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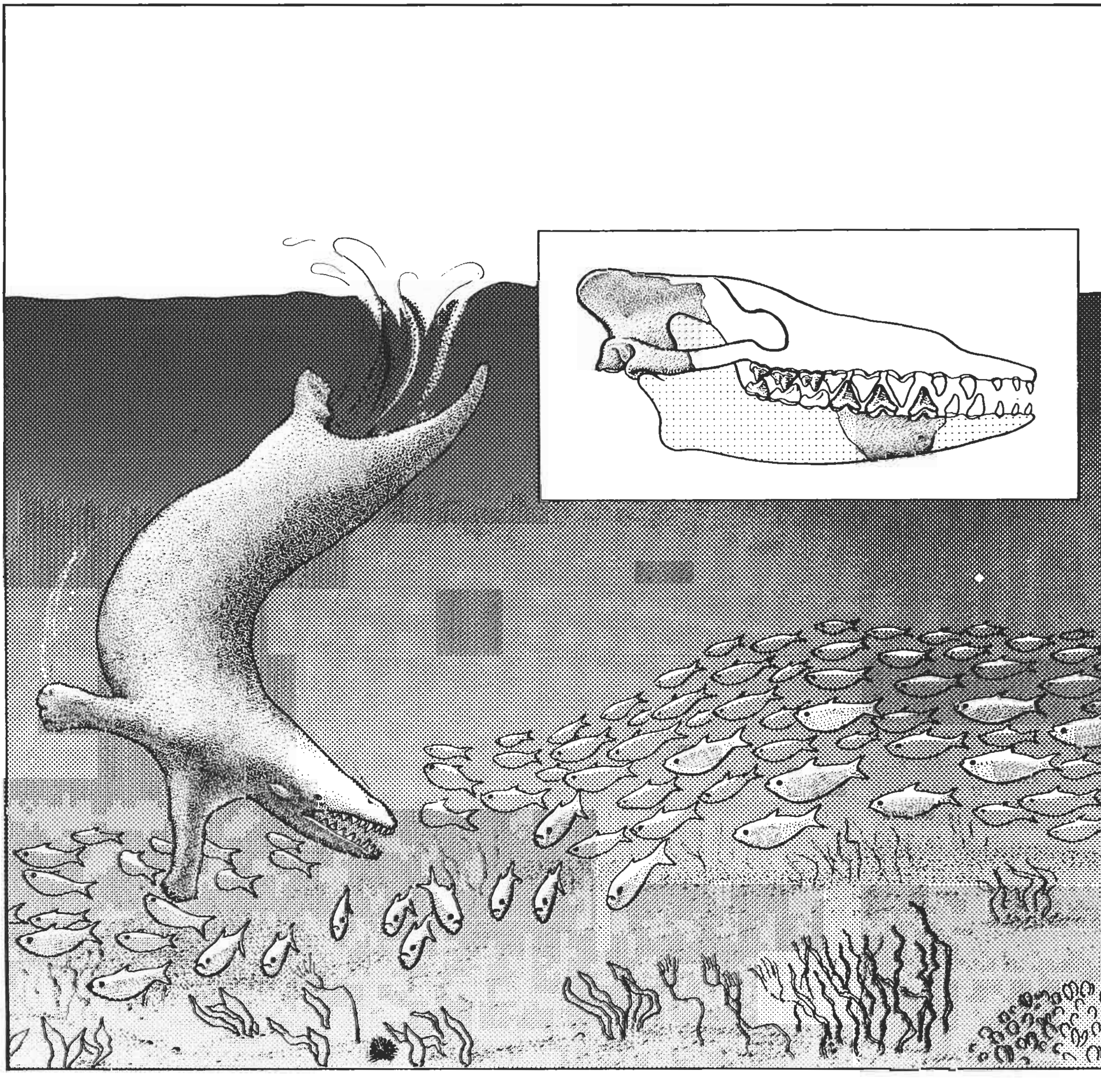

