The Misnamed, Mistreated, and Misunderstood Irish Elk

Nature herself seems by the vast magnitude and stately horns, she has given this creature, to have singled it out as it were, and showed it such regard, with a design to distinguish it remarkably from the common herd of all other smaller quadrupeds.

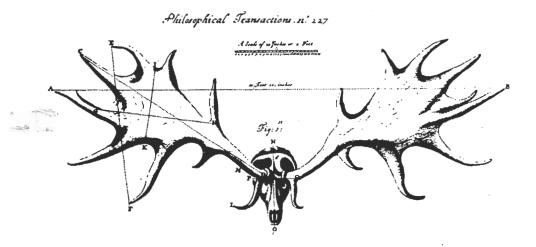
THOMAS MOLYNEUX, 1697

THE IRISH ELK, the Holy Roman Empire, and the English Horn form a strange ensemble indeed. But they share the common distinction of their completely inappropriate names. The Holy Roman Empire, Voltaire tells us, was neither holy, nor Roman, nor an empire. The English horn is a continental oboe; the original versions were curved, hence "angular" (corrupted to English) horn. The Irish Elk was neither exclusively Irish, nor an elk. It was the largest deer that ever lived. Its enormous antlers were even more impressive. Dr. Molyneux marveled at "these spacious horns" in the first published description of 1697. In 1842, Rathke described them in a language unexcelled for the expression of enormity as bewunderungswuerdig. Although the Guiness book of world records ignores fossils and honors the American moose, the antlers of the Irish Elk have never been exceeded, or even approached, in the history of life. Reliable estimates of their total span range up to 12 feet. This figure seems all the more impressive when we recognize that the antlers were probably shed and regrown annually, as in all other true deer.

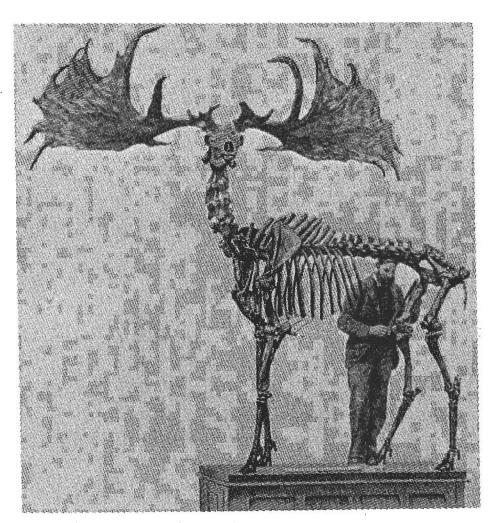
Fossil antlers of the giant deer have long been known in Ireland, where they occur in lake sediments underneath peat deposits. Before attracting the attention of scientists, they had been used as gateposts, and even as a temporary bridge to span a rivulet in County Tyrone. One story, probably apocryphal, tells of a huge bonfire made of their bones and antlers in County Antrim to celebrate the victory over Napoleon at Waterloo. They were called elk because the European moose (an "elk" to Englishmen) was the only familiar animal with antlers that even approached those of the giant deer in size.

The first known drawing of giant deer antlers dates from 1588. Nearly a century later, Charles II received a pair of antlers and (according to Dr. Molyneux) "valued them so highly for their prodigious largeness" that he set them up in the horn gallery of Hampton Court, where they "so vastly exceed" all others in size "that the rest appear to lose much of their curiosity."

Ireland's exclusive claim vanished in 1746 (although the name stuck) when a skull and antlers were unearthed in Yorkshire, England. The first continental discovery followed in



A drawing of the giant deer in Thomas Molyneux's 1697 article shows the antlers incorrectly rotated forward ninety degrees.



A worthy predecessor of the author measures the other end of an Irish Elk. Figure originally published by J. G. Millais in 1897.

1781 from Germany, while the first complete skeleton (still standing in the museum of Edinburgh University) was exhumed from the Isle of Man in the 1820s.

We now know that the giant deer ranged as far east as Siberia and China and as far south as northern Africa. Specimens from England and Eurasia are almost always fragmentary, and nearly all the fine specimens that adorn so many museums throughout the world come from Ireland. The giant deer evolved during the glacial period of the last few million years and may have survived to historic times in continental Europe, but it became extinct in Ireland about 11,000 years ago.

"Among the fossils of the British empire," wrote James Parkinson in 1811, "none are more calculated to excite astonishment." And so it has been throughout the history of paleontology. Putting aside both the curious anecdotes and the sheer wonder that immensity always inspires, the importance of the giant deer lies in its contribution to debates about evolutionary theory. Every great evolutionist has used the giant deer to defend his favored views. The controversy has centered around two main issues: (1) Could antlers of such bulk be of any use? and (2) Why did the giant deer become extinct?

