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Stephen Jay Gould: *Hooking Leviathan by Its Past*

THE LANDSCAPE of every career contains a few crevasses*, and usually a more extensive valley or two – for every Ruth's bat a Buckner's legs; for every lopsided* victory at Agincourt, a bloodbath at Antietam. Darwin's *Origin of Species* contains some wonderful insights and magnificent lines, but this masterpiece also includes a few notable clunkers*. Darwin experienced most embarrassment from the following passage, curtailed* and largely expunged* from later editions of his book:

In North America the black bear was seen by Hearne swimming for hours with widely open mouth, thus catching, like a whale, insects in the water. Even in so extreme a case as this, if the supply of insects were constant, and if better adapted competitors did not already exist in the country, I can see no difficulty in a race of bears being rendered*, by natural selection, more aquatic in their structure and habits, with larger and larger mouths, till a creature was produced as monstrous as a whale.

Why did Darwin become so chagrined* about this passage? His hypothetical tale may be pure speculation and conjecture, but the scenario is not entirely absurd. Darwin's discomfort arose, I think, from his failure to follow a scientific norm of a more sociocultural nature. Scientific conclusions supposedly rest upon facts and information. Speculation is not entirely taboo, and may sometimes be necessary *faute de mieux*. But when scientists propose truly novel and comprehensive* theories – as Darwin tried to do in advancing natural selection as the primary mechanism of evolution – they need particularly good support, and invented hypothetical cases just don't supply sufficient confidence for crucial conclusions.

Natural selection (or the human analogue of differential breeding) clearly worked at small scale* – in the production of dog breeds and strains of wheat, for example. But could such a process account for the transitions of greater scope* that set our concept of evolution in the fullness of time – the passage of reptilian lineages to birds and mammals; the origin of humans from an ancestral stock* of apes? For these larger changes, Darwin could provide little direct evidence, for a set of well-known and much-lamented reasons based on the extreme spottiness* of the fossil record.

Some splendid cases began to accumulate in years following the *Origin of Species*, most notably the discovery of *Archaeopteryx*, an initial bird chock-full of reptilian features*, in 1861; and the first findings of human fossils late in the nineteenth century. But Darwin had little to present in his first edition of 1859, and he tried to fill this factual gap with hypothetical fables about swimming bears eventually turning into whales – a fancy* that yielded far more trouble in easy ridicule than aid in useful illustration. Just two years after penning his bear-to-whale tale, Darwin lamented to a friend (letter to James Lamont, February 25, 1861), “It is laughable how often I have been attacked and misrepresented about this bear.”

The supposed lack of intermediary forms in the fossil record remains the fundamental canard of current antievolutionism. Such transitional forms are sparse, to be sure, and for two sets of good reasons – geological (the gappiness* of the fossil record) and biological (the episodic nature of evolutionary change, including patterns of punctuated equilibrium*, and transition within small populations of limited geographic extent). But paleontologists have discovered several superb examples of intermediary forms and sequences, more than enough to convince any fair-minded skeptic about the reality of life's physical genealogy.

The first “terrestrial” vertebrates retained six to eight digits on each limb (more like a fish paddle than a hand), a persistent tailfin, and a lateral-line system for sensing sound vibrations underwater. The anatomical transition from reptiles to mammals is particularly well documented in the key anatomical change of jaw articulation* to hearing bones. Only one bone, called the dentary, builds the mammalian jaw, while reptiles retain several small bones in the rear portion of the jaw. We can trace, through a lovely sequence of intermediates, the reduction of these small reptilian bones, and their eventual disappearance or exclusion from the jaw, including the remarkable passage of the reptilian articulation bones into the mammalian middle ear (where they became our malleus and incus, or hammer and anvil). We have even found the transitional form that creationists often proclaim inconceivable in theory – for how can jawbones become ear bones if intermediaries must live with an unhinged* jaw before the new joint* forms? The transitional species maintains a double jaw joint, with both the old articulation of reptiles (quadrate to articular bones) and the new connection of mammals (squamosal to dentary) already in place! Thus, one joint could be lost, with passage of its bones into the ear, while the other articulation continued to guarantee a properly hinged jaw.

Still, our creationist incubi*, who would never let facts spoil* a favorite argument, refuse to yield, and continue to assert* the absence of *all* transitional forms by ignoring those that have been found, and continuing to taunt* us with admittedly frequent examples of absence. Darwin's old case for the origin of whales remains a perennial favorite, for if Darwin had to invent a fanciful swimming bear, and if paleontologists haven't come to the rescue by discovering an intermediary form with functional legs and potential motion on land, then Jonah's scourge* may gobble* up the evolutionary heathens as well. God's taunt to Job might be sounded again: "Canst thou draw out leviathan with an hook?" (The biblical Leviathan is usually interpreted as a crocodile, but many alternate readings favor whales.)

