Comparative analysis of the mammoth populations on Wrangel Island and the Channel Islands


At the end of the Pleistocene the range of distribution of the woolly mammoth (Mammuthus primigenius) appreciably moved to the extreme northern portions of Eurasia. At the boundary of the Late Pleistocene and early Holocene the distribution was divided into isolate groups. In the early Holocene the last mammoth populations were present on the Taimyr Peninsula and on Wrangel Island, in the Siberian Arctic Ocean. In the latter location, mammoths survived to the middle Holocene (3,000-4,000 years ago). In Northern America the range of distribution of the Columbian mammoth (Mammuthus columbi) also changed appreciably ate the end of the Pleistocene, producing separate, isolated populations. One of these isolate groups was established on the Californian Channel Islands. Comparisons of the morphological features of dentition and skeleton were made, to reflect the adaptations to habitation in the separate environments. The Holocene Wrangel Island molars have a narrow crown and a frequency of enamel plates slightly exceeding late Pleistocene Siberian mammoths. On the Channel Islands the lamellar frequency increased 20% for M. exilis. By comparison of parameters of the bones it is apparent that the American mammoth generally had a smaller size, although some individual bones are quite comparable. Our conclusions indicate that the Channel Islands mammoths are dwarfed, whereas the Wrangel mammoths are no longer considered to be dwarfs. It is probable that the major difference between the two populations is the length of isolation. For Wrangel Island it was not more than 6,000-7,000 years. Also, during the winters, Wrangel Island was connected to the mainland by ice, allowing migration in both directions. For the Channel Islands the time of isolation is not fully known, but it apparently exceeds 40,000 years. It is possible that additional migration of M. columbi from the mainland took place, but no dwarf mammoths have been discovered on the Californian coast. On the Channel Islands selective forces acted towards smaller animals, resulting in a new species (M. exilis) with 150-180 cm shoulder height. Holocene mammoths from Wrangel Island ranged from 180-230 cm shoulder height and probably corresponded to the last Late Pleistocene populations in northern Siberia.

Correspondence: A. Tikhonov, Zoological Institute of the Russian Academy of Sciences, Universitetskaya nab.1, St. Petersburg 199034, Russia; L. D. Agenbroad, Dept.of geology, Northern Arizona University, Flagstaff, AZ 86011 USA / Santa Barbara Museum of Natural History, Santa Barbara, CA 93105 USA; and Mammoth Site of Hot Springs, Hot Springs, SD 57747 USA.; Sergey Vartanyan, Wrangel Island State Reserve, Ushakovskoe, Russia.

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INTRODUCTION
Isolated island populations of animals are one of the most attractive subjects for scientific research and speculation on the rapid evolutionary changes that often produced reduced sizes of animals and unique specialisations. This is especially true if we talk about famous giants of the mammal world such as an elephant. It is always hard to believe that these enormous terrestrial animals can be the same size as a shepherd dog. As we know, this is really possible on islands and the most famous example we have from Mediterranean islands, where dwarf elephants (*Elephas falconeri*) existed in the Pleistocene. Isolation of these elephants continued many hundreds of thousands of years, so time was a major factor.

WRANGLER ISLAND AND THE CALIFORNIAN CHANNEL ISLANDS
Until recent times, no dwarfs were described among another Pleistocene groups of elephants belonging to the genus *Mammuthus*. So, when the first information about dwarf mammoths from Santa Rosa and Wrangel Islands appeared (Agenbroad 1998; Orr 1968; Vartanyan et al. 1993), it was not very unusual because dwarfs come from island populations. After that, more and more information and collections gathered on these islands raised new questions. On the Channel Islands, California, which includes Santa Rosa Island, real dwarfs coexisted with the mammoths of reduced and moderate sizes. Comparative analysis of Wrangel Holocene mammoth teeth with teeth of mammoths from the last populations on the mainland in Eurasia demonstrated that both sets were very close to one another (Averianov et al. 1995). Dozens of postcranial bones were collected during expeditions of the last few years on Wrangel Island (Fig. 1), before that only teeth were known. Some of them were dated. Now we can conclude that during the Holocene mammoths of different sizes coexisted on Wrangel Island. We thus have a good parallel between the Santa Rosa and Wrangel cases. These islands are very far from one another, not only by distance but also in geographical zones. Wrangel is situated in the high Arctic and Santa Rosa in the temperate zone. There

Figure 1  The Late Pleistocene and Holocene finds of woolly mammoth on Wrangel Island, Russia.
are some similarities too. Both islands are close to the mainland and comparable in size. Our primary aim thus was a comparison of the two mammoth populations to look for similarities and differences.