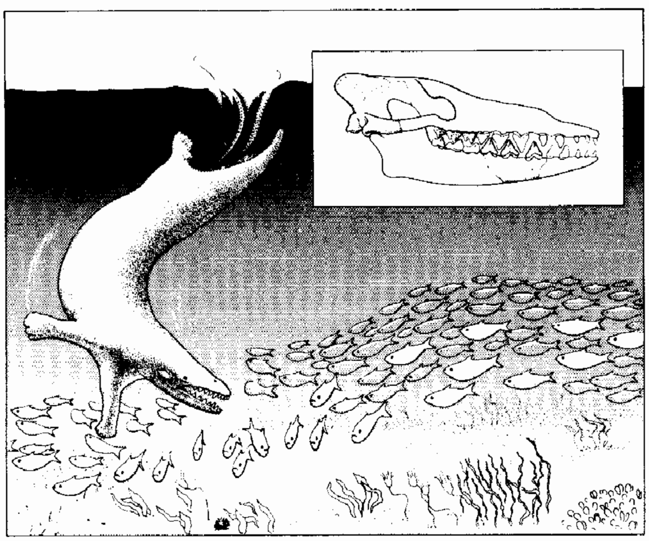

COVER PHOTO

Artist's interpretation of the oldest fossil whale, *Pakicetus*, based on fossils from the late early Eocene Kuldana Formation, Pakistan. "The age, environment of deposition, associated fauna, and functional morphology of *Pakicetus* indicate not only that it is the oldest and most primitive whale yet discovered, but that it is an important transitional form linking Paleocene carnivorous land mammals and later, more advanced marine whales. Whales apparently made the transition from land to sea in the early Eocene when protocetids like *Pakicetus* entered shallow epicontinental seas to feed on abundant planktivorous fishes living there." See article on pages 140-144.

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Evidence for Evolution from the Vertebrate Fossil Record

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Abstract

The paucity of intermediate transitional forms linking species and higher taxa in the fossil record is commonly cited by creationists (and sometimes by scientists) as a weakness in our current understanding of organic evolution. Evolutionary studies in the fossil record rely on stratigraphic superposition to document temporal change in individual lineages and in whole faunas. Evolution at the species level is illustrated for the early Cenozoic primates *Plesiadapis* and *Cantius*, based on stratigraphic superposition and faunal succession documented in western North America. Evolutionary change across an ordinal boundary is illustrated by discovery of the earliest fossil whale, *Pakicetus*, which indicates the timing and sequence of transitional stages involved in the origin of whales. Creationists confuse science with religion, and they will continue to promote a false debate over evolution as long as they confuse material and spiritual realms of being.

Key words: Creationism; geology — public affairs; paleontology — vertebrate; philosophy of science.

Introduction

I finished teaching a large lecture course on primate and human evolution recently. Just before I started the final lecture, a student in the course got up and addressed the class. He urged that they not believe what I was teaching, since "evolution is just a theory, and the Biblical story of creation makes more sense." The student further promised that after the final examination he would distribute a paper he had written presenting the truth about creation and evolution. Somehow the idea that a classmate would have more insight into evolution than the professor teaching a course was more than the class would tolerate, and they soon stopped listening and told the creationist student to sit down.

As promised, the student did pass out copies of his paper after the final exam. I received and read a copy, and the central question it raised provides a fitting starting point for this essay: *Where are the intermediate transitional forms linking different kinds of animals in the fossil record?* This problem of transitional forms has been a topic of considerable interest recently in evolutionary paleontology, and I hope that what I have to say here might be of interest to my professional colleagues, as well as to those concerned more generally with evolution and creationism.

The paper distributed by the student concluded:

> One has two choices, take your pick. We are either a hand-me-down product of a cosmic crap game, or we are created by Wisdom, Love, and Power beyond comprehension. These are the options, accident or design, chance or creation, and these options have profound implications for the way you feel about yourself and others in this world.

I can't say very much on the question of accident vs. benevolent design, but since it is, perhaps, the heart of the evolution/creationism debate, I can't entirely avoid it either. I shall return to this problem in closing.