Since debate on the Irish Elk has long centered on the reasons for its extinction, it is ironic that the primary purpose of Molyneux's original article was to argue that it must still be alive. Many seventeenth-century scientists maintained that the extinction of any species would be inconsistent with God's goodness and perfection. Dr. Molyneux's article of 1697 begins:

That no real species of living creatures is so utterly extinct, as to be lost entirely out of the World, since it was first created, is the opinion of many naturalists; and 'tis grounded on so good a principle of Providence taking care in general of all its animal productions, that it deserves our assent.

Yet the giant deer no longer inhabited Ireland, and Molyneux was forced to search elsewhere. After reading traveler's reports of antler size in the American moose, he concluded that the Irish Elk must be the same animal; the tendency toward exaggeration in such accounts is apparently universal and timeless. Since he could find neither figure nor an accurate description of the moose, his conclusions are not as

absurd as modern knowledge would indicate. Molyneux attributed the giant deer's demise in Ireland to an "epidemick distemper," caused by "a certain ill constitution of air."

For the next century arguments raged along Molyneux's line—to which modern species did the giant deer belong? Opinion was equally divided between the moose and the reindeer.

As eighteenth-century geologists unraveled the fossil record of ancient life, it became more and more difficult to argue that the odd and unknown creatures revealed by fossils were all still living in some remote portion of the globe. Perhaps God had not created just once and for all time; perhaps He had experimented continually in both creation and destruction. If so, the world was surely older than the six thousand years that literalists allowed.

The question of extinction was the first great battleground of modern paleontology. In America, Thomas Jefferson maintained the old view, while Georges Cuvier, the great French paleontologist, was using the Irish Elk to prove that extinction did occur. By 1812 Cuvier had resolved two pressing issues: by minute anatomical description, he proved that the Irish Elk was not like any modern animal; and by placing it among many fossil mammals with no modern counterparts, he established the fact of extinction and set the basis for a geologic time scale.

Once the fact of extinction had been settled, debate moved to the time of the event: in particular, had the Irish elk survived the flood? This was no idle matter, for if the flood or some previous catastrophe had wiped out the giant deer, then its demise had natural (or supernatural) causes. Archdeacon Maunsell, a dedicated amateur, wrote in 1825: "I apprehended they must have been destroyed by some overwhelming deluge." A certain Dr. MacCulloch even believed that the fossils were found standing erect, noses elevated—a final gesture to the rising flood, as well as a final plea: don't make waves.

If, however, they had survived the flood, then their exterminating angel could only have been the naked ape himself. Gideon Mantell, writing in 1851, blamed Celtic tribes; in

1830, Hibbert implicated the Romans and the extravagant slaughters of their public games. Lest we assume that our destructive potential was recognized only recently, Hibbert wrote in 1830: "Sir Thomas Molyneux conceived that a sort of distemper, or pestilential murrain, might have cut off the Irish Elks. . . . It is, however, questionable, if the human race has not occasionally proved as formidable as a pestilence in exterminating from various districts, whole races of wild animals."

In 1846, Britain's greatest paleontologist, Sir Richard Owen, reviewed the evidence and concluded that in Ireland at least, the giant deer had perished before man's arrival. By this time, Noah's flood as a serious geologic proposition had passed from the scene. What then had wiped out the giant deer?

Charles Darwin published the *Origin of Species* in 1859. Within ten years virtually all scientists had accepted the *fact* of evolution. But the debate about causes and mechanisms was not resolved (in Darwin's favor) until the 1940s. Darwin's theory of natural selection requires that evolutionary changes be adaptive—that is, that they be useful to the organism. Therefore, anti-Darwinians searched the fossil record for cases of evolution that could not have benefited the animals involved.

The theory of orthogenesis became a touchstone for anti-Darwinian paleontologists, for it claimed that evolution proceeded in straght lines that natural selection could not regulate. Certain trends, once started, could not be stopped even if they led to extinction. Thus certain oysters, it was said, coiled their valves upon each other until they sealed the animal permanently within; saber-toothed "tigers" could not stop growing their teeth or mammoths their tusks.

But by far the most famous example of orthogenesis was the Irish Elk itself. The giant deer had evolved from small forms with even smaller antlers. Although the antlers were useful at first, their growth could not be contained and, like the sorceror's apprentice, the giant deer discovered only too late that even good things have their limits. Bowed by the weight of their cranial excrescences, caught in the trees or mired in the ponds, they died. What wiped out the Irish Elk? They themselves or, rather, their own antlers did.