At first we need to stress that our island mammoths belong to different species or species groups. Mammoths from Wrangel are representatives of woolly mammoth (*Mammuthus primigenius*), whereas Channel Islands mammoths (*Mammuthus exilis*) belong to the lineage of Columbian mammoths (*Mammuthus columbi*). At the end of the Pleistocene, the distribution range of the woolly mammoth (*Mammuthus primigenius*) appreciably moved to the extreme north of Eurasia. Around the Pleistocene/Holocene boundary it divided into small populations isolated from each other. In early Holocene times the last populations of mammoths were preserved on the Taimyr Peninsula and on Wrangel Island; on the latter, mammoths survived until the middle of the Holocene (3,000-4,000 years ago). The existence of an isolated population on the Arctic island has resulted in appreciable morphological changes, reduction of size, and narrow molars with high density of enamel plates. All this has allowed the description of a new subspecies, *M. primigenius vrangeliensis* GARUTT, AVERIANOV ET VARTANYAN, 1993.

In North America the distribution range of the Columbian mammoth (*Mammuthus columbi*) also changed appreciably at the end of the Pleistocene and probably also became divided into separate, isolated populations. One of these remained on the Channel Islands off the coast of California, where mainland mammoths had penetrated earlier. A long isolation has resulted in appreciably reduced sizes and a series of other morphological changes. Mammoths from the Channel Islands were described as a separate taxon, *Parelephas exilis* (STOCK et FURLONG 1928). Now, the majority of specialists refer this form to a separate species *M. exilis*.

Despite the huge ecological differences in the compared territories, it is of great interest to present the analysis of paleogeographical conditions in which the two island populations of mammoths existed. Initially, morphological features of skeleton and teeth were taken that reflect adaptations of the animals to their respective ecological conditions. However, it is necessary to take into account the length (duration) of the existence of the mammoths in both territories. The separation of Wrangel Island from the mainland took place on the Pleistocene/Holocene boundary (approximately 10,000 yBP). Isolated mammoth populations existed on this island no more than 6,000 years. A very short period of time for island dwarfing, even in the extreme north. Moreover, the individual age of mammoths can reach 65-70 years (Vereschagin & Tikhonov 1987) so during 6,000 years nearly 100 mammoth generations existed on Wrangel Island. During the late Pleistocene larger mammoths were abundant on the island also, thus the separation of Pleistocene and Holocene remains is possible only with radiocarbon dating. In the past few years we processed more than 100 dates, although the majority of the bones of the skeleton are not yet dated.

The Channel Islands were separated from mainland much earlier than Wrangel. Isolated populations existed here for a relatively long time and had enough time to evolve into animals of unusually small size. One of the most interesting questions, as with the Wrangel mammoths, is connected with the dating. Is it possible that the last mammoths on the Channel Islands were only dwarfs, or a mixed population? How long have the Santa Rosa dwarfs existed on the island? Current radiocarbon chronology indicates dwarfs were present for more than 40,000 years.

In both cases we see how important it is to consider the length of the time of existence on the islands. Unfortunately, in comparison with representative collections of bones from the Channel Islands, we hardly have dated postcranial mammoth material from Wrangel. Nevertheless, we are trying to compare some dimensional characteristics of the bones that can help us to imagine a life-size of animals from both populations.
TUSKS
On Wrangel Island no entire mammoth skull was found, so it is not possible to compare with skulls from the Channel Islands. But we can consider the measurements of tusks, which indicate a probable size of the skulls. The length of two Holocene Wrangel tusks with a large curvature is 255 and 280 cm; the diameter at the alveoli is 120 and 121 mm, respectively. On the skulls from the Channel Islands the diameter of the edge of the alveoli is 57 and 105 mm, which probably corresponds to tusks with the diameters at the alveoli of 30-40 and 70-80 mm. It is obvious that the tusks from Wrangel belonged to normal-sized mammoths with a shoulderheight of at least 230 cm. Mammoths from the Channel Islands represent all ages; measurements are taken for adults. The skull and tusks are about one half the size of mainland mammoths, with shoulder heights less than 200 cm. Comparable mammoths from the Channel Islands were adult animals with very small skulls and tusks.