Transitional Forms

What about the paucity of transitional forms linking species and higher taxonomic categories in the fossil record? In Darwin's day the paucity of transitional forms could easily be explained as a direct, if unfortunate, result of the many large gaps in the known geological record. Much more is known today about geology, stratigraphy, and paleontology worldwide, and in some places it has been estimated that the stratigraphic record is 50 percent or more complete when studied on a scale of tens or hundreds of thousands of years. Stratigraphic sections yielding abundant fossils are beginning to be studied with new intensity, and these are yielding remarkably detailed patterns of change for organisms living in the geographic areas being sampled. Unfortunately, large areas inhabited by organisms in the past can never be sampled, and gaps in the fossil record will always be a serious problem in evolutionary paleontology. We study what we can, recognizing that processes producing patterns similar to those actually observed in one area were undoubtedly operating outside the study area as well.

In the following sections I want to discuss three examples of evolutionary transition in the vertebrate fossil record. I had originally intended to concentrate on classic examples, reviewing *Archaeopteryx* and the origin of birds, mammal-like reptiles and the origin of mammals, etc., but these major transitions have been much discussed in the literature already (e.g., Ostrom, 1975, 1976; and Crompton and Jenkins, 1973, 1979) and I think I can make the points I want to more effectively using examples from my own work. First I will discuss evolutionary transitions at the species level, using archaic squirrel-like Paleocene primates (*Plesiadapis* and its allies) and the earliest primates of modern aspect (Eocene *Cantius* in particular) as examples. Second, I will review new evidence on a classic problem in paleontology, the origin of whales and their transition from land to sea.

First Principles

The theoretical background necessary for interpreting patterns in the fossil record is not complicated. Evolutionary paleontology rests on two familiar principles:

1. Steno's principle of original horizontality and superposition of sedimentary strata;
2. Smith's principle of faunal succession and correlation in fossiliferous strata.

As students, we first encounter these principles in discussing stratigraphy, and our geological time scale is largely based upon them. They have a wider import:

