



Evolutionary biology is a field plagued by more misunderstanding and misrepresentation than practically any other in science. Adaptive evolution by natural selection is a simple concept, yet the ways in which selection operates are exceedingly subtle and the patterns it generates are easy to misinterpret. Especially in India, the meagre treatment that evolution gets in biology curricula is rife with misinterpretations and over-simplifications; it is also shockingly out of date by over half a century. Stephen Jay Gould wrote extensively and elegantly about misunderstandings of pattern and process in evolution. In the essay reproduced here, which appears as Chapter 11 in *'Bully for Brontosaurus'*, he takes up the tale of the evolution of modern horses, a tale that is familiar to most of us from high school biology texts. Gould shows in his inimitable style how the prejudiced notion of evolution leading to some kind of clear progression up a ladder of increasing perfection was projected onto the data on fossil horses, leading to figures reproduced in biology texts world-wide as canonical examples of adaptive evolution that are, nevertheless, plain wrong.

Amitabh Joshi

Life's Little Joke

Stephen Jay Gould

I STILL DON'T UNDERSTAND why a raven is like a writing desk, but I do know what binds Hernando Cortés and Thomas Henry Huxley together.

On February 18, 1519, Cortés set sail for Mexico with about 600 men and, perhaps more important, 16 horses. Two years later, the Aztec capital of Tenochtitlán lay in ruins, and one of the world's great civilizations had perished.

Cortés's victory has always seemed puzzling, even to historians of an earlier age who did not doubt the intrinsic superiority of Spanish blood and Christian convictions. William H Prescott, master of this tradition, continually emphasizes Cortés's diplomatic skill in making alliances to divide and conquer – and his good fortune in despoiling Mexico during a period of marked internal dissension among the Aztecs and their vassals. (Prescott published his *History of the Conquest of Mexico* in 1843; it remains among the most exciting and literate books ever written.)

Prescott also recognized Cortés's two "obvious advantages on the score of weapons" – one inanimate and one animate. A gun is formidable enough against an obsidian blade, but

consider the additional impact of surprise when your opponent has never seen a firearm. Cortés's cavalry, a mere handful of horses and their riders, caused even more terror and despair, for the Aztecs, as Prescott wrote,

had no large domesticated animals, and were unacquainted with any beast of burden. Their imaginations were bewildered when they beheld the strange apparition of the horse and his rider moving in unison and obedient to one impulse, as if possessed of a common nature; and as they saw the terrible animal, with "his, neck clothed in thunder," bearing down their squadrons and trampling them in the dust, no wonder they should have regarded him with the mysterious terror felt for a supernatural being.

On the same date, February 18, in 1870, Thomas Henry Huxley gave his annual address as president of the Geological Society of London and staked his celebrated claim that Darwin's ideal evidence for evolution had finally been uncovered in the fossil record of horses – a sequence of continuous transformation, properly arrayed in temporal order:

It is easy to accumulate probabilities – hard to make out some particular case, in such a way that it will stand rigorous criticism. After much search, however, I think that such a case is to be made out in favor of the pedigree of horses.

Huxley delineated the famous trends to fewer toes and higher-crowned teeth that we all recognize in this enduring classic among evolutionary case histories. Huxley viewed this lineage as a European affair, proceeding from fully three-toed, *Anchitherium*, to, *Hipparion* with side toes “reduced to mere dew-claws [that] do not touch the ground,” to modern *Equus*, where, “finally, the crowns of the grinding-teeth become longer... . The phalanges of the two outer toes in each foot disappear, their metacarpal and metatarsal bones being left as the ‘splints’.”

In *Cat's Cradle*, Kurt Vonnegut speaks of the subtle ties that can bind people across worlds and centuries into aggregations forged by commonalities so strange that they must be meaningful. Cortés and Huxley must belong to the same karass (Vonnegut's excellent word for these associations) – for they both, on the same date, unfairly debased America with the noblest of animals. Huxley was wrong and Cortés, by consequence, was ever so lucky.

Horses evolved in America, through a continuity that extends unbroken across 60 million years. Several times during this history, different branches migrated to Europe, where Huxley arranged three (and later four) separate incursions as a false continuity. But horses



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then died in America at the dawn of human history in our hemisphere, leaving the last European migration as a source of recolonization by conquest. Huxley's error became Montezuma's sorrow, as an animal more American than Babe Ruth or apple pie came home to destroy her greatest civilization. (Montezuma's revenge would come later, and by another route.)