POST CRANIAL BONES
Among other bones we can compare some bones of the extremities. The collection of Holocene bone remains from Wrangel includes three femurs (Fig. 2) and one tibia. All other bones are of unknown age. Among them a whole pelvis, its width, 1300 mm. The sizes of American mammoths are appreciably less; the width of pelvis varies from 540 to 942 mm. Three Holocene Wrangel femurs have lengths of 836 mm (subadult specimen with unfused epiphyses), 985, and 1010 mm. Mammoths from the Channel Islands had smaller femurs, varying from 590 to 842 mm (n=14). The length of the tibia with fused epiphyses from Wrangel Island ranges from 431 to 519 mm (n=5). Tibia sizes from the Channel Islands did not exceed 505 mm (n=1), though the majority were between 300 and 400 mm (n=11); there were 4 bones ranging between 400 and 500 mm.

Figure 2  Femurs of the Holocene mammoths from Wrangel Island.
DENTITION

Molars from Wrangel Island
The molars of Holocene Wrangel mammoths had a narrow crown (46-74 mm width of m3) and the frequency of enamel plates (in average 10.1 in M3) slightly exceeds average parameters of Late Pleistocene Siberian mammoths. This can be attributed to feeding on bush branches which were the main food supply for mammoth on the Wrangel Island during the Holocene.

Molars from the Channel Islands
*M. exilis* from the Channel Islands have an occlusal width (m3) of 30-65 mm with a mean of 48.8 (n=15) and a plate frequency of 5.5-9 with a mean of 7.2 (n=14). It is estimated that the ancient islands had grasses as well as bushes.

DISCUSSION

A comparison of parameters of bones indicates that American island mammoths, on the average, were smaller. Although some separate bones (tibia) are quite comparable, in general the mammoths from Channel Islands were real dwarfs, whereas Wrangel mammoths were not dwarfs. Probably the main difference between two populations is found in the length of the time of isolation. On the Channel Islands this time lasted at least 40,000 years; on Wrangel Island it was no more than 6,000-7,000 years. Moreover, Wrangel Island was connected to the mainland by ice during winters, mammoths could migrate in both directions.

American *M. exilis* (from Santa Rosa Island) was really a dwarf form (shoulder height 150-180 cm), and separate on the species level. On the other hand, the existence of normal-sized mammoths on the Channel Islands together with dwarfs can be explained by possible migration of animals from the mainland as the straits between islands and the mainland are rather narrow and mammoths could cross them swimming. As we know, recent elephants can cross very wide ocean straits, such as to the Andaman and Nikobar Islands in the Indian Ocean. A working hypothesis is that the Pleistocene "super island" of Santarosae was colonised by Columbian mammoths in the Late Pleistocene. As the island shrank due to eustatic sea level rise, smaller forms had adaptive advantages and the ancestral mammoths (and late mainland migrants) declined. It is important to note that no dwarf (pygmy) forms have been reported from the mainland.

The Holocene mammoths from Wrangel Island were of different sizes (from 180 to 230 cm at the shoulders) and probably corresponded to the last late Pleistocene populations of mammoths in northern Siberia. Some adult individuals were very small as we can see from the size of the last molars and one undated tibia (431 mm). Radiocarbon dating of the smallest m3/M3’s suddenly show that these small animals belong not only to the latest known mammoth population (on Wrangel Island, 5,000-3,000 years ago), but also to more ancient periods (8,000-6,000 years ago). The comparison of Wrangel and Berelekh populations of the last Siberian mammoths shows that in both populations, small and normal size animals coexisted which can show on one hand a sexual dimorphism and on the other hand a very high level of individual variability in the last isolated mammoth populations.

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