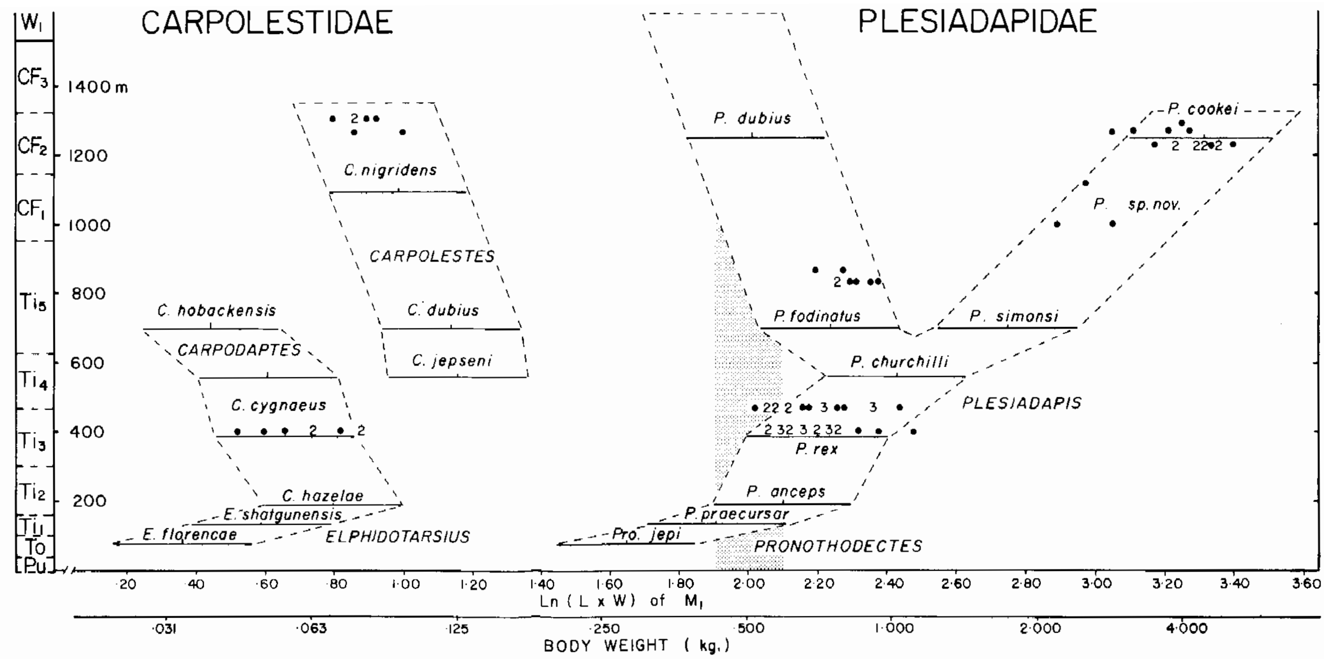

Figure 1. Stratigraphic distribution and interpreted phylogenetic relationships of North American Paleocene Carpolestidae and Plesiadapidae. Ordinate is stratigraphic level (in meters) above Cretaceous-Tertiary boundary in Clark's Fork Basin, Wyoming, with appropriate *Plesiadapis* biochrons indicated at left. Abscissa is standard measure of tooth size: log of length multiplied by width of the first lower molar. Solid lines with vertical slash are sample mean and expected range for the largest sample of each species. Dashed lines show phylogenetic hypotheses based on stratophenetic linking of published information for all species. New undescribed specimens collected recently are shown as solid circles (or integers where two or more specimens are of same size). New specimens provide a test of the proposed phylogeny and appear to corroborate it except for several minor adjustments in means and expected ranges. Body weights shown on abscissa are estimated from tooth size using regression for living primates. Figure reproduced from Gingerich (1980).

faunal succession ordered in time by stratigraphic superposition is the empirical evidence for organic evolution. Evolution as a description of the history of life was an established scientific fact 200 years ago, a result of careful study of the stratigraphic succession of fossil faunas in the classic sedimentary basins of western Europe.

Evolution at the Species Level

It is one thing to show that life evolved, and quite another to explain how the process works. Darwin's great insight was that extrinsic environmental factors are sufficient to cause organisms to change through time by a process of natural selection. This process is still not fully understood, and it is the focus of very active research by systematists, ecologists, ethologists, geneticists, and paleontologists. No single discipline covers evolution in all its dimensions, and progress will come only through coordinated research in all of these disciplines.

As a graduate student, I was surprised (and disappointed) to realize that the most cited example of evolution in the fossil record, the evolutionary history of the horse, was always shown in terms of genera (cf. Simpson, 1953) while evolution itself is a process occurring at the level of species. At the same time, my colleagues Niles Eldredge and Stephen Gould published a seminal paper interpreting the evolutionary process in such a way that intermediate transitional forms linking established species would rarely, if ever, be preserved in the fossil record (Eldredge and Gould, 1972). Their idea of "punctuated equilibria" ran counter to my field experience collecting mammalian fossils in early Cenozoic strata of the Clark's Fork and Bighorn Basins in Wyoming, and I set out to test this idea by looking at species-level transitions in the mammalian fossil record. This required careful stratigraphic documentation and procurement of large collections of fossils from many successive stratigraphic intervals. In a sense, ten years later, the work has just begun. It has taken nearly ten years to accumulate fossil collections large enough to show unequivocally how lineages of the more common taxa changed through time. As a result it is now possible to say something about species-level evolutionary transitions in the mammalian fossil record.