During our centennial year of 1876, Huxley visited America to deliver the principal address for the founding of Johns Hopkins University. He stopped first at Yale to consult the eminent paleontologist Othniel C Marsh. Marsh, ever gracious, offered Huxley an architectural tour of the campus, but Huxley had come for a purpose and would not be delayed. He pointed to the buildings and said to Marsh: "Show me what you have got inside them; I can see plenty of bricks and mortar in my own country." Huxley was neither philistine nor troglodyte; he was simply eager to study some particular fossils: Marsh's collection of horses.

Two years earlier, Marsh had published his phylogeny of American horses and identified our continent as the center stage, while relegating Huxley's European sequence to a periphery of discontinuous migration. Marsh began with a veiled and modest criticism (*American Journal of Science*, 1874):

Huxley has traced successfully the later genealogy of the horse through European extinct forms, but the line in America was probably a more direct one, and the record is more complete.

Later, he stated more baldly (p.258): "The line of descent appears to have been direct, and the remains now known supply every important intermediate form."

Marsh had assembled an immense collection from the American West (prompted largely by a race for priority in his bitter feud with Edwin D Cope – see Essay 5 for another consequence of this feud!). For every query, every objection that Huxley raised, Marsh produced a specimen. Leonard Huxley describes the scene in his biography of his father:

At each inquiry, whether he had a specimen to illustrate such and such a point or to exemplify a transition from earlier and less specialized forms to later and more specialized ones, Professor Marsh would simply turn to his assistant and bid him fetch box number so and so, until Huxley turned upon him and said, "I believe you are a magician; whatever I want, you just conjure it up."

Years before, T H Huxley had coined a motto; now he meant to live by it: "Sit down before fact as a little child, be prepared to give up every preconceived notion." He capitulated to Marsh's theory of an American venue. Marsh, with growing pleasure and retreating

modesty, reported his impression of personal triumph:

He [Huxley] then informed me that this was new to him, and that my facts demonstrated the evolution of the horse beyond question, and for the first time indicated the direct line of descent of an existing animal. With the generosity of true greatness, he gave up his own opinions in the face of new truth and took my conclusions.

A few days later, Huxley was, if anything, more convinced. He wrote to Marsh from Newport, his next stop: "The more I think of it the more clear it is that your great work is the settlement of the pedigree of the horse." But Huxley was scheduled to lecture on the evolution of horses less than a month later in New York. As he traveled about eastern America, Huxley rewrote his lecture from scratch. He also enlisted Marsh's aid in preparing a chart that would show the new evidence to his New York audience in pictorial form. Marsh responded with one of the most famous illustrations in the history of paleontology – the first pictorial pedigree of the horse.