In 1925, the American paleontologist R. S. Lull invoked the giant deer to attack Darwinism: "Natural selection will not account for overspecialization, for it is manifest that, while an organ can be brought to the point of perfection by selection, it would never be carried to a condition where it is an actual menace to survival . . . [as in] the great branching antlers of the extinct Irish deer."

Darwinians, led by Julian Huxley, launched a counterattack in the 1930s. Huxley noted that as deer get larger—either during their own growth or in the comparison of related adults of different sizes—the antlers do not increase in the same proportion as body size; they increase faster, so that the antlers of large deer are not only absolutely larger but also relatively larger than those of small deer. For such regular and orderly change of shape with increasing size, Huxley used the term allometry.

Allometry provided a comfortable explanation for the giant deer's antlers. Since the Irish Elk had the largest body size of any deer, its relatively enormous antlers could have been a simple result of the allometric relationship present among all deer. We need only assume that increased body size was favored by natural selection; the large antlers might have been an automatic consequence. They might even have been slightly harmful in themselves, but this disadvantage was more than compensated by the benefits of larger size, and the trend continued. Of course, when problems of larger antlers outweighted the advantages of larger bodies, the trend would cease since it could no longer be favored by natural selection.

Almost every modern textbook of evolution presents the Irish Elk in this light, citing the allometric explanation to counter orthogenetic theories. As a trusting student, I had assumed that such constant repetition must be firmly based on copious data. Later I discovered that textbook dogma is self-perpetuating; therefore, three years ago I was disappointed, but not really surprised, to discover that this widely touted explanation was based on no data whatsoever. Aside

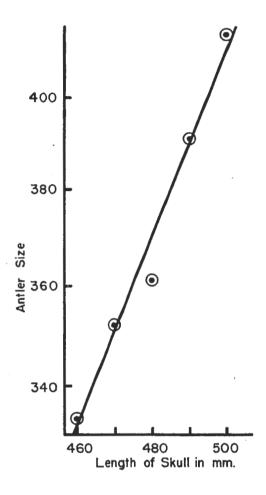
from a few desultory attempts to find the largest set of antlers, no one had ever measured an Irish Elk. Yardstick in hand, I resolved to rectify this situation.

The National Museum of Ireland in Dublin has seventeen specimens on display and many more, piled antler upon antler, in a nearby warehouse. Most large museums in western Europe and America own an Irish Elk, and the giant deer adorns many trophy rooms of English and Irish gentry. The largest antlers grace the entranceway to Adare Manor, home of the Earl of Dunraven. The sorriest skeleton sits in the cellar of Bunratty Castle, where many merry and slightly inebriated tourists repair for coffee each evening after a medieval banquet. This poor fellow, when I met him early the morning after, was smoking a cigar, missing two teeth, and carrying three coffee cups on the tines of his antlers. For those who enjoy invidious comparisons, the largest antlers in America are at Yale; the smallest in the world at Harvard.

To determine if the giant deer's antlers increased allometrically, I compared antler and body size. For antler size, I used a compounded measure of antler length, antler width, and the lengths of major tines. Body length, or the length and width of major bones, might be the most appropriate measure of body size, but I could not use it because the vast majority of specimens consist only of a skull and its attached antlers. Moreover, the few complete skeletons are invariably made up of several animals, much plaster, and an occasional ersatz (the first skeleton in Edinburgh once sported a horse's pelvis). Skull length therefore served as my measure of overall size. The skull reaches its final length at a very early age (all my specimens are older) and does not vary thereafter; it is, therefore, a good indicator of body size. My sample included seventy-nine skulls and antlers from museums and homes in Ireland, Britain, continental Europe, and the United States.

My measurements showed a strong positive correlation between antler size and body size, with the antlers increasing in size two and one-half times faster than body size from small to large males. This is not a plot of individual growth; it is a relationship among adults of different body size. Thus, the allometric hypothesis is affirmed. If natural selection favored large deer, then relatively larger antlers would appear as a correlated result of no necessary significance in itself.

Yet, even as I affirmed the allometric relationship, I began to doubt the traditional explanation—for it contained a curious remnant of the older, orthogenetic view. It assumed that



Graph showing relative increase in antler size with increasing skull length in Irish Elks. Each point is the average for all skulls in a 10 mm. interval of length; the actual data include 81 individuals. Antler size increases more than $2\frac{1}{2}$ times as fast as skull length—a line with a slope of 1.0 (45 degree angle with the x-axis) would indicate equal rates of increase on these logarithmic scales. The slope here is obviously very much higher.

the antlers are not adaptive in themselves and were tolerated only because the advantages of increased body size were so great. But why must we assume that the immense antlers had no primary function? The opposite interpretation is equally possible: that selection operated primarily to increase antler size, thus yielding increased body size as a secondary consequence. The case for inadaptive antlers has never rested on more than subjective wonderment born of their immensity.