The first example I want to discuss is the stratigraphic succession of species of the Paleocene primate *Plesiadapis* and its allies. In terms of general form, *Plesiadapis* and related genera most closely resembled modern squirrel-like rodents. They lived at a time before rodents invaded North America, and rodents make the best structural models for many archaic Paleocene primates. In the mid-1970s, Kenneth Rose and I published extensive systematic reviews of two families of plesiadapiform primates, Carpolestidae (Rose, 1975) and Plesiadapidae (Gingerich, 1976). We approached these groups in similar ways, first determining how many species were represented at each of the known North American fossil localities yielding carpolestids and plesiadapids, respectively, and then determining how the various species samples at individual localities were related to those at other localities. Our results are shown graphically in Figure 1, where tooth size is plotted on the abscissa and relative geological age is plotted on the ordinate. Mammals like Carpolestidae and Plesiadapidae are advantageous for study because they have hard parts, teeth, that preserve well as fossils, do not show ontogenetic variations, and accurately reflect both the body size and diet of the species they represent. Geological age is determined, in Figure 1, by stratigraphic superposition and faunal correlation in the Clark's Fork and northern Bighorn Basins.

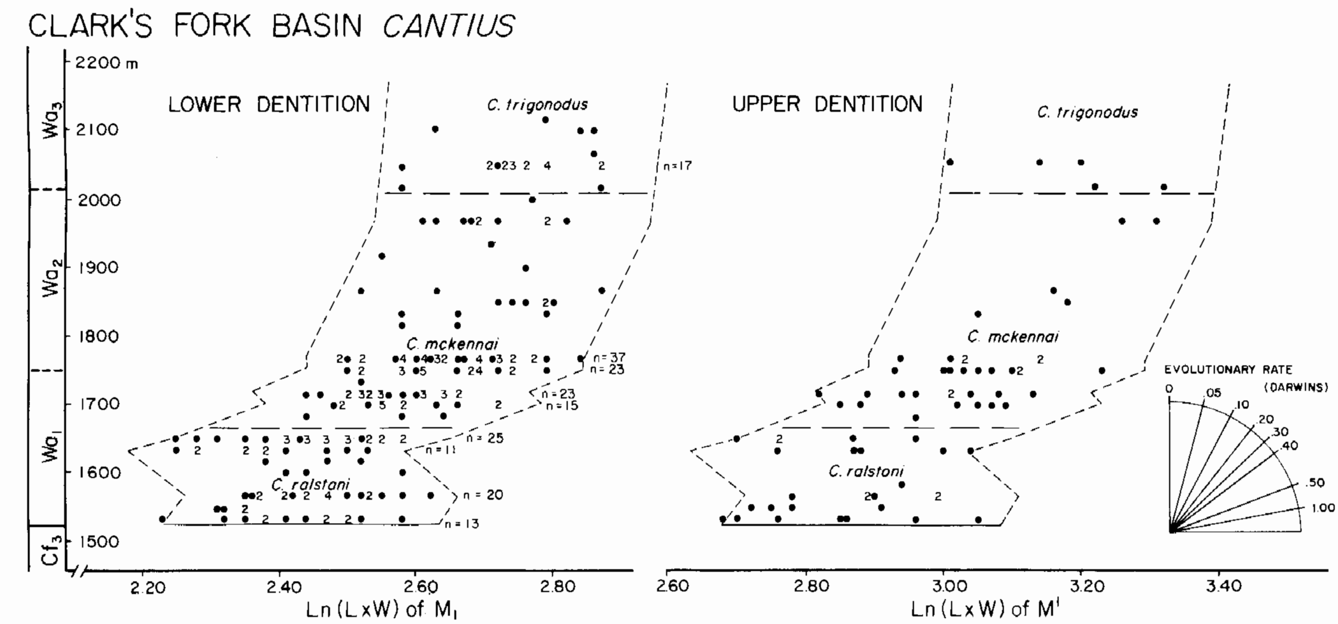

Figure 2. Stratigraphic change in size of lower and upper molars of the early Eocene primate *Cantius* based on collections from the Clark's Fork Basin, Wyoming. Note rapid transition from *C. ralstoni* to *C. mckennai* (ca. 0.50 darwins) and the much slower transition from *C. mckennai* to *C. trigonodus* (ca. 0.10 darwins). Symbols, tooth size scale (abscissa), and stratigraphic scale (ordinate) as in Figure 1. Figure reproduced from Gingerich (1982).