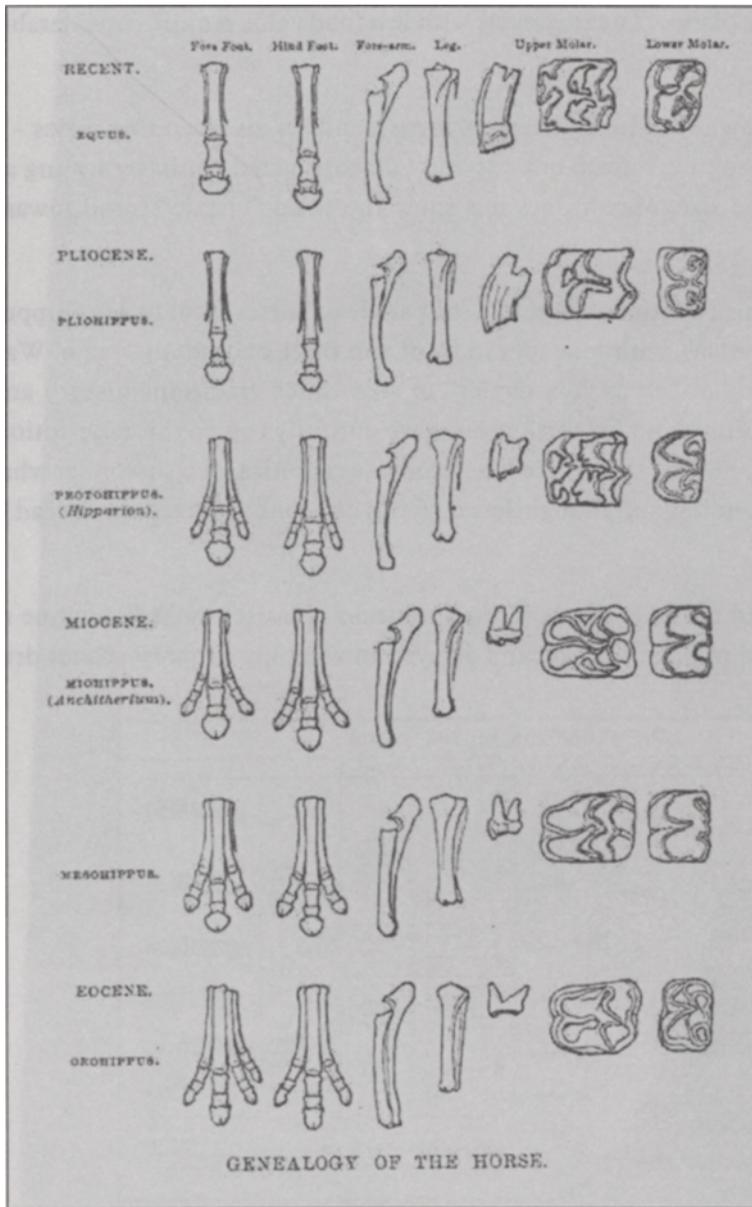
Scholars are trained to analyze words. But primates are visual animals, and the key to concepts and their history often lies in iconography. Scientific illustrations are not frills or summaries; they are foci for modes of thought. The evolution of horse – both in textbook charts and museum exhibits – has a standard iconography. Marsh began this traditional display in his illustration for Huxley. In so doing he also initiated an error that captures pictorially the most common of all misconceptions about the shape and pattern of evolutionary change.

Errors in science are diverse enough to demand a taxonomy of categories. Some make me angry, particularly those that arise from social prejudice, masquerade as objectively determined truth, and directly limit the lives of those caught in their thrall (scientific justifications for racism and sexism, as obvious examples). Others make me sad because honest effort ran headlong into unresolvable complexities of nature. Still others, as errors of logic that should not have occurred, bloat my already extended ego when I discover them. But I reserve a special place in perverse affection for a small class of precious ironies – errors that pass nature through a filter of expectation and reach a particular conclusion only because nature really works in precisely and unlikely, but bear with me for the premier example of life's little joke – as displayed in conventional iconography (and interpretation) for the most famous case study of all, the evolution of the horse.

In his original 1874 article, Marsh recognized the three trends that define our traditional view of old dobbin's genealogy: increase in size, decrease in the number of toes (with the



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The celebrated original figure drawn by O C Marsh for T H Huxley's New York lecture on the evolution of horses. This version appeared in an article by Marsh in the American Journal of Science for 1879. NEG. NO. 123823. Courtesy Department of Library Services, American Museum of Natural History.

hoof of modern horses made from a single digit, surrounded by two vestigial splints as remnants of side toes), and increase in the height and complexity of grinding teeth. (I am not treating the adaptive significance of these changes here, but wish to record the conventional explanation for the major environmental impetus behind trends in locomotion and dentition: a shift from browsing on lush lowland vegetation to grazing of newly

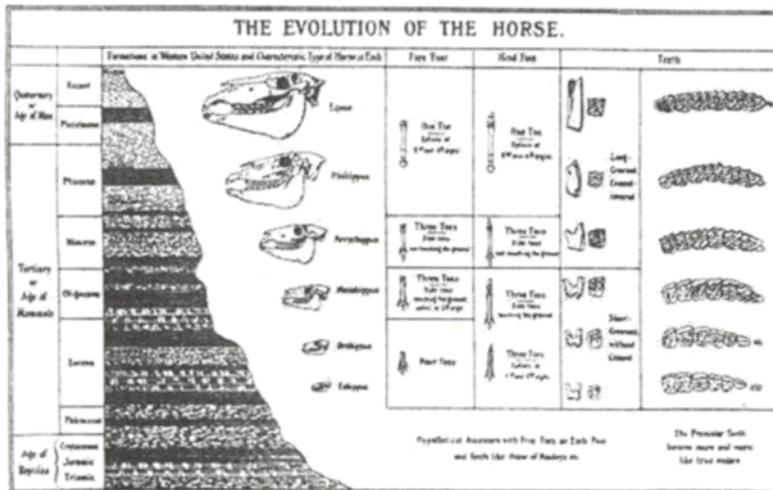
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evolved grasses upon drier plains. Tough grasses with less food value require considerably more dental effort.)