Every creationist book on my shelf cites the actual absence and inherent inconceivability of transitional forms between terrestrial mammals and whales. Alan Haywood, for example, writes in his *Creation and Evolution* (see bibliography):

Darwinists rarely mention the whale because it presents them with one of their most insoluble problems. They believe that somehow a whale must have evolved from an ordinary land-dwelling animal, which took to the sea and lost its legs ... A land mammal that was in process of becoming a whale would fall between two stools – it would not be fitted for life on land or at sea, and would have no hope of survival.

Duane Gish, creationism's most ardent debater, makes the same argument in his more colorful style (*Evolution: The Challenge of the Fossil Record*):

There simply are no transitional forms in the fossil record between the marine mammals and their supposed land mammal ancestors ... It is quite entertaining, starting with cows, pigs, or buffaloes, to attempt to visualize what the intermediates may have looked like. Starting with a cow, one could even imagine one line of descent which prematurely became extinct, due to what might be called an "udder failure."

The most "sophisticated"* (I should really say "glossy"*) of creationist texts, *Of Pandas and People* by P. Davis, D. H. Kenyon, and C. B. Thaxton says much the same, but more in the lingo of academesese:

The absence of unambiguous transitional fossils is strikingly illustrated by the fossil record of whales ... If whales did have land mammal ancestors, we should expect to find some transitional fossils. Why? Because the anatomical differences between whales and terrestrial mammals are so great that innumerable in-between stages must have paddled and swam the ancient seas before a whale as we know it appeared. So far these transitional forms have not been found.

Three major groups of mammals have returned to the ways of distant ancestors in their seafaring modes of life (while smaller lineages within several other mammalian orders have become at least semi-aquatic, often to a remarkable degree, as in river and sea otters): the suborder Pinnepedia (seals, sea lions, and walruses) within the order Carnivora (dogs, cats, and Darwin's bears among others); and two entire orders – the Sirenia (dugongs and manatees) and Cetacea (whales and dolphins). I confess that I have never quite grasped the creationists' point about inconceivability of transition – for a good structural (though admittedly not a phylogenetic) series of intermediate anatomies may be extracted from these groups. Otters have remarkable aquatic abilities, but retain fully functional limbs for land. Sea lions are clearly adapted for water, but can still flop about on land with sufficient dexterity to negotiate* ice floes, breeding grounds, and circus rings.

But I admit, of course, that the transition to manatees and whales represents no trivial extension, for these fully aquatic mammals propel themselves by powerful, horizontal tail flukes and have no visible hind limbs at all – and how can a lineage both develop a flat propulsive tail from the standard mammalian length of rope, and then forfeit* the usual equipment of back feet so completely? (Sirenians have lost every vestige of back legs; whales often retain tiny, splintlike pelvic and leg bones, but no foot or finger bones, embedded in musculature of the body wall, but with no visible expression in external anatomy.)

The loss of back legs, and the development of flukes, fins, and flippers by whales, therefore stands as a classic case of a supposed cardinal problem in evolutionary theory – the failure to find intermediary fossils for major anatomical transitions, or even to imagine how such a bridging form might look or work. Darwin acknowledged the issue by constructing a much-criticized fable about swimming bears, instead of

presenting any direct evidence at all, when he tried to conceptualize the evolution of whales. Modern creationists continue to use this example and stress the absence of intermediary forms in this supposed (they would say impossible) transition from land to sea.

Goethe told us to “love those who yearn* for the impossible.” But Pliny the Elder, before dying of curiosity by straying too close to Mount Vesuvius at the worst of all possible moments, urged us to treat impossibility as a relative claim: “How many things, too, are looked upon as quite impossible until they have been actually effected.” Armed with such wisdom of human ages, I am absolutely delighted to report that our usually recalcitrant fossil record has come through in exemplary fashion. During the past fifteen years, new discoveries in Africa and Pakistan have greatly added to our paleontological knowledge of the earliest history of whales. The embarrassment of past absence has been replaced by a bounty of new evidence – and by the sweetest series of transitional fossils an evolutionist could ever hope to find. Truly, we have met* the enemy and he is now ours. Moreover, to add blessed insult to the creationists’ injury*, these discoveries have arrived in a gradual and sequential fashion – a little bit at a time, step by step, from a tentative hint fifteen years ago to a remarkable smoking gun early in 1994. Intellectual history has matched life’s genealogy by spanning the gaps in sequential steps. Consider the four main events in chronological order.

CASE ONE. *Discovery of the oldest whale*. Paleontologists have been fairly confident, since Leigh Van Valen’s demonstration in 1966, that whales descended from mesonychids, an early group of primarily carnivorous running mammals that spanned a great range of sizes and habits from eating fishes at river edges to crushing bones of carrion. Whales must have evolved during the Eocene epoch, some 50 million years ago, because Late Eocene and Oligocene rocks already contain fully marine cetaceans, well past any point of intermediacy.