Several patterns are apparent in Figure 1. Carpolestids and plesiadapids both appear during the Torrejonian Land-Mammal Age (middle Paleocene, ca. 62 million years ago [*Ma*]) and both groups became extinct near the end of the Clarkforkian Land-Mammal Age (earliest Eocene, ca. 54 *Ma*). Both families are represented by a single lineage in the Torrejonian and by two lineages during the Tiffanian Land-Mammal Age (late Paleocene). Division of one lineage into two is reasonably well dated in *Plesiadapis*, but it is not so well documented in Carpolestidae. Of the principal lineage segments shown in Figure 1, three became larger through time while three became smaller. None appears to have remained static in size for very long.

Figure 1 illustrates how hypotheses are formulated in evolutionary paleontology, based on the stratigraphic sequence of different forms, and how these hypotheses can be tested by additional fossil collecting. Horizontal solid bars in Figure 1 show the means and ranges of samples originally described by Rose (1975) and Gingerich (1976), and dashed lines link these into lineages through time. Specimens collected subsequently are shown by solid circles (or integers, in the case of multiple specimens of the same size), and in almost every case the specimens collected after the initial hypothesis of lineage relationships was drawn fall within the dashed lines, thus corroborating the initial hypotheses.

Each of the samples represented by a solid bar in Figure 1 represents what a paleontologist considers a distinct species. The distribution of these species in time permits one to trace lineages outlining the overall radiation of Carpolestidae and Plesiadapidae in North America, but this distribution does not tell us very much about actual transitions from one species to another. In an attempt to learn more about intermediate transitional forms linking successive species, we began collecting intensively in strata of the Wasatchian Land-Mammal Age (early Eocene, ca. 53.5 - 51 *Ma*) in beds overlying those yielding Carpolestidae and Plesiadapidae. Here jaws and teeth of the earliest dawn horse to appear in North America, *Hyracotherium*, are common, as are remains of the earliest modern primates. Systematic review of *Hyracotherium* is not yet completed and it would be premature to discuss this genus here, but the common modern primate *Cantius* has been revised recently (Gingerich and Simons, 1977) and it is represented in our study area by several hundred new specimens.

Three species of *Cantius* are recognized in the Clark's Fork Basin, and these are shown in stratigraphic sequence in Figure 2. Specimens of *Cantius ralstoni* differ from later species of the genus in being smaller and in having very simple molars and premolars. Specimens of *C. mckennai* are larger than those of *C. ralstoni* and there is a greater tendency to add cusps and crenulations, especially on the last molars. Specimens of *C. trigonodus* tend to be larger than those of *C. mckennai* and they usually have a rudimentary mesostyle cusp present on the upper molars. The principal difference between the three species is overall size, and this is the morphological characteristic plotted against time in Figure 2. As shown, each sample of *Cantius* from successive stratigraphic levels is itself intermediate and transitional between earlier and later samples. There is relatively little change from one sample to the next, yet the net change over two million years or so of geological time is profound. Change here is so gradual that the boundaries between successive species (heavier dashed lines in Figure 2) are necessarily arbitrary. *Cantius ralstoni* and its descendant *C. trigonodus* are linked by an insensibly graded sequence of intermediate transitional forms.

Origin of Major Groups

The search for intermediate transitional forms in paleontology proceeds on a macroevolutionary level as well. Many of the major groups of organisms appear abruptly in the fossil record, with no obvious ancestral forms in lower geological strata. The abrupt appearance of *Cantius* and *Hyracotherium* in North America at the beginning of the Wasatchian Land-Mammal Age, discussed above, are two such examples. Both genera are unknown in North America before the Wasatchian Land-Mammal Age, but they are represented by slightly older and more primitive forms in Europe. Thus it is plausible

