The Island Sweepstakes

Why did pygmy elephants, dwarf deer, and large mice once populate the Mediterranean?

by Paul Y. Sondaar

The inhabitants of some Mediterranean islands thought the unusual bones they came across were those of saints or of dragons, but nineteenth-century paleontologists saw them for what they were: the fossils of pig-sized elephants and hippos. Most attributed the origin of these peculiar dwarf, or pygmy, mammals to the occurrence of degeneration (the deterioration or loss of function or structure in the course of evolution). They thought that the ancestors of these animals had been of normal size but that degeneration had occurred as the result of the inbreeding inevitable in small, isolated populations.

At the turn of the century, Dorothea Bate, a British scientist, began to collect these fossils systematically. In 1901, she visited Cyprus and obtained fossils of dwarf hippos for the British Museum (Natural History). A few years later she went to Crete, then under Turkish rule where she masqueraded as a man in order to travel freely. Again she came home with a wealth of remains: dwarf hippos dwarf elephants, dwarf deer, and large mice. The prevailing theory was that the ancestors of these creatures had originally reached the islands by crossing bridges of land and that the populations had been cu

Illustrations by D. L. Cramer

from the mainland when these land dges subsequently submerged.

Sixteen Mediterranean islands (or for- r islands) have been found to contain sils of endemic, or unique local, mmals. There are elephants on ten is- ds, deer on nine, hippos on four, and elopelike bovids on two; most of these atures are dwarfed. Another special ture of the fossil fauna of these islands is the absence of large predators, although there is a disproportionate number of birds of prey, especially owls. A few groups of small mammals (insectivores, such as shrews, and rodents) are also represented, and some of these species are larger than their mainland counterparts. Interestingly, similar "unbalanced" fossil fauna—limited to a few animal groups—occur on islands elsewhere in the world: the Japanese islands, the Philippines, the Lesser Sunda Islands, and the Channel Islands off California. When this large fossil record is taken into account, the land-bridge/degeneration hypothesis does not explain the consistent picture that emerges. Why did mainly the same mammals become isolated (deer, elephants, and hippos), and why do they often show the same trends in body structure?

od swimmers, elephants at times have colonized islands far from the inland, leaving their descendants to evolve in relative isolation.

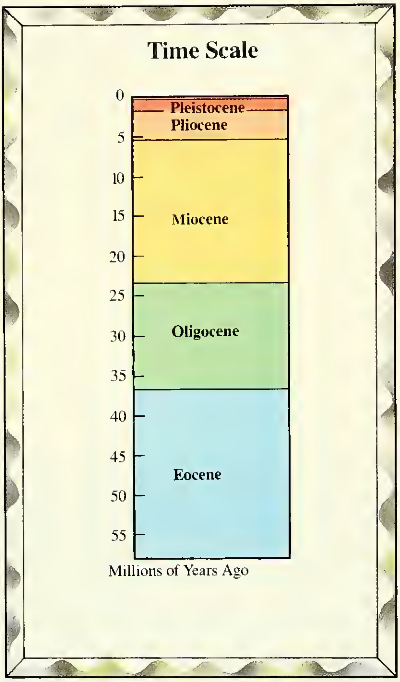
If we look at living elephants, deer, and hippos, however, we begin to see alternative explanations—all these land animals are excellent swimmers. Elephants love bathing, and there are numerous reports of them island hopping in the open sea off India and Sri Lanka (their trunks make excellent snorkels). Deer flee to water if they are in danger and have often been observed swimming. Hippos, which live in or near rivers, have been known to swim from the African mainland to the island of Zanzibar—a distance of more than twenty-three miles. Not noted for swimming long distances, rodents and insectivores are sometimes swept across water on natural rafts, such as floating mats of vegetation. All these creatures, then, can overcome a water barrier and reach islands without benefit of a land bridge.

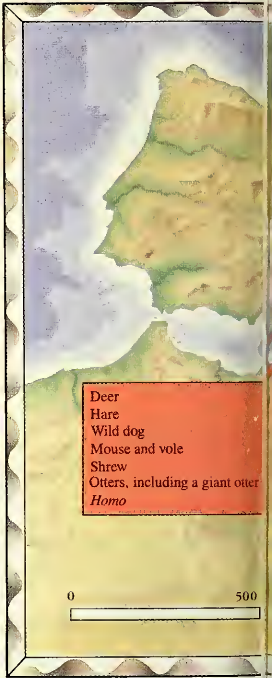
If an island is close to the coast, animals that visit it remain in genetic contact with their parent population, by returning to the mainland themselves or because new arrivals periodically join the island inhabitants. In exceptional cases, however, owing to strong currents or stressful situations, animals may venture far from the coast, reach an isolated island from which they cannot return, and be forced to settle there. Such an event could be a chance occurrence or the outcome of special circumstances, such as a population increase. The late paleontologist George G. Simpson called this sweepstakes dispersal, meaning that the geographical route is impossible for most species and possible only on rare occasions for others. In most cases, dispersal on such a route is a one-way affair.