Marsh's famous chart, drawn for Huxley, depicts these trends as an ascending series – a ladder of uninterrupted progress toward one toe and tall, corrugated teeth (by scaling all his specimens to the same size, Marsh does not show the third “classic” trend toward increasing bulk).

We are all familiar with this traditional picture – the parade of horses from little eohippus (properly called *Hyracotherium*), with four toes in front and three behind, to Man o' War. (*Hyracotherium* is always described as “fox terrier” in size. Such traditions disturb and captivate me. I know nothing about fox terriers but have dutifully copied this description. I wonder who said it first, and why this simile has become so canonical. I also wonder what the textbook tradition of endless and thoughtless copying has done to retard the spread of original ideas.*)

In conventional charts and museum displays, the evolution of horses looks like a line of schoolchildren all pointed in one direction and arrayed in what my primary-school drill



Most widely reproduced of all illustrations showing the evolution of horses as a ladder towards progress. Note increase in skull size, decrease in the number of toes, and increase in the height of the teeth. The skulls are also arranged in stratigraphic order. WD Matthew used this illustration in several publications. This version comes from an article in the Quarterly Review of Biology for 1926. NEG NO. 37969. Courtesy Department of Library Services, American Museum of Natural History.

* This parenthetical inspired Roger Angell's letter and led directly to research and writing of the essay preceding this piece.

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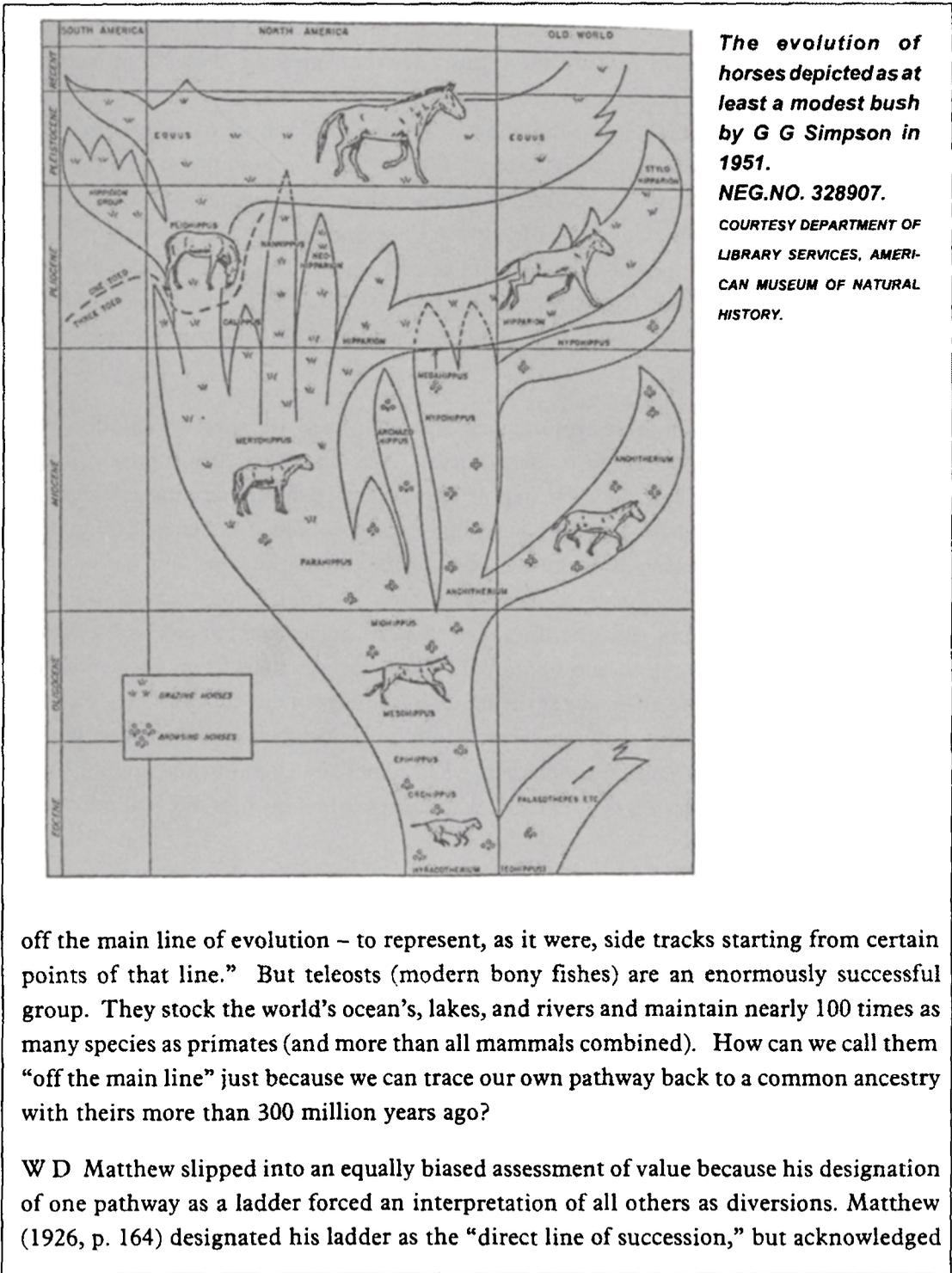
instructors called “size place” (also stratigraphic order in this case). The most familiar of all illustrations, first drawn early in the century for the American Museum of Natural History’s pamphlet on the evolution of horses, by W D Matthew, but reproduced hundreds of times since then, shows the whole story: size, toes, and teeth arranged in a row by order of appearance in the fossil record. To cite just one example of this figure’s influence, George W Hunter reproduced Matthew’s chart as the primary illustration of evolution in his high-school textbook of 1914, *A Civic Biology*. John Scopes assigned this book to his classes in Tennessee and was convicted for teaching its chapters on evolution, as William Jennings Bryan issued his last hurrah (see Essay 28): “No more repulsive doctrine was ever proclaimed by man ... may heaven defend the youth of our land from [these] impious babblings.”