In 1983, my colleague Phil Gingerich from the University of Michigan, along with N. A. Wells, D. E. Russell, and S. M. Ibrahim Shah, reported their discovery of the oldest whale, named *Pakicetus* to honor its country of present residence, from Middle Eocene sediments some 52 million years old in Pakistan. In terms of intermediacy, one could hardly have hoped for more from the limited material available, for* only the skull of *Pakicetus* has been found. The teeth strongly resemble those of terrestrial mesonychids, as anticipated, but the skull, in feature after feature, clearly belongs to the developing lineage of whales.

Both the anatomy of the skull, particularly in the ear region, and the inferred habitat of the animal in life, testify to transitional status. The ears of modern whales contain modified bones and passageways that permit directional hearing in the dense medium of water. Modern whales have also evolved enlarged sinuses that can be filled with blood to maintain pressure during diving. The skull of *Pakicetus* lacks both these features, and this first whale could neither dive deeply nor hear directionally with any efficiency in water.

In 1993, J. G. M. Thewissen and S. T. Hussain affirmed these conclusions and added more details on the intermediacy of skull architecture in *Pakicetus*. Modern whales achieve much of their hearing through their jaws, as sound vibrations pass through the jaw to a “fat pad” (the technical literature, for once, invents no jargon and employs the good old English vernacular in naming this structure), and thence to the middle ear. Terrestrial mammals, by contrast, detect most sound through the ear hole (called the “external auditory meatus,” which means the same thing in more refined language). Since *Pakicetus* lacked the enlarged jaw hole that holds the fat pad, this first whale probably continued to hear through the pathways of its terrestrial ancestors. Gingerich concluded that “the auditory mechanism of *Pakicetus* appears more similar to that of land mammals than it is to any group of extant* marine mammals.”

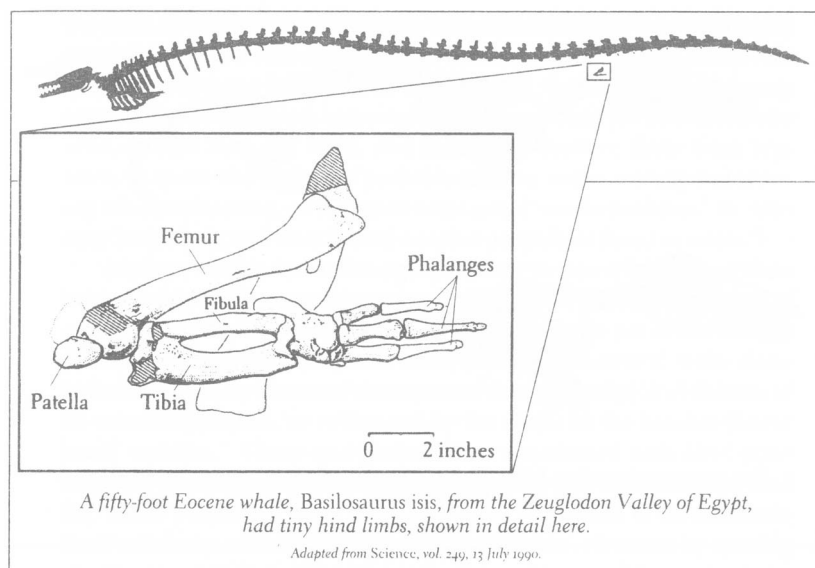
As for place of discovery, Gingerich and colleagues found *Pakicetus* in river sediments bordering an ancient sea – an ideal habitat for the first stages of such an evolutionary transition (and a good explanation for lack of diving specializations if *Pakicetus* inhabited the mouths of rivers and adjacent shallow seas). My colleagues judged *Pakicetus* as “an amphibious stage in the gradual evolutionary transition of primitive whales from land to sea ... *Pakicetus* was well equipped to feed on fishes in the surface waters of shallow seas, but it lacked auditory adaptations necessary for a fully marine existence.”

Verdict: In terms of intermediacy, one could hardly hope for more from the limited material of skull bones alone. But the limit remains severe, and the results therefore inconclusive. We know nothing of the limbs, tail, or body form of *Pakicetus*, and therefore cannot judge transitional status in these key features of anyone’s ordinary conception of a whale.