Sweepstakes dispersal explains—in a way that the land-bridge model does not—the limited selection of animal species found on the various Mediterranean islands. In addition, since islands populated by the sweepstakes route are by nature relatively isolated, the animals that settle on them are likely candidates to evolve into endemic species. Faunas with both of these characteristics (low diversity, endemic forms) can be easily recognized in fossil deposits even where a former island is now part of the mainland. For example, the northern Italian region of Tuscany was an island about 7 million years ago, with a monotonous fauna consisting of a few species of monkeys, some antelopelike bovids (including one with ever growing incisors), and a pig. Similarly, from roughly 20 to 6 million years ago, the present peninsula of Gargano, on Italy's Adriatic coast, was an island with its own unusual fauna—a five-horned ruminant closely related to deer, a giant hedgehog, and giant rodents.

Most of today's Mediterranean islands acquired their present form during the Pleistocene epoch (1.6 million to 12,500 years ago), and this is the period from which we have the most fossils of island fauna. Some of these places were once part of a mainland. Sicily was connected to Africa sometime late in the Miocene epoch (23.5 to 5.3 million years ago), as shown by fossil mammals of African origin found there. The region was submerged in the Pliocene epoch (5.3 to 1. million years ago) and then became a island, connected for a time with mai land Italy at the end of the Pleistocen Similarly, Crete was part of mainland E rope for most of the Miocene, submerge near the end of the Miocene, and rea peared as an island during the Pleistocen In contrast, on Majorca, Menorca, an Sardinia, island faunas appear without i terruption as far back as the Eocene epoc (58 to 36.8 million years ago). The places seem to have remained isolate from the mainland even when, at the er of the Miocene, the Mediterranean is b lieved to have dried up (the so-calle Messinian Event, caused by a tempora closing of the Strait of Gibraltar).

While each Mediterranean island h its own geological history, many were a parently populated by the sweepstak route. The animals of a particular speci





'ften of dwarf size, elephants, deer, and hippos, along with other unique local species, nce inhabited many Mediterranean islands. As shown on the map, below, the animals iat lived on widely separated islands were often similar, reflecting parallel events in ie founding of island populations and their subsequent evolution. Each island has its wn geological history, however, and may yield fossils of various ages. Gargano and 'uscany, for example, now both part of mainland Italy, were islands during the Aiocene epoch, at which time they were populated by the animal species listed. leistocene-age species are shown for the other islands indicated on the map. On Sardinia, ne set of island inhabitants was replaced by another during the Pleistocene. The more ecent group included humans who were unlike their mainland contemporaries.
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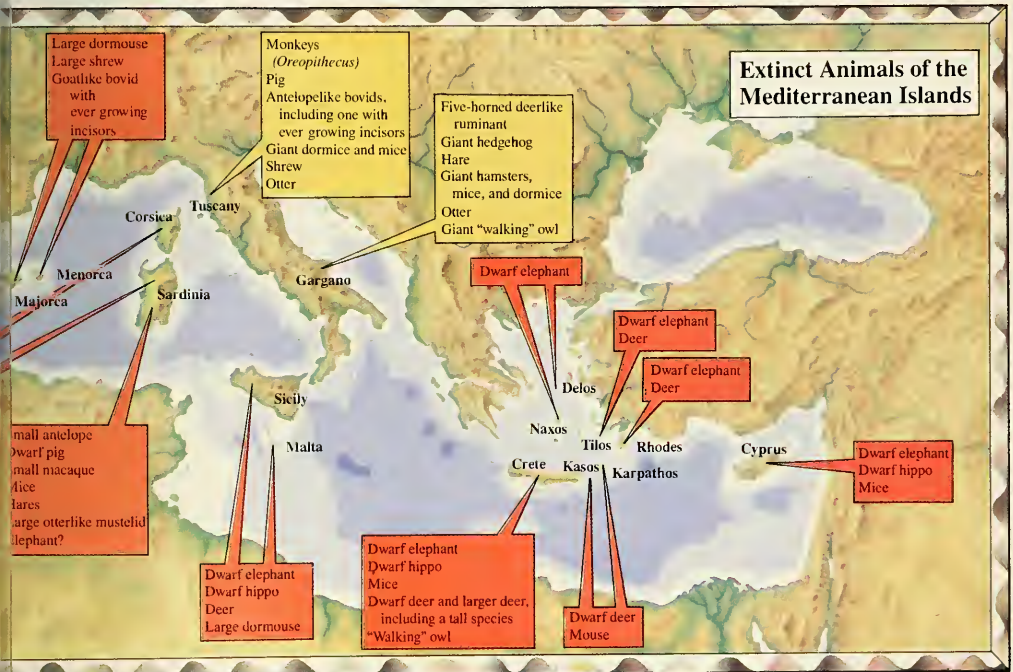