But what is so wrong with these evolutionary ladders? Surely we can trace an unbroken continuity from *Hyracotherium* to modern horses. Yes, but continuity comes in many more potential modes than the lock step of the ladder. Evolutionary genealogies are copiously branching bushes – and the history of horses is more lush and labyrinthine than most. To be sure, *Hyracotherium* is the base of the trunk (as now known), and *Equus* is the surviving twig. We can, therefore, draw a pathway of connection from a common beginning to a lone result. But the lineage of modern horses is a twisted and tortuous excursion from one branch to another, a path more devious than the road marked by Ariadne’s thread from the Minotaur at the center to the edge of our culture’s most famous labyrinth. Most important, the path proceeds not by continuous transformation but by lateral stepping (with geological suddenness when punctuated equilibrium applies, as in this lineage, at least as read by yours truly, who must confess his bias as coauthor of the theory).

Each lateral step to a new species follows one path among several alternatives. Each extended lineage becomes a set of decisions at branching points – only one among hundreds of potential routes through the labyrinth of the bush. There is no central direction, no preferred exit to this maze – just a series of indirect pathways to every twig that ever graced the periphery of the bush.

As an example of distortions imposed by converting tortuous paths through bushes into directed ladders, consider the men associated with the two classical iconographies reproduced here. When Huxley made his formal capitulation to Marsh’s interpretation in print (1880), he extended the ladder of horses as a metaphor for all vertebrates. Speaking of modern reptiles and teleost fishes, Huxley wrote (1880, p.61): “They appear to me to be

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The evolution of horses depicted as at least a modest bush by G G Simpson in 1951.

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off the main line of evolution – to represent, as it were, side tracks starting from certain points of that line.” But teleosts (modern bony fishes) are an enormously successful group. They stock the world’s ocean’s, lakes, and rivers and maintain nearly 100 times as many species as primates (and more than all mammals combined). How can we call them “off the main line” just because we can trace our own pathway back to a common ancestry with theirs more than 300 million years ago?

