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On the type material and evolution of North American mammoths

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ABSTRACT

The type material (holotypes, paratypes, syntypes and neotypes) and nomenclatural history of North American mammoth species are described in detail, focusing on names that have been in recent use: *Mammuthus columbi, M. imperator, M. jeffersonii, M. meridionalis, M. hayi, M. haroldcooki* and *M. primigenius.* Biometric study of the type specimens of *M. meridionalis nebrascensis, M. hayi and M. haroldcooki* shows them to be within the range of variation of *M. columbi*. These and other specimens referred to these species have a misleadingly 'primitive' appearance that is due to advanced individual age or, in the case of *M. hayi*, to inaccurate reconstruction of fragmentary fossils. The type material of *M. imperator* is also indistinguishable from *M. columbi*, but this taxon has been used to categorise mammoth fossils thought to be of intermediate grade between *M. meridionalis* and *M. columbi*. Biometric data indicate no clear morphocline in North American mammoths through the Pleistocene, except for 'advancement' in some Late Pleistocene samples that have been categorised as *Mammuthus jeffersonii*. Genetic and morphometric data suggest that these represent part of a complex metapopulation that arose with the immigration of *M. primigenius* into the continent, followed by varying degrees of hybridization with endemic *M. columbi.* Where adequate single-site Late Pleistocene samples are available they span the whole range of morphologies from 'typical' *M. columbi* to '*M. jeffersonii*'. It is difficult to impose taxonomic boundaries on a complex evolutionary process, but a suggested compromise is to treat the whole range of Late Pleistocene variation as *M. columbi* but informally, if desired, using 'Jeffersonian' as a descriptive term for the more advanced individuals or samples.

1. Introduction

The taxonomy of North American mammoths has had a confused history. In part this is due to issues of nomenclatural priority, inadequate type material and disputes on synonymy, but in retrospect it can be seen also to result from the complexities of the evolutionary process itself. In this contribution I review in some detail the type specimens of the most important taxa, which have their own historical interest, and then briefly assess the evolutionary models which these taxa have been thought to embody. I do not attempt to review all the numerous names that have been given to North American mammoths over the past 200 years, or their type material, but restrict myself to those taxa that have been employed in more recent literature. These are the species *columbi*, *imperator*, *jeffersonii*, *hayi*, *haroldcooki*, and *meridionalis*, with shorter notes on *primigenius*. Lists of the numerous other historical names for North American mammoths, and their likely synonyms, can be found in Osborn (1942), Maglio (1973) and Madden (1981). I exclude from consideration *Mammuthus exilis* of the California Channel Islands; see Roth (1982, 1996) and Agenbroad (2003, 2012) for taxonomic discussion of this form.

2. Materials and methods

All of the specimens discussed here have been examined by the author with the exception of the type material of *Elephas jacksoni, Elephas americanus* and *Archidiskodon haroldcooki*, which are lost, and the Brunswick Canal molars at ANSP. Dental measurements are based on Lister and Sher (2015), modified after Maglio (1973) and Lister and van Essen (2003), and are in mm. Enamel thickness is the mode of several measurements across the occlusal surface.

Abbreviations: ABDSP, Anza-Borrego Desert State Park; AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; DMNS, Denver Museum of Nature and Science; MTA, General Directorate of Mineral Research and Exploration, Ankara; NHMUK, Natural History Museum, London; SMG, Sedgwick Museum of Geology, Cambridge, UK; UDSH, Utah Division of State History, Salt Lake City; UNSM, University of Nebraska State Museum, Lincoln; M^3 and M_3, upper and lower third molars, respectively. Further abbreviations are given in the caption to Table 1.

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Lamellar frequency is averaged top and bottom of crown in uppers (LF), bottom of crown only (LFB) in lowers. LF is inverted to give average length of one lamella-cement interval using the formula LL = 100/LF or LLB = 100/LFB, where LL and LLB are lamella length and basal lamella length, respectively. Crown height, lamella length and enamel thickness are standardised to a crown width of 100 mm using the formulae HI = 100 × H/W, LLI = 100 × LL/W, LLBI = 100 × LLB/W, and ETI = 100 × ET/W, respectively, where H = maximum unworn crown height, W = maximum crown width including cement, ET = modal enamel thickness, HI = hypsodonty index, LLI = lamella length index, LLBI = basal lamella length index and ETI = enamel thickness index. The standardizing procedure allows these variables to be compared irrespective of molar size, while not affecting the comparison between molars of the same size. However, data and plots for the unstandardized variables can be found in Lister and Sher (2015, supplementary materials). In the case of matched left/right pairs, either the most complete of the pair was measured, or in some cases, available measurements were combined from both teeth.