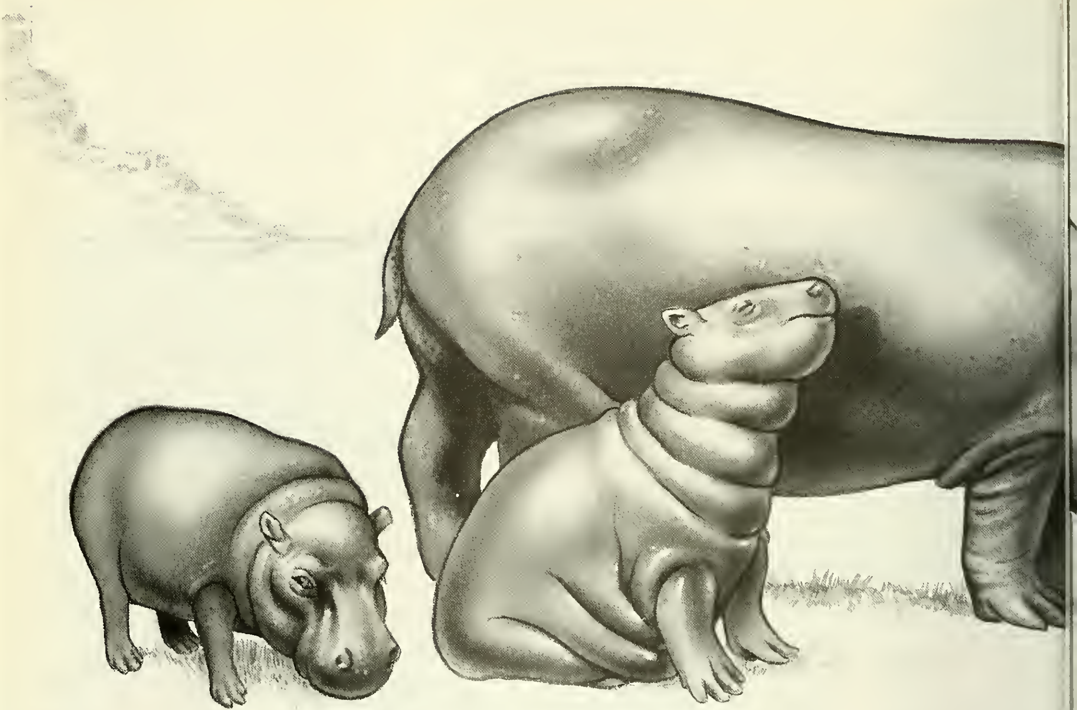
ıat arrived on an island constituted a ɔunding group. Since these founders ʼere few in number, they represented only small sample of the genetic variation in ıe mainland population. No two islands ʼould have had the same sample, with the ɛsult that the descendants would tend to ary in a random way from island to isınd. If inbreeding affected these populaons, they would be apt to vary from each ther to an even greater extent. Instead, ʼe find that the elephants on the different slands, for example, all deviated in the ame direction from the ancestral mainınd form, which was related to the resent-day Indian elephant.

This parallel development on various slands suggests that the island environıents strongly determined how the foundıg populations evolved and that this was ıore than a process of degeneration. The sland fossil species were the results of a repeated experiment in natural selection: the immigrants were compelled to adapt to similar conditions on the different islands, and the outcome was therefore also similar. Some trends—most notably the diminution in size—even held across species lines.

Careful consideration of the taxonomy, dating, and distribution of island dwarf species confirms that larger mainland forms were their ancestors. While the various Mediterranean dwarf hippos, for example, are close in size to the living Liberian hippo (the so-called pygmy hippo), they are not closely related to it. Geographically they are widely separated, and more important, the dwarf species and the Liberian hippo differ anatomically. The arrangement of the skull bones, which paleontologists use to distinguish different members of the hippo family, shows that the island dwarfs are more closely related to large hippos. The placement of the premolar teeth and the shape of the canines also point to the same conclusion. The Liberian hippo, on the other hand, is simply a small mainland form; its ancestors were also small.