CASE TWO. *Discovery of the first complete hind limb in a fossil whale.* In the most famous mistake of early American paleontology, Thomas Jefferson, while not engaged in other pursuits usually judged more important, misidentified the claw of a fossil ground sloth* as a lion. My prize for second worst error must go to R. Harlan, who, in 1834, named a marine fossil vertebrate *Basilosaurus* in the *Transactions of the American Philosophical Society*. *Basilosaurus* means “king lizard,” but Harlan’s creature is an early whale. Richard Owen, England’s greatest anatomist, corrected Mr. Harlan before the decade’s end, but the name sticks and must be retained by the official rules of zoological nomenclature. (The Linnaean naming system is a device for information retrieval, not a guarantor of appropriateness. The rules require that each species have a distinctive name, so that data can be associated unambiguously with a stable tag. Often, and inevitably, the names originally given become literally inappropriate for the unsurprising reason that scientists make frequent mistakes, and that new discoveries modify old conceptions. If we had to change names every time our ideas about a species altered, taxonomy would devolve into chaos. So *Basilosaurus* will always be *Basilosaurus* because Harlan followed the rules when he gave the name. And we do not change ourselves to *Homo horribilis* after Auschwitz, or to *Homo ridiculosis* after Tonya Harding – but remain, however dubiously, *Homo sapiens*, now and into whatever forever we allow ourselves.)

Basilosaurus, represented by two species, one from the United States and the other from Egypt, is the “standard” and best-known early whale. A few fragments of pelvic and leg bones had been found before, but not enough to know whether *Basilosaurus* bore working hind legs – the crucial feature for our usual concept of a satisfying intermediate form in both anatomical and functional senses.

In 1990, Phil Gingerich, B. H. Smith, and E. L. Simons reported their excavation and study of several hundred partial skeletons of the Egyptian species *Basilosaurus isis*, which lived some 5 to 10 million years after *Pakicetus*. In an exciting discovery, they reported the first complete hind-limb skeleton found in any whale – a lovely and elegant structure (put together from several partial specimens), including all pelvic bones, all leg bones (femur, tibia, fibula, and even the patella, or kneecap), and nearly all foot and finger bones, right down to the phalanges (finger bones) of the three preserved digits.



This remarkable find might seem to clinch our proof of intermediacy, but for one small problem. The limbs are elegant but tiny (see the accompanying illustration), a mere 3 percent of the animal’s total length. They are anatomically complete, and they did project from the body wall (unlike the truly vestigial* hind limbs of modern whales), but these miniature legs could not have made any important contribution to locomotion – the real functional test of intermediacy. Gingerich et al. write: “Hind limbs of *Basilosaurus* appear to have been too small relative to body size to have assisted in swimming, and they could not

possibly have supported the body on land.” The authors strive bravely to invent some potential function for these minuscule limbs, and end up speculating that they may have served as “guides during copulation, which may otherwise have been difficult in a serpentine aquatic mammal.” (I regard such guesswork as unnecessary, if not ill-conceived*. We need not justify the existence of a structure by inventing some putative Darwinian function. All bodies contain vestigial features of little, if any, utility. Structures of lost usefulness in genealogical transitions do not disappear in an evolutionary overnight.)

Verdict: Terrific and exciting, but no cigar, and no bag-packer for creationists. The limbs, though complete, are too small to work as true intermediates must (if these particular limbs worked at all) – that is, for locomotion on both land and sea. I intend no criticism of *Basilosaurus*, but merely point out that this creature had already crossed the bridge (while retaining a most informative remnant of the other side). We must search for an earlier inhabitant of the bridge itself.

CASE THREE. *Hind limb bones of appropriate size.* *Indocetus ramani* is an early whale, found in shallow-water marine deposits of India and Pakistan, and intermediate in age between the *Pakicetus* skull and the *Basilosaurus* hind legs (cases one and two above). In 1993, P. D. Gingerich, S. M. Raza, M. Arif, M. Anwar, and X. Zhou reported the discovery of leg bones of substantial size from this species.

Gingerich and colleagues found pelvic bones and the ends of both femur and tibia, but no foot bones, and insufficient evidence for reconstructing the full limb and its articulations. The leg bones are large and presumably functional on both land and sea (the tibia, in particular, differs little in size and complexity from the same bone in the related and fully terrestrial mesonychid *Pachyaena ossifraga*). The authors conclude: “The pelvis has a large and deep acetabulum [the socket for articulation of the femur, or thigh-bone], the proximal femur is robust, the tibia is long ... All these features, taken together, indicate that *Indocetus* was probably able to support its weight on land, and it was almost certainly amphibious, as early Eocene *Pakicetus* is interpreted to have been ... We speculate that *Indocetus*, like *Pakicetus*, entered the sea to feed on fish, but returned to land to rest and to birth and raise its young.”

Verdict: Almost there, but not quite. We need better material. All the right features are now in place – primarily leg bones of sufficient size and complexity – but we need more and better-preserved fossils.