W D Matthew slipped into an equally biased assessment of value because his designation of one pathway as a ladder forced an interpretation of all others as diversions. Matthew (1926, p. 164) designated his ladder as the “direct line of succession,” but acknowledged

that “there are also a number of side branches, more or less closely related.” Three pages later, Matthew adds the opprobrium of near indecency to his previous charge of mere laterality, as he describes (p. 167) “a number of side branches leading up in a similar manner to aberrant specialized Equidae now extinct.” But in what way are extinct lineages more specialized than a modern horse or in any sense more peculiar? Their historical death is the only possible rationale for a designation of aberrancy, but more than 99 percent of all species that ever lived are extinct – and disappearance cannot be the biological equivalent of a scarlet letter. We might as well call modern horses aberrant because, much to Montezuma's later sorrow, they became extinct in the land of their birth.

Yet we have recognized the bushiness of horse evolution from the very beginning. How else did Marsh forestall Huxley but by convincing him that his European “genealogy” of horses formed a stratigraphic sequence of discontinuous stages, falsely linking several side branches that had disappeared without issue?

As an example of bushiness, and a plug for the value of appropriate metaphors in general, consider the finest book on the evolution of horses ever written for popular audiences – G G Simpson's *Horses* (1951). Simpson redrew the genealogy of horses as a modest bush with no preferred main line. He also criticized the conceptual lock, imposed by the bias of the ladder when he noted that modern one-toed horses are a side branch and extinct three-toed creatures the main line (if any center can be designated at all).

As nearly as there is a straight line in horse evolution, it culminated and ended with these animals [the three-toed anchitheres], which, like their ancestors, were multiple-toed browsers. From this point of view, it is the line leading to modern horses that was the side branch, even though it outlasted the straighter line of horse evolution [p. 130].

Yet Simpson, who held a lifelong commitment to the predominant role of evolution by transformational change within populations rather than by accumulation across numerous events of discrete, branching speciation, could not entirely let go of biases, imposed by the metaphor of the ladder. In one revealing passage, he accepts bushiness, but bemoans the complexities thus introduced, as though they clouded evolution's essence of transformational change:

Miohippus ... intergraded with several different descendant groups. It is sad that this introduces possible confusion into the story, but there is not much point in criticizing nature for something that happened some millions of years ago. It would also be foolish to try to ignore the complications, which did occur and which are a very important part of the record.

But these “complications” are not a veil upon the essence of lineal descent; they are the primary stuff of evolution itself.

Moreover, Simpson restricted his bushiness as much as possible and retained linearity wherever he could avoid an inference of branching. In particular, he proposes the specific and testable hypothesis (see his illustration) that the early part of the record – the sequence of *Hyracotherium*–*Orohippus*–*Epihippus*–*Mesohippus*–*Miohippus*–*Hypohippus* – tells a story of linear descent, only later interrupted by copious branching among three-toed browsers: “The line from *Eohippus* to *Hypohippus*, for example, exemplifies a fairly continuous phyletic evolution” (p. 217). Simpson especially emphasizes the supposedly gradual and continuous transformation from *Mesohippus* to *Miohippus* near the top of this sequence:

The more progressive horses of the middle Oligocene and all the horses of the late Oligocene are placed by convention in a separate genus, Miohippus. In fact Mesohippus and Miohippus intergrade so perfectly and the differences between them are so slight and variable that even experts find it difficult, at times nearly impossible, to distinguish them clearly.

The enormous expansion of collections since Simpson proposed this hypothesis has permitted a test by vertebrate paleontologists Don Prothero and Neil Shubin. Their results falsify Simpson’s gradual and linear sequence for the early stages of horse evolution and introduce extensive bushiness into this last stronghold of the ladder.

Prothero and Shubin have made four major discoveries in the crucial segment of history that Simpson designated as the strongest case for a gradualistic sequence of lineal transformation – the transition from *Mesohippus* to *Miohippus*.