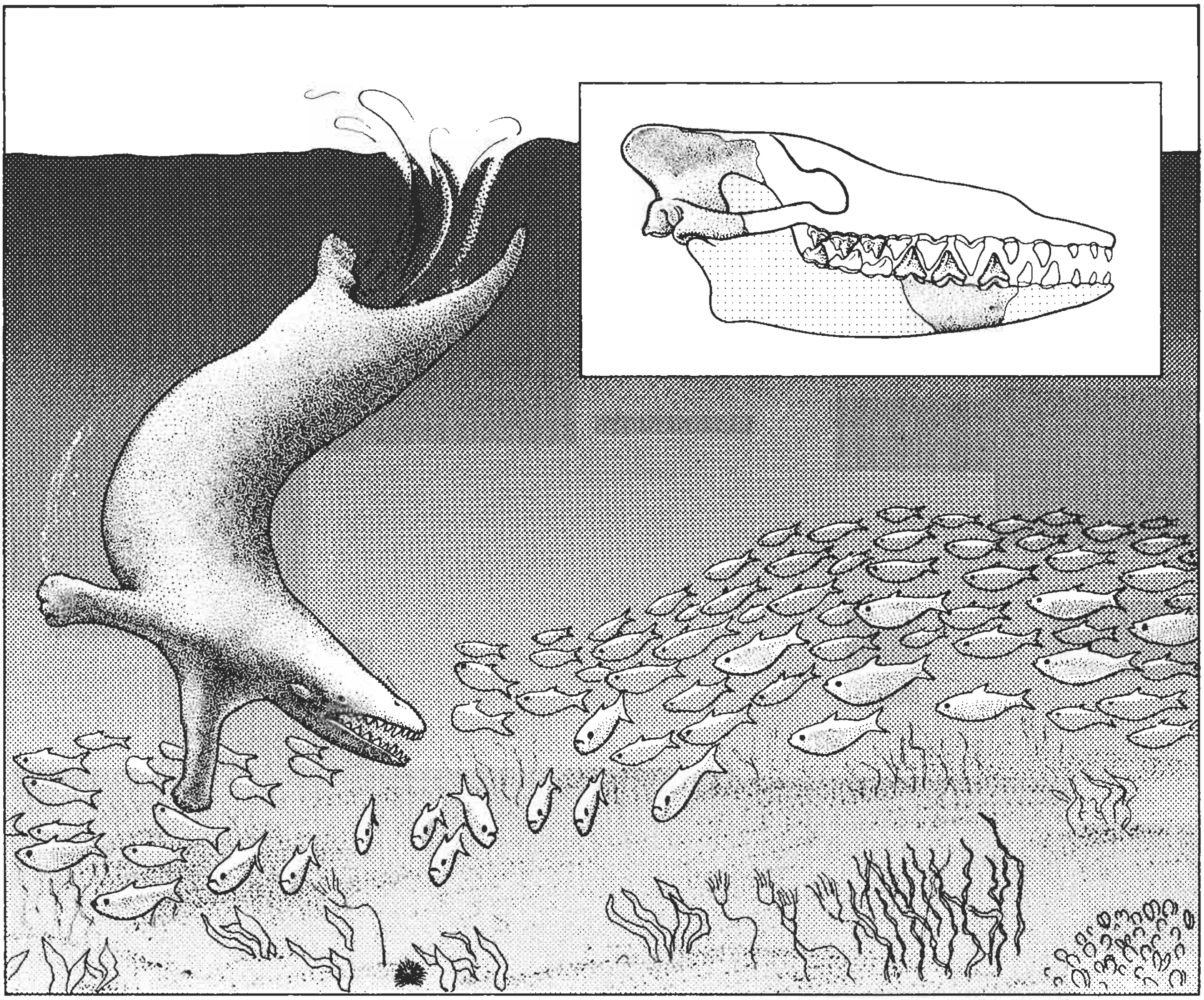

Figure 3. Artist's reconstruction of the oldest fossil whale, *Pakicetus*, known from the early Eocene of Pakistan. Preserved parts of skull are shown in inset with shading or stippling — remainder of skeleton is unknown. Functional morphology and mode of occurrence of the fossils indicate that *Pakicetus* was not yet adapted for a fully aquatic existence, but it probably entered shallow, saline, highly productive remnants of eastern Tethys to feed on abundant planktivorous fishes. Reconstruction drawn by Karen Klitz.

that they immigrated into North America from elsewhere, as did other characteristic Wasatchian genera (Gingerich, 1980).