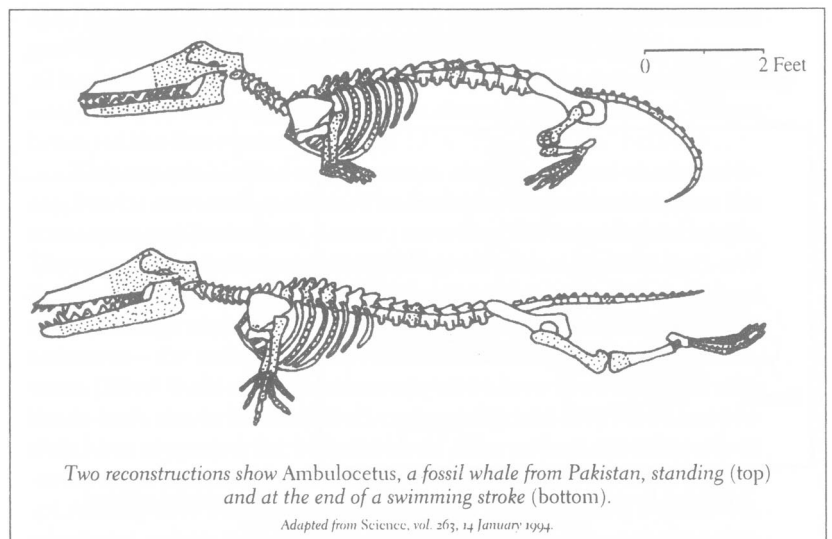
CASE FOUR. *Large, complete, and functional hind legs for land and sea – finding the smoking gun.* The first three cases, all discovered within ten years, surely indicate an increasingly successful paleontological assault* upon an old and classic problem. Once you know where to look, and once high interest spurs great attention, full satisfaction often follows in short order. I was therefore delighted to read, in the January 4, 1994, issue of *Science*, an article by J. G. M. Thewissen, S. T. Hussain, and M. Arif, titled “Fossil evidence for the origin of aquatic locomotion in archaeocete whales.”

In Pakistan, in sediments 120 meters above the beds that yielded *Pakicetus* (and therefore a bit younger in age), Thewissen and colleagues collected a remarkable skeleton of a new whale – not complete, but far better preserved than anything previously found of this age, and with crucial parts in place to illustrate a truly transitional status between land and sea. The chosen name, *Ambulocetus natans* (literally, the swimming walking-whale) advertises the excitement of this discovery.

Ambulocetus natans weighed some 650 pounds, the size of a hefty sea lion. The preserved tail vertebra is elongated, indicating that *Ambulocetus* still retained the long, thin mammalian tail, and had not yet transmuted this structure to a locomotory blade (as modern whales do in shortening the tail and evolving a prominent horizontal fluke as the animal’s major means of propulsion). Unfortunately, no pelvic bones have been found, but most elements of a large and powerful hind leg were recovered – including a complete femur, parts of the tibia and fibula, an astragalus (ankle bone), three metatarsals (foot bones), and several phalanges (finger bones). To quote the authors: “The feet are enormous.” The fourth metatarsal, for example, is nearly six inches long, and the associated toe almost seven inches in length. Interestingly, the last phalanx of each toe ends in a small hoof, as in terrestrial mesonychid ancestors.

Moreover, this new bounty of information allows us to infer not only the form of this transitional whale, but also, with good confidence, an intermediary style of locomotion and mode of life (an impossibility with the first three cases, for *Pakicetus* is only a skull, *Basilosaurus* had already crossed the bridge, and *Indocetus* is too fragmentary). The forelimbs were smaller than the hind, and limited in motion; these front legs were, to quote the authors, “probably used in maneuvering and steering while swimming, as in extant cetaceans [“modern whales” in ordinary language], and they lacked a major propulsive force in water.”

Modern whales move through the water by powerful beats of their horizontal tail flukes – a motion made possible by strong undulation of a flexible rear spinal column. *Ambulocetus* had not yet evolved a tail fluke, but the spine had requisite flexibility. Thewissen et al. write: “*Ambulocetus* swam by means of



dorsoventral [back-to-belly] undulations of its vertebral column, as evidenced by the shape of the lumbar [lower back] vertebra.” These undulations then functioned with (and powered) the paddling of *Ambulocetus*’s large feet – and these feet provided the major propulsive force for swimming. Thewissen et al. conclude their article by writing: “Like modern cetaceans, it swam by moving its spine up and down, but like seals, the main propulsive surface was provided by its feet. As such, *Ambulocetus* represents a critical intermediate between land mammals and marine cetaceans.”

Ambulocetus was no ballet dancer on land, but we have no reason to judge this creature as any less efficient than modern sea lions, which do manage*, however inelegantly. Forelimbs may have extended out to the sides, largely for stability, with forward motion mostly supplied by extension of the back and consequent flexing of the hind limbs – again, rather like sea lions.

Verdict: Greedy paleontologists, used to working with fragments in reconstructing wholes, always want more (some pelvic bones would be nice, for starters), but if you had given me both a blank sheet of paper and a blank check, I could not have drawn you a theoretical intermediate any better or more convincing than *Ambulocetus*. Those dogmatists who can make white black, and black white, by verbal trickery will never be convinced by anything, but *Ambulocetus* is the very animal that creationists proclaimed impossible in theory.