Particular care was taken to assess the completeness or incompleteness of preserved molars. Much of the confusion or misidentification in past assessment of elephantid molars has arisen due to the misinterpretation of incomplete specimens. The peculiar mode of dental eruption and wear in elephantid molars means that, starting around the middle of the lifetime of the tooth, the anterior end of the crown has worn to the root and that, with continuing forward movement of the molar, it gradually loses length and lamellae from the front end. Molars thus affected retain progressively shorter length and fewer lamellae than they started with (Lister and Sher, 2015, Fig. 3). Their measured width will also often become reduced from its original value, as wear extends behind the point of original maximum width (usually in the anterior part of a third molar), and eventually also below the maximum width of each lamella (usually at some height above its base). At the time of writing the latter article I was unaware that precisely the same point had been forcibly made by Graham (1986: 168–169) thirty years previously, when he wrote: “variation in dental characteristics as a result of tooth wear must be considered in mammoth taxonomy” and went on to state, “As mammoth teeth wear the number of plates is reduced, the spacing between plates is increased and the enamel thickness is greater”. Osborn at one point (Osborn, 1942, p. 1087) showed recognition of this issue, although he elsewhere usually ignored it. Methods of recognizing, and where possible compensating for, wear effects are discussed in detail in Sher and Garutt (1987) and Lister and Sher (2015, supplementary materials). Both Sher and I were also unaware that in a remarkable but obscure paper, Hay (1922) had presaged some of these observations, writing: “a complete lower molar of an elephant possesses a strong anterior root which is distinctly separated from the more or less coalesced hinder roots. This root supports three, four, or possibly five plates. When the tooth is worn down so that this root is gone, one can no longer be certain just how many front plates are missing”. This corresponds closely to the observations on woolly mammoths by Sher and Garutt (1987), who introduced a method of estimating the number of missing plates, provided the anterior-most set of paired roots and their ‘marker plate’ (behind the isolated anterior and second roots) are preserved. In less derived elephants, the number of plates above the first root is fewer (see Lister and Sher, 2015).

All of the species here discussed were originally placed in the genus *Elephas* by their founders. Osborn (1924) subsequently created the genus *Parelephas* for *columbi* and *jeffersonii*, while other species (*meridionalis, imperator, hayi* and *haroldcooki*) were transferred to the genus *Archidiskodon* (Osborn, 1942). Since Maglio (1973), most authors have included all these species in the genus *Mammuthus*. To use *Mammuthus* throughout the historical accounts, however, would obscure the pattern of name changes which is part of the story; I have therefore kept to the original terminology, switching to *Mammuthus* when describing recent research. I trust this will not cause any significant confusion as the species names remain constant throughout.

3. Results

3.1. *Mammuthus columbi*

The Columbian mammoth owes its name to the endeavours of two Scotsmen. In January 1846 the celebrated geologist Charles Lyell (1797–1875), on a tour of the United States, visited the excavations for the ill-fated Brunswick Canal, intended to link the Altamaha and Turtle rivers near Darien, Georgia. Local planter and scholar Hamilton Couper had there collected fossil remains from a superficial clay deposit, including a partial skeleton of *Megatherium* and elements of *Mammut, Mylodon, Equus* and *Bison* (Couper, 1843; Lyell, 1849), strongly suggesting Late Pleistocene age. Most of the remains were presented by Couper to the Academy of Natural Sciences in Philadelphia, where they were identified by Richard Harlan, but some (including an elephant tooth) were given to Lyell who took them back to Britain and handed them in turn to Scottish paleontologist Hugh Falconer (1808–1865), a specialist of fossil elephants.

In 1846 Falconer examined but did not describe the elephant molar. The name *Elephas (Euelephas) columbi* first appears in a synoptic table for proboscidean species in Part I of Falconer's monograph on fossil mastodons and elephants (Falconer, 1857a). The species is said to occur in Mexico, Georgia and Alabama, but no specimens are named or illustrated. Falconer notes a questionable synonymy with *E. jacksoni* of Mather (1838) (see later). Later in 1857 Falconer presented Part II of his account to the Geological Society of London, but only a short abstract was published (Falconer, 1857b), including, however, the line ‘In the southern United States and Mexico a distinct fossil species, *E. (Euelephas) columbi*, hitherto undescribed, occurs’. Not until several years later did Falconer publish a full account of *E. columbi* including detailed description of the Brunswick Canal molar (Falconer, 1863).

Thus, although *E. columbi* has become universally accepted as the valid name for the American mammoth, with Falconer (1857a) as its source, the situation is not entirely clear due to the lack of any description or type specimen in that publication. However, we know from Falconer (1863) that Lyell had shown him the Brunswick Canal fossils in 1846, and that the reference to ‘Georgia’ in Falconer (1857a) did refer to these specimens, which is sufficient to establish the priority of the name. The Code of Zoological Nomenclature (Art. 72.4.1.1) states: ‘For a nominal species or subspecies established before 2000, any evidence, published or unpublished, may be taken into account to determine what specimens constitute the type series’ (ICZN, 1999). The principal challenger is *E. texianus*, a name first coined by Richard Owen (1859, p. lxxxvi) for the elephant of the ‘warm and temperate latitudes of North America’, but without any indication of its material basis. In 1862 Owen's protégé Charles Carter Blake described *E. texianus* with reference to a molar from San Felipe de Austin on the Brazos River, Texas (Blake, 1862; the specimen still exists as NHMUK PV OR 33218). The trajectory of the two names is similar but all subsequent authors (Osborn, 1942; Maglio, 1973; Madden, 1981) have accepted that Falconer (1857a) takes priority over Owen (1859) or Blake (1862). They have also all agreed (as did both Falconer and Blake) that *texianus* and *columbi* are synonyms. Lister and Sher (2015) measured and plotted the San Felipe ‘*E. texianus*’ molar, together with others from the same locality in the NHMUK collection, and found them fully