1. Previous experts were so convinced about the imperceptibly gradual transition between these two genera that they declared any search for distinguishing characters as vain, and arbitrarily drew the division between *Mesohippus* and *Miohippus* at a stratigraphic boundary. But far richer material available to Prothero and Shubin has permitted the identification of characters that cleanly distinguish the two genera. (Teeth are the hardest part of a vertebrate skeleton and the fossil record of mammals often contains little else. A technical course in the evolution of mammals is largely an exercise in the identification of teeth, and an old professional quip holds that mammalian evolution is the interbreeding of two sets of teeth to produce some slightly modified descendant choppers. *Miohippus* and *Mesohippus* do not have distinctive dentitions, and previous failure to find a clear separation should not surprise us. The new material is rich in skull and limb bones.) In particular, Prothero



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and Shubin found that *Miohippus* develops a distinctive articulation, absent in ancestral *Mesohippus*, between the enlarging third metatarsal (the foot bone of the digit that will become the entire hoof of modern horses) and the cuboid bone of the tarsus (ankle) above.

2. *Mesohippus* does not turn into *Miohippus* by insensible degrees of gradual transition. Rather, *Miohippus* arises by branching from a *Mesohippus* stock that continues to survive long afterward. The two genera overlap in time by at least 4 million years.

3. Each genus is itself a bush of several related species, not a rung on a ladder of progress. These species often lived and interacted in the same area at the same time (as different species of zebra do in Africa today). One set of strata in Wyoming, for example, has yielded three species of *Mesohippus* and two of *Miohippus*, all contemporaries.

4. The species of these bushes tend to arise with geological suddenness, and then to persist with little change for long periods. Evolutionary change occurs at the branch points themselves and trends are not continuous marches up ladders, but concatenations of increments achieved at nodes of branching on evolutionary bushes. Of this phenomenon Prothero and Shubin write:

There is no evidence of long-term changes within these well-defined species [of Mesohippus and Miohippus] through time. Instead, they are strikingly static through millions of years. Such stasis is apparent in most Neogene [later] horses as well, and in Hyracotherium. This is contrary to the widely-held myth about horse species as gradualistically varying parts of a continuum, with no real distinctions between species. Throughout the history of horses, the species are well-marked and static over millions of years. At high resolution, the gradualistic picture of horse evolution becomes a complex bush of overlapping, closely related species.

Bushiness now pervades the entire phylogeny of horses.

We can appreciate this fundamental shift in iconography and meaning, but where is the “precious irony” that I promised? What is “life’s little joke” of my title? Simply this. The model of the ladder is much more than merely wrong. It never could provide the promised illustration of evolution progressive and triumphant – for *it could only be applied to unsuccessful lineages.*

Bushes represent the proper topology of evolution. Ladders are false abstractions, made by running a steamroller over a labyrinthine pathway that hops from branch to branch through a phylogenetic bush. We cannot force a successful bush of evolution into a ladder



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because we may follow a thousand pathways through the maze of twigs, and we cannot find a criterion for preferring one route over another. Who ever heard of the evolutionary trend of rodents or of bats or of antelopes? Yet these are the greatest success stories in the history of mammals. Our proudest cases do not become our classic illustrations because we can draw no ladder of progress through a vigorous bush with hundreds of surviving twigs.

But consider the poor horses. Theirs was once a luxuriant bush, yet they barely survive today. Only one twig (the genus *Equus*, with horses, zebras, and asses) now carries all the heritage of a group that once dominated the history of hoofed mammals – and with fragility at that, for *Equus* died in the land of its birth and had to be salvaged from a stock that had migrated elsewhere. (In a larger sense, horses form one of three dwindling lines – tapirs and rhinos are the others – that now represent all the diversity of the formerly dominant order Perissodactyla, or odd-toed ungulates, among hoofed mammals. This mighty group once included the giant titanotheres, the clawed chalicotheres, and *Baluchitherium*, the largest land mammal that ever lived. It now hangs on as a remnant in a world increasingly dominated by the Artiodactyla, or even-toed ungulates – cows, deer, antelope, camels, hippos, giraffes, pigs, and their relatives.)

This is life's little joke. By imposing the model of the ladder upon the reality of bushes, we have guaranteed that our classic examples of evolutionary progress can only apply to unsuccessful lineages on the very brink of extermination – for we can linearize a bush only if it maintains but one surviving twig that we can falsely place at the summit of a ladder. I need hardly remind everybody that at least one other mammalian lineage, preeminent among all in our attention and concern, shares with horses the sorry state of reduction from a formerly luxuriant bush to a single surviving twig – the very property of extreme tenuousness that permits us to build a ladder reaching only to the heart of our own folly and hubris.

Acknowledgements

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