo and Bucine (Italy) with 5 and 3 lithics, respectively, Fuente Nueva 3 (Spain) with 17, Lehringen and Gröbern (Germany) with 25 and 27, respectively, Áridos 2 (Spain) with 34, Notarchirico (Italy) with 42, Ebbsfleet (U.K.) with 80, etc. At the other extreme are sites containing hundreds or thousands of lithics, such as at the large multilevel sites of Gesher Benot Ya'aqov in Israel and Neumark-Nord in Germany. Not all lithics at the larger sites were associated with the killing or butchering of individual proboscideans. Such variations in the numbers of associated killing or butchering materials have been interpreted as the outcomes of one or a few events of on-site and opportunistic knapping by hominins making butchering tools after procuring or encountering a carcass, or the long-term accumulations of flint knapping from recurring visits to locales where animals were serially killed and butchered.

Cut marking in late Quaternary sites varies from site to site, perhaps inspiring the different interpretations of hominin motivations for the intensity of butchering. A complicating factor in some published analyses is the lack of supportable definitions of true cut marks. Scratches and slices that have been classified as cuts from stone tools in fact might have been inflicted by animal trampling, carnivore gnawing, sedimentary abrasion or excavators' tools. These types of marks are sometimes visually similar. Nowell and d'Errico [319] analyzed Molodova I's so-called "symbolic" engravings, including a claimed depiction of a deer on a mammoth scapula, and concluded that none of the marks in their sample had been made by Middle Palaeolithic Neanderthals. White and Toth [367] noted that the Engis 2 Neanderthal child's cranium from Belgium, which had been interpreted as cut during scalping, was in fact marked by preparator tools, as were other Neanderthal crania from Spy I and II. Wiest et al. [368] illustrated unintentional marks made by air scribe tools that were used to clean fossil bones from the non-cultural Waco (Texas, USA) Columbian mammoth site, some of which could be mistaken for carnivore teeth marks.

Research efforts are continuing into finding the least ambiguous criteria for differentiating true cuts from other bone surface marks, with some important results to show. For example, re-examinations of the Acheulean site of Torralba in Spain have significantly reduced the original estimated frequency of lithic cuts and scrape marks on elephant bones [135,307].

Recent experimental butchering and ethnographic observations of elephant carcass processing can contribute to more reliable recognition of true cut marks by predicting where marks are expected to be made on specific proboscidean elements [361]. However, experimental and ethnographic data do not necessarily provide reliable predictions of the quantities of cut marks to be expected on fossil proboscidean bones. Ethnographic data from historic-era people, such as Efe foragers in central Africa [369,370] and Bisa agropastoral people in southern Africa [371], show that elephants butchered for subsistence or sale were often completely stripped of meat by metal tools and that bones were extensively broken apart. Metal tools allow for the heavy-handed removal of meat and disarticulating

of elements. Crader [371] (p. 135, Table 7) recorded that the number of chop marks (*n* = 62) and "shear" faces from chopping through bone (*n* = 17) on 72 bones of 7 adult elephants killed and butchered by agropastoral people in Zambia were much higher than the number of cut marks (*n* = 16) in the sample. Over 77% of all of the marks were on vertebrae and ribs. The chops were most abundant on non-meaty elements and appeared to be related to the disarticulation of elements. Any finer knife-edge work that might have been carried out on meaty bones left few or no identifiable marks on elements, other than ribs and vertebrae [371] (p. 136, Figure 8), partly because weathering had obscured the marks. In five of the seven bone sites that Crader observed, whenever more than a single fragment of rib or vertebra was found, the proportions of fragments with cuts varied from a low of 0% to a high of 38.7% (12 fragments marked out of 31 present).

Proboscidean bone breakage is another feature that inspires different interpretive explanations. Bone might have been deliberately broken by hominins to extract marrow fats and oils or to reduce bones into packages of raw material for making tools and other objects. Bone fragments could also have been used as exigent cutting implements. The sharp edges of bone and ivory flakes might have been useful for slicing through the soft tissue on carcasses.

Proboscidean compact bone was flaked into bifaces in several Lower and Middle Palaeolithic sites in Africa and Eurasia [372]. Interpretations differ as to why this was carried out, ranging from a purely functional explanation (useful cutting edges were made available by the shaping) to an "act of reverence" that reflected a cosmologically significant relationship that hominins are thought to have had with elephants [373] (p. 354). The oldest proboscidean bone that was flaked into a handaxe dates to 1.4 Ma in Konso (Ethiopia) (not listed in Table 1 because the assemblage does not have evidence of elephant butchering). The manufacture of proboscidean bone bifaces apparently disappeared after 40 ka [318,374].

Localized polish on bones in some of the assemblages in Table 1 has been diagnosed as the effects of tool use. In some cases, perhaps this interpretation needs further analysis to remove the possibility of error. For example, a fragment of cortical bone from a mastodon site in North America [375] was first considered to be a possible expedient tool used for butchering the mastodon because of its spiral fracture shape and pointed end with rounded edges. The scanning electron photomicrographs of one area on the specimen revealed that the polish was created after a drying crack had developed, rounding the edges of the crack, and then another drying crack appeared later, after the polish was created. This sequence of events does not firmly disprove the idea that humans had used a weathered bone fragment as a tool that afterwards weathered further, but it does allow for questioning and further study.