Because of their large size, elephants and hippos did not have natural enemies on the mainland. On the Mediterranean islands, which were generally free of large predators, large size lost its significance, while small size may have been advantageous, offering greater mobility in what was generally a mountainous environment and, thus, better access to island food resources. The animals' smaller size also made it easier for them to keep cool (dwarf hippos, for example, did not have to spend the whole day in the water as their mainland ancestors did). Finally, small size permitted a larger population.

Island dwarf species commonly resem-



bled each other in having heavy limb bones. Smaller mammals normally have slender limb bones, indicative of fleetness, but the island dwarf species have heavily built legs with shortened lower parts. Because there were no big carnivores on the islands, speed was no longer a necessary requirement for survival, while solidly constructed feet provided a useful "low gear" locomotion.

The phalanges, or toe bones, of the hippos on Crete and Cyprus, for example, are much shorter than those in the large hippo, and their articulation surfaces are different. In the large hippo, the phalanges support a large foot cushion; but the island hippos apparently lost their foot pads and walked on the tips of their toes, more like goats. This type of locomotion is unique in the hippo family and shows a major adaptational shift. These dwarf forms could have walked very well in mountainous regions—and the location of fossil finds shows that they did.

Paleontologist Gerard Willemsen recently studied the anatomy of present-day reindeer from the island of Spitsbergen, and he found clear parallels with the fossil deer and other ruminants of the Mediterranean islands: they are small and have relatively short legs. The reindeer on Spitsbergen have no natural enemies (even the polar bear does not hunt them), so they do not have to be fast runners. Instead, their short legs give them better stability in the rugged environment. After the brief summer season, they are extremely fat and heavy, having stored up extra food for the winter. Thus their short legs are also probably an adaptation to carrying this extra seasonal weight. Similar explanations may apply to the heavily built dwarf ruminants on the Mediterranean islands.

On the islands, we sometimes find evidence of mass starvation. The fossils occur mainly in caves and fissures where the animals sought shelter and died or into which their remains were washed. On Crete, in a small cave near Rethymnon, I found evidence of an ancient drama: the remains of more than a hundred individuals of a small endemic deer species, *Candiacervus ropalophorus*. The animals were mainly newborns, one-year-olds, or very old individuals. This age distribution suggests that they all died about the same time, probably in a bad season, and that only the strongest adults survived. A cli on Cyprus (called Dragon Mountain b the local residents because of the fossi found there) is another example of a ric bone bed—in this case not a cave bu perhaps part of a small river or pool. I deposit of dwarf hippo bones seems to b the result of one event, pointing to a ma starvation. Fossils of endemic deer foun there, as well as at a locality on Cret show osteoporosis, a bone defect cause by chronic malnutrition. This type of ev dence suggests that overpopulation, fo lowed by food shortage, was the princip selective pressure on the islands. The a sence of carnivores probably allowed he bivore populations to grow out of balan with the environment, causing overgra ing and destruction of otherwise suitab habitats. This may have been a recurrin phenomenon, causing drastic changes population size and thus favoring a quic rate of evolution.

Along with the islands' rugged terrai such conditions account fairly well for th evolution of the short-legged, heavily bu dwarf species found on the islands. Th other endemic species that evolved ma represent more complex adaptations

A dwarf hippo, far left, was among the mammals that inhabited Cyprus in Pleistocene times. The arrangement of its skull bones and other details of its anatomy show that this species must have descended from mainland hippos similar to the large modern hippo, left. Despite a superficial resemblance, the modern "pygmy" hippo, foreground, a mainland animal from Liberia, is not a close relative. Because of its small size, the Cyprus species was well adapted to negotiating the island's mountainous terrain. The dwarf hippo's foot bones, below left (in rest position), enabled it to walk on the tips of its toes, as a goat does. The modern pygmy and large hippos, which rest their weight on large foot pads, have differently shaped foot bones, center and right.

ese island environments. On Crete, for ample, in addition to several species of arf deer, there were some of normal e and one large deer with long, slender s, which probably had a giraffelike way life. The variety of deer species was ssible, in part, because of the absence of mpetition from most mainland animal ecies. Oversized rodents and insecti-es, on the other hand, may have olved because their large size afforded m protection against birds of prey, ich were the only dangerous carnivores the islands.