Some discoveries in science are exciting because they revise or reverse previous expectations, others because they affirm with elegance something well suspected, but previously undocumented. Our four-case story, culminating in *Ambulocetus*, falls into this second category. This sequential discovery of picture-perfect intermediacy in the evolution of whales stands as a triumph in the history of paleontology. I cannot imagine a better tale for popular presentation of science, or a more satisfying, and intellectually based, political victory over lingering creationist opposition. As such, I present the story in this series of essays with both delight and relish*.

Still, I must confess that this part of the tale does not intrigue me most as a scientist and evolutionary biologist. I don’t mean to sound jaded or dogmatic, but *Ambulocetus* is so close to our expectation for a transitional form that its discovery could not provide a professional paleontologist with the greatest of all pleasures in science – surprise. As a public illustration and sociopolitical victory, transitional whales may provide the story of the decade, but paleontologists didn’t doubt their existence or feel that a central theory would collapse if their absence continued. We love to place flesh upon our expectations (or put bones under them, to be more precise), but this kind of delight takes second place to the intellectual jolting of surprise.

I therefore find myself far more intrigued by another aspect of *Ambulocetus* that has not received much attention, either in technical or popular reports. For the anatomy of this transitional form illustrates a vital principle in evolutionary theory – one rarely discussed, or even explicitly formulated, but central to any understanding of nature’s fascinating historical complexity.

In our Darwinian traditions, we focus too narrowly on the adaptive nature of organic form, and too little on the quirks and oddities encoded into every animal by history. We are so overwhelmed – as well we should be – by the intricacy of aerodynamic optimality of a bird’s wing, or by the uncannily precise mimicry of a dead leaf by a butterfly. We do not ask often enough why natural selection had homed in upon this particular optimum – and not another among a set of unrealized alternatives. In other words, we are dazzled by good design and therefore stop our inquiry too soon when we have answered, “How does this feature work so well?” – when we should also be asking the historian’s questions: “Why *this* and not *that*?” or “Why *this* over here, and *that* in a related creature living elsewhere?”

To give the cardinal example from seagoing mammals: The two fully marine orders, Sirenia and Cetacea, both swim by beating horizontal tail flukes up and down. Since these two orders arose separately from terrestrial ancestors, the horizontal tail fluke evolved twice independently. Many hydrodynamic studies have documented both the mode and the excellence of such underwater locomotion, but researchers too often stop at an expression of engineering wonder, and do not ask the equally intriguing historian’s question. Fishes swim in a truly opposite manner – also by propulsion from the rear, but with vertical tail flukes that beat from side to side (seals also hold their rear feet vertically and move them from side to side while swimming).

Both systems work equally well; both may be “optimal.” But why should ancestral fishes favor one system, and returning mammals the orthogonal alternative? We do not wish to throw up our hands, and simply say “six of one, half a dozen of the other.” Either way will do, and the manner chosen by evolution

is effectively random in any individual case. “Random” is a deep and profound concept of great positive utility* and value, but some vernacular meanings amount to pure cop-out*, as in this case. It may not matter in the “grand scheme of things” whether optimality be achieved vertically or horizontally, but one or the other solution occurs for a reason in any particular case. The reasons may be unique to an individual lineage, and historically bound – that is, not related to any grand concept of pattern or predictability in the overall history of life – but local reasons do exist and should be ascertainable.

This subject, when discussed at all in evolutionary theory, goes by the name of “multiple adaptive peaks.” We have developed some standard examples, but few with any real documentation; most are hypothetical, with no paleontological backup. (For example, my colleague Dick Lewontin loves to present the following case in our joint introductory course in evolutionary biology: some rhinoceros species have two horns, others one horn. The two alternatives may work equally well for whatever rhinos do with their horns, and the pathway chosen may not matter. Two and one may be comparable solutions, or multiple adaptive peaks. Lewontin then points out that a reason must exist for two or one in any case, but that the explanation probably resides in happenstances of history, rather than in abstract predictions based on universal optimality. So far, so good. History’s quirkiness, by populating the earth with a *variety* of *unpredictable* but sensible and well-working anatomical designs, does constitute the main fascination of evolution as a subject. But we can go no further with rhinos, for we have no data for understanding the particular pathway chosen in any individual case.)