Bone preservation also differs from site to site. Many fossil sites were preserved in environments of rapid burial, which were conducive to better preservation. Rapid burial in windblown sediments was possible at certain times and places, such as many multi-mammoth archeological sites dated to the Pleistocene in Europe; bones in loess could be well preserved or affected by post-burial cryogenic processes. The presence of moving water is often a key factor in relatively rapid burial and the preservation of bones; it is sometimes indicated by abraded or waterworn materials, in addition to the texture of the sediments themselves. Streamside settings imply overbank sedimentation. Some sites appear to have been buried when the bones themselves created impediments to waterborne sediments, leading to the creation of lag deposits. Some bones from the Table 1 sites were found in channel deposits. In many of these and other cases, such as bones buried in frozen ground, some redeposition or spatial disturbance occurred. These processes not only moved bones around but may have also added materials that were never behaviorally associated with the proboscidean's death, such as lithics or the bones of other animals.

Many late Quaternary proboscidean sites also contain background faunal remains, usually of mixed body sizes and often with non-patterned bone representation and diverse weathering stages. These could be a form of lag deposit, left behind after different

kill/butchering events, periods of post-mortem weathering, episodes of carnivore subtraction of bones, or non-cultural transport events.

As mentioned above in Section 3.3, mortality profiling is thought to provide clues about the origins of anthropogenic and non-anthropogenic proboscidean assemblages. Examples of different mortality profiles resulting from specific causes of death can be found in the literature. For example, mortality profiles in modern African elephant bone sites that were created during drought and starvation periods are greatly dominated by subadults. This was documented over 30 years ago in African field studies [305,306,376,377] and was more recently re-discovered by wildlife field researchers in Africa [378,379]. Other kinds of mortality profiles result from different causes of death or from time-averaging, which can be a challenge to interpret. Therefore, mortality profiles are not always straightforward indicators that proboscideans were either actively hunted or passively scavenged.

Mortality profiles vary in the late Quaternary hominin-related sites in Table 1. Some of the assemblages contain post-adolescent/adults associated with Lower or Middle Palaeolithic artifacts [344] (p. 83) or other evidence of hominin presence, such as cut marks. Questions remain about whether the animals were killed or scavenged. Younger archeological sites dating from near the end of the Pleistocene also contain adults, but there are plenty of sites dominated by subadults and/or juveniles (such as Spy [178], Milovice I and Kraków Spadzista [209], Dolní Věstonice II [213], and Yudinovo [248]). The juveniles might have been the least difficult to kill and provided more than enough meat and fat for forager groups. Hominins selecting to kill adults might have been opportunistic reactions to a perceived higher vulnerability of older animals. The choice might also have followed from the desires of some hunters to show off hunting prowess or from a need to acquire larger amounts of meat and fat or bigger tusks to use as raw material.

The shaping of proboscidean bones into standardized artifact forms differs substantially in proboscidean assemblages. As mentioned above, proboscidean bones that appear to be knapped bifaces have been found in a number of Acheulean sites. Sharp points made from bone and ivory have been found at many Middle and Upper Palaeolithic sites. Other functional implements include forms interpreted as mattocks, shovels, awls, and spatulate scoops, such as at Avdeevo (Russia). Carved ivory figurines have also been found at European Upper Palaeolithic sites (e.g., Dolní Věstonice in the Czech Republic and Vogelherd Cave in Germany), as are incised/decorated tusk segments, such as those at Eliseevichi and Avdeeva (Russia) and Předmostí and Pavlov 1 (Czech Republic). The inventory of proboscidean osseous tool types in the Americas is very small compared to Old World inventories, perhaps partly because the hominin co-existence with proboscideans in Eurasia and Africa lasted so much longer.

4. Conclusions

This sampling of sites and brief review of apparent patterning may serve to show that the importance of proboscideans for human subsistence varied over time and space, but greatly increased near the end of the Pleistocene. Non-anthropic processes also probably varied greatly over time and space, such as carnivore competition for proboscidean carcasses and environmental conditions that fostered or hindered bone preservation.

A compendium of currently known sites will always be incomplete because new discoveries are made regularly and different interpretations often result when known sites are re-analyzed. Taphonomic or experimental studies of proboscidean butchering [294,361] and ethnographic studies of the social implications of elephant hunting [380–382] can provide new clues for understanding the origins of ancient proboscidean bone assemblages. A wide battery of analytical methods that has been applied to the oldest assemblages has significantly increased our appreciation of how adaptable Palaeolithic people were in their subsistence behavior and their exploitation of proboscideans (e.g., [383]). Zooarchaeological syntheses of proboscidean assemblages in different world regions (e.g., [384]) are valuable reflections on patterning and uniqueness that should inspire the further analysis of understudied materials.

The differences or similarities apparent in fossil bone sites cannot be explained by a few hypothetical principles or universal patterns that are attributable to a limited set of natural and human actions. The archeological record of hominin associations with proboscideans is less complete and less clear than one may hope for, but it is still rich and in need of further interpretation.

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