One curiosity is that on Sardinia (and bably also on nearby Corsica, although re is less fossil evidence from that is-d) a drastic change occurred in the ddle Pleistocene. About one million rs ago, an assortment of animals, in-ding macaques, a small pig, and an elopelike bovid, was replaced by a new oup dominated by a deer, a small hare, d a dholelike dog. This second fauna of rdinia is endemic and unbalanced, wing that Sardinia remained an island, t the deer is of mainland proportions. To rn why, in 1982 I, along with other eontologists from Utrecht University, excavated an ancient cave once used for human habitation. (Its last occupant had been a Robin Hood-like bandit, who had lived there for twenty years until he was shot by the carabinieri in 1900.) When we dug down to the cave's Pleistocene sediment we saw unexpected accumulations of deer bones. The fossils were arranged in an unusual way and showed all kinds of cuts and grooves that could not be explained by natural causes. The discovery, in 1983, of a human temporal bone in the same sediment put an end to any doubt we may have had: humans must have lived in the Pleistocene island environment of Sardinia and preyed on the deer.

In 1985 we found more human fossils (an upper jaw and an ulna, the larger bone of the forearm), three flint scrapers, and small, curious pieces of animal bone. These last, which we consider to be artifacts, were all made from the same part of a deer ulna. Carbon-14 assessment puts the age of these finds at about 14,000 years. The possibility that these people, like other island species, were endemic to Sardinia needs to be studied; the fossils show that they were anatomically different from contemporaneous humans from the mainland. In northern Sardinia, Italian archeologists found a paleolithic tool industry of a type different from the mainland. This evidence, provisionally estimated to be about 200,000 years old, points to a long human occupation of Sardinia. The arrival of these people might have caused the extinction of Sardinia's earlier island fauna, and their presence there was almost certainly the reason why the deer did not lose their mainland proportions.

The early human colonization of Sardinia is an exceptional case among the Mediterranean islands. (Discoveries at Franchthi Cave, on the southern Greek mainland, show that people traveled to Melos about 9,500 years ago to collect obsidian, but they did not settle there.) Continuous human settlement was generally not possible on the islands before the advent of agriculture and animal husbandry. While dwarf elephants, deer, and hippos would have been easy prey for paleolithic hunters, the reproductive rate of these mammals is low, and hunting would have quickly reduced or exterminated them. Small rodents with a high reproductive rate were present on most of the islands, but they were probably too small to provide sufficient protein. As a result, no ecological equilibrium could have been established. A reasonably large mammal with a high rate of reproduction seems to be an essential resource to support a permanent hunting population. The larger hares of Pleistocene Sardinia may have fulfilled this requirement and, along with the island's size and position not too far from the mainland, rendered Sardinia the only island in the Mediterranean suitable for permanent colonization by paleolithic humans.

With the exception of Sardinia (and possibly Corsica), humans moved relatively recently onto the Mediterranean islands. The larger islands like Cyprus, Crete, and Sardinia were colonized about 8,000 years ago by neolithic humans, who brought their sheep, agriculture, and pottery and drastically changed the life on the islands. The arrival of neolithic humans was followed by the extinction of all surviving Pleistocene island endemic types (including, perhaps, a remnant paleolithic human population on Sardinia). Nikos Symeonidis of Athens University has learned that dwarf elephants were still living on the Greek island of Tilos 7,000 years ago, and neolithic people were using their ivory.

Neolithic humans should not be held entirely responsible for the extinctions. Environmental factors also played a role. The fluctuation of the Pleistocene glaciers caused drastic changes in sea level. When the glaciers melted and the sea level rose, islands may have become too small to supply enough food for a population of mammals. On the other hand, during periods when sea water was trapped in glaciers, islands might have become connected with the mainland—this happened to Sicily at the end of the Pleistocene. Once an island became connected with the mainland, its endemic mammals would have had no chance of surviving since they were easy prey for the large mainland predators. In many cases, however, human population of the islands must have dealt a final blow, and the peculiar mammals vanished, leaving only fossils as a trace of their existence. □

he fossils of at least seven species of deer have been found on Crete. They ranged from ‹varf forms to two of normal size to one that was taller than any known mainland deer. he tall deer may have exploited its habitat much the way a giraffe does. The absence ' dangerous carnivores apparently allowed these species to exhibit unusual mbinations of size and proportion. Small mainland animals, for example, typically ve slender limbs, indicative of fleetness. The island dwarfs, however, had sturdy, ortened limbs, reminiscent of those of large mainland creatures. Conversely, the tall er on Crete had slender limbs, giving it the proportions of a small mainland animal.

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Cover: *The common loon is becoming less common on many northern lakes. Story on page 58. Photograph by Peter M. Roberts; Wildlife Photography.*

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