I love the story of *Ambulocetus* because this transitional whale has provided hard data on reasons for a chosen pathway in one of our best examples of multiple adaptive peaks. Why did both orders of fully marine mammals choose the solution of horizontal tail flukes? Previous discussions have made the plausible argument that particular legacies of terrestrial mammalian ancestry established an anatomical predisposition. In particular, many mammals (but not other terrestrial vertebrates), especially among agile and fast-moving carnivores, run by flexing the spinal column up and down (conjure up a running tiger in your mind, and picture the undulating back). Mammals that are not particularly comfortable in water – dogs dog-paddling, for example – may keep their backs rigid and move only by flailing their legs. But semi-aquatic mammals that swim for a living – notably the river otter (*Lutra*) and the sea otter (*Enhydra*) – move in water by powerful vertical bending of the spinal column in the rear part of the body. This vertical bending propels the body forward both by itself (and by driving the tail up and down), and by sweeping the hind limbs back and forth in paddling as the body undulates.

Thus, horizontal tail flukes may evolve in fully marine mammals because inherited spinal flexibility for movement up and down (rather than side to side) directed this pathway from a terrestrial past. This scenario has only been a good story up to now, with limited symbolic support from living otters, but no direct evidence at all from the ancestry of whales or sirenians. *Ambulocetus* provides this direct evidence in a most elegant manner – for all pieces of the puzzle lie within the recovered fossil skeleton.

We may infer from a tail vertebra that *Ambulocetus* retained a long and thin mammalian tail, and had not yet evolved the horizontal fluke. We know from the spinal column that this transitional whale retained its mammalian signature of flexibility for up and down movement – and from the large hind legs that undulation of the back must have supplied propulsion to powerful paddling feet, as in modern otters.

Thewissen and colleagues draw the proper evolutionary conclusion from these facts, thus supplying beautiful evidence to nail down a classic case of multiple adaptive peaks with paleontological data: “*Ambulocetus* shows that spinal undulation evolved before the tail fluke ... Cetaceans have gone through a stage that combined hindlimb paddling and spinal undulation, resembling the aquatic locomotion of fast swimming otters.” The horizontal tail fluke, in other words, evolved because whales carried their terrestrial system of spinal motion to the water.

History channels a pathway among numerous theoretical alternatives. In his last play, Shakespeare noted that “what’s past is prologue; what to come, in yours and my discharge.” But present moments build no such wall of separation between a past that molds* us and a future under our control. The hand of the past reaches forward right through us and into an uncertain future that we cannot fully specify.

EPILOGUE

I wrote this essay in a flush of excitement during the week that Thewissen and colleagues published their discovery of the definitive intermediate whale *Ambulocetus*, in January 1994. With my lead time of three months from composition to the first publication of these essays in *Natural History* magazine, “Hooking Leviathan by Its Past” appeared in April 1994 – complete with central theme of a chronologically developing story in four stages.

I think of the old spiritual: “Sometimes I get discouraged, and think my work’s in vain. But then the Holy Spirit revives my soul again.” I’m actually a fairly cheerful soul but we all need replenishment now and then. If “there is a balm in Gilead” (the song’s title) for scientists, that elixir, that infusion of the holy spirit, takes the form of new discoveries. On the very week of my essay’s publication, Phil Gingerich and colleagues (see bibliography) published their description of yet another intermediate fossil whale, a fifth tale for this gorgeous* sequence of evolutionary and paleontological affirmation. (I did feel a bit funny about the superannuation of my essay on the day of its birth, but all exciting science must be obsolescent from inception – and I knew I could write this epilogue for my next book!)

Gingerich and colleagues discovered and named a new fossil Eocene whale from Pakistan, *Rodhocetus kasrani* (*Rodho* for the local name of the region, *kasrani* for the group of Baluchi people living in the area. *Rodhocetus*, estimated at some ten feet in length, lived about 46.5 million years ago. This new whale is thus about 3 million years younger than the “smoking gun” *Ambulocetus* (Case Four and the key story in the main essay), and about the same age as *Indocetus* (stage three in the main essay). No forelimb bones have been found, and the spinal column lacks tail vertebrae, but much of the skull has been recovered with, perhaps more important, a nearly complete vertebral column from the neck all the way back to the beginning of the tail. Most of the pelvis has also been found and, crucial to evidence about intermediacy, a complete femur (but no other elements of the hind limb).

We may summarize the importance of *Rodhocetus*, and its gratifying extension of our story about “hard” evidence for intermediacy in the evolution of whales from terrestrial ancestors, by summarizing evidence in the three great categories of paleontological data: form (anatomy), habitat (environment), and function.

FORM. I was most struck by two features of *Rodhocetus*’s anatomy. First, the excellent preservation of the vertebral column provides good evidence of intermediacy in a mixture of features retained from a terrestrial past with others newly acquired for an aquatic present. The high neural spines (upward projections) of the anterior thoracic vertebrae (just behind the neck) support muscles that help to hold up the head in terrestrial animals (not a functional necessity in the buoyancy* of marine environments, whales evolved from a terrestrial group, the mesonychids, with particularly large heads). Direct articulation of the pelvis with the sacrum (the adjacent region of the vertebral column) also characterizes both *Rodhocetus* and terrestrial mammals (where gravity requires this extra strength), but does not occur in modern whales. Gingerich and colleagues conclude: “These are primitive characteristics of mammals that support their weight on land, and both suggest that *Rodhocetus* or an immediate predecessor was still partly terrestrial.”