Views long abandoned often continue to exert their influence in subtle ways. The orthogenetic argument lived on in the allometric context proposed to replace it. I believe that the supposed problem of "unwieldy" or "cumbersome" antlers is an illusion rooted in a notion now abandoned by students of animal behavior.

To nineteenth-century Darwinians, the natural world was a cruel place. Evolutionary success was measured in terms of battles won and enemies destroyed. In this context, antlers were viewed as formidable weapons to be used against predators and rival males. In his Descent of Man (1871), Darwin toyed with another idea: that antlers might have evolved as ornaments to attract females. "If, then, the horns, like the splendid accounterments of the knights of old, add to the noble appearance of stags and antelopes, they may have been modified partly for this purpose." Yet he quickly added that he had "no evidence in favor of this belief," and went on to interpret antlers according to the "law of battle" and their advantages in "reiterated deadly contests." All early writers assumed that the Irish Elk used its antlers to kill wolves and drive off rival males in fierce battle. To my knowledge this view has been challenged only by the Russian paleontologist L. S. Davitashvili, who asserted in 1961 that the antlers functioned primarily as courtship signals to females.

Now, if antlers are weapons, the orthogenetic argument is appealing, for I must admit that ninety pounds of broadpalmed antler, regrown annually and spanning twelve feet from tip to tip, seems even more inflated than our current military budget. Therefore, to preserve a Darwinian explanation, we must invoke the allometric hypothesis in its original form.

But what if antlers do not function primarily as weapons? Modern studies of animal behavior have generated an exciting concept of great importance to evolutionary biology: many structures previously judged as actual weapons or devices for display to females are actually used for ritualized combat among males. Their function is to prevent actual battle (with consequent injuries and loss of life) by establishing hierarchies of dominance that males can easily recognize and obey.

Antlers and horns are a primary example of structures used for ritualized behavior. They serve, according to Valerius Geist, as "visual dominance-rank symbols." Large antlers confer high status and access to females. Since there can be no evolutionary advantage more potent than a guarantee of successful reproduction, selective pressures for larger antlers must often be intense. As more and more horned animals are observed in their natural environment, older ideas of deadly battle are yielding to evidence of purely ritualized display without body contact, or fighting in ways clearly designed to prevent bodily injury. This has been observed in red deer by Beninde and Darling, caribou by Kelsall, and in mountain sheep by Geist.

As devices for display among males, the enormous antlers of the Irish Elk finally make sense as structures adaptive in themselves. Moreover, as R. Coope of Birmingham University pointed out to me, the detailed morphology of the antlers can be explained, for the first time, in this context. Deer with broad-palmed antlers tend to show the full width of their antlers in display. The modern fallow deer (considered by many as the Irish Elk's nearest living relative) must rotate its head from side to side in order to show its palm. This would have created great problems for giant deer, since the torque produced by swinging ninety-pound antlers would have been immense. But the antlers of the Irish Elk were arranged to display the palm fully when the animal looked straight ahead. Both the unusual configuration and the enormous size of the antlers can be explained by postulating that they were used for display rather than for combat.

If the antlers were adaptive, why did the Irish Elk become

extinct (at least in Ireland)? The probable answer to this old dilemma is, I am afraid, rather commonplace. The giant deer flourished in Ireland for only the briefest of times—during the so-called Alleröd interstadial phase at the end of the last glaciation. This period, a minor warm phase between two colder epochs, lasted for about 1,000 years, from 12,000 to 11,000 years before the present. (The Irish Elk had migrated to Ireland during the previous glacial phase when lower sea levels established a connection between Ireland and continental Europe.) Although it was well adapted to the grassy, sparsely wooded, open country of Alleröd times, it apparently could not adapt either to the subarctic tundra that followed in the next cold epoch or to the heavy forestation that developed after the final retreat of the ice sheet.

Extinction is the fate of most species, usually because they fail to adapt rapidly enough to changing conditions of climate or competition. Darwinian evolution decrees that no animal shall actively develop a harmful structure, but it offers no guarantee that useful structures will continue to be adaptive in changed circumstances. The Irish Elk was probably a victim of its own previous success. Sic transit gloria mundi.