But other features of the spinal column indicate adaptation for swimming: short cervical (neck) vertebrae, implying rigidity for the front end of the body (good for cutting through the water as the rear parts of the animal provide propulsion); and, especially, the seamless flexibility of posterior vertebrae (sacral vertebrae are fused together in most large terrestrial mammals, but unfused in both modern whales and *Rodhocetus*), an important configuration for providing forward thrust in swimming. Gingerich and colleagues conclude: “These are derived characteristics of later archaeocetes [ancient whales] and modern whales associated with aquatic locomotion.”

Second, and even more striking for this essay’s case of graded intermediacy, sequentially discovered during the past twenty years, *Rodhocetus* is about 3 million years younger than the “smoking gun” *Ambulocetus* (a marine whale with limbs large enough for movement on land as well), and a good deal older than later whales that had already crossed the bridge to fully marine life (*Basilosaurus*, my Case Two, with well-formed but tiny hind limbs that could not have functioned on land, and probably didn’t do much in water either). In the most exciting discovery of this new Case Five, the femur of *Rodhocetus* is about two thirds as long as the same bone in the older *Ambulocetus* – still functional on land (probably), but already further reduced after 3 million additional years of evolution.

HABITAT. *Rodhocetus* is the oldest whale from fully and fairly deep marine waters. The oldest of all whales, *Pakicetus* of Case One, lived around the mouths of rivers; *Ambulocetus* and *Indocetus* of Cases Three and Four inhabited very shallow marine waters. Interestingly, the more fully marine habitat of *Rodhocetus* correlates with greater reduction of the hind limb, for *Indocetus* is a contemporary of *Rodhocetus*, yet grew a larger femur comparable in length with the earlier *Ambulocetus*. (All three creatures had about the same body size). Thus, admittedly on limited evidence, limbs decreased in size over time and became smaller faster in whales from more fully marine environments. (Perhaps *Rodhocetus* had already ceased making excursions on land, while the earlier *Ambulocetus*, with a larger femur, almost surely inhabited both land and water.) In any case, the contemporaneity of *Rodhocetus* (shorter femur and deeper water) and *Indocetus* (longer femur with life in shallower water) illustrates the diversity that already existed in cetacean evolution. Evolution, as I always say, no doubt to the point of reader's boredom, is a copiously branching bush, not a ladder.

FUNCTION. *Rodhocetus* lacks tail vertebrae, so we can't tell for sure whether or not this whale had yet evolved a tail fluke. But evidence of the beautifully preserved spinal column – particularly the unfused sacral vertebrae, “making,” in the words of Gingerich et al., “the lumbocaudal [back to tail] column seamlessly flexible” – indicates strong dorsoventral (back to belly) flexion at the rear end of the body – the prerequisites for swimming in the style of modern whales (with propulsion provided by a horizontal tail fluke, driven up and down by bending the vertebral column). I was particularly pleased by this result, since I closed my essay with a mini-disquisition on multiple adaptive peaks and the importance of historical legacies, as illustrated by vertical tail fins in fishes vs. horizontal flukes in whales – both solutions working equally well, but with whales limited to this less familiar alternative because they evolved from terrestrial ancestors with backs that flexed dorsoventrally in running. Gingerich and colleagues conclude: “This indicates that the characteristic cetacean mode of swimming by dorsoventral oscillation of a heavily muscled tail evolved within the first three million years or so of the appearance of the archaeocetes.”

A tangential comment in closing: The sociology of science includes much that I do not like, but let us praise what we do well. Science at its best is happily and vigorously international (see essay 20) – and I can only take great pleasure in the following list of authors for research done in an American lab based on fieldwork in Asia, supported by the Geological Survey of Pakistan: Philip D. Gingerich, S. Mahmood Raza, Muhammad Arif, Mohammad Anwar, and Xiaoyuan Zhou. Bravo to you all. I also couldn't help noting the paper's first sentence: “The early evolution of whales is illustrated by partial skulls and skeletons of five archaeocetes of Ypresian (Early Eocene) ... age.” The geological time scale is just as international, for our fossil record is a global scheme for correlating the ages of rocks. So a layer of sediments in Pakistan may be identified as representing a time named for a place that later became the bloodiest European battle site of World War I – the dreaded Ypres (or “Wipers” as British soldiers named and pronounced their hecatomb).

But so much for lugubrious* and sentimental thoughts. Let's just end in the main essay's format for our new case of *Rodhocetus*:

CASE FIVE. Open and shut.

Verdict: sustained in spades*, wine and roses.