One of the greatest mysteries in mammalian evolution has always been the origin of whales. Whales are found in marine sedimentary rocks of middle Eocene age at localities as widely distributed as Egypt, India, Pakistan, Nigeria, and Texas. They have never been found in early Eocene or older marine sediments. Where did whales come from? How did they enter the sea? These questions have been partially answered in recent years, with evidence coming from an unexpected source.

In 1977 I organized an expedition to search for new Eocene mammal sites in Pakistan in collaboration with Drs. Donald E. Russell of the Museum National d'Histoire Naturelle in Paris and S.M. Ibrahim Shah of the Geological Survey of Pakistan in Quetta. The first year of the project we found only one good locality, in Panoba Dome not far from the village of Chorlakki (Kohat District). The site is located high on a folded ridge overlooking the River Indus. Here we found one dentary of a small artiodactyl and some isolated teeth of other land mammals. All were found in a sequence of bright red continental sediments of the lower Kuldana Formation. We returned to the locality in 1978 and found, among other fossils, a partial cranium with a surprisingly small braincase (even for an Eocene mammal). Continued work produced a piece of a large lower jaw with three pointed premolar teeth and some large sharply cusped molars belonging to a carnivorous mammal of some kind. Most of the fossils we found belonged to artiodactyls, perissodactyls, rodents, a creodont, a primate, and other land mammals, but the cranium, the large lower jaw, and the sharply cusped carnivorous molars proved to represent a new genus of whale that we named *Pakicetus* after its country of origin.

A student of mine, Neil Wells, joined our expedition in 1978 and began careful study of the Eocene environment of deposition of the Chorlakki locality and surrounding areas. He has determined that the principal fossiliferous stratum at Chorlakki was deposited by a river draining into shallow, saline, epicontinental remnants of the Tethyan seaway confined between Indo-Pakistan and central Asia as these two tectonic plates converged. Careful study of the fauna from Chorlakki shows that it is entirely non-marine in origin. Study of the vertical sequence of formations near Chorlakki confirmed earlier authors' suggestions that the red continental facies of the lower Kuldana Formation are latest early Eocene in age.

Finally, study of the teeth of *Pakicetus* indicates that this early cetacean fed on fishes as did middle Eocene whales, while study of the cranium indicates that *Pakicetus* had none of the modifications of the skull and hearing apparatus characteristic of later whales and necessary for a fully aquatic existence. The age, environment of deposition, associated fauna, and functional morphology of *Pakicetus* indicate not only that it is the oldest and most primitive whale yet discovered, but that it is an important transitional form linking Paleocene carnivorous land mammals and later, more advanced marine whales. Whales apparently made the transition from land to sea in the early Eocene when protocetids like *Pakicetus* entered shallow epicontinental seas to feed on abundant planktivorous fishes living there (Gingerich and others, 1983; see Figure 3).

Transitional forms linking some of the other distinctively specialized orders of mammals, like bats for example, to more generalized ancestors are not yet known. However, discovery of *Pakicetus* in a sedimentary and faunal facies not previously well studied suggests that careful attention to new sedimentary facies and modes of fossil preservation will contribute to our understanding of the origin of other groups in the future.

Conclusion

The examples presented here indicate that intermediate transitional forms linking older ancestral species to their evolutionary descendants *are* known in the fossil record. The examples briefly described here are a small sample of the evolutionary transitions documented to date, and many more are reported in the paleontological literature every year. In addition, the primate fossil record, not reviewed here, is sufficiently well known to indicate that humans, like whales, are inextricably linked through our evolutionary past to progressively older and more primitve ancestors. Humans can be traced in the fossil record to primates of ape grade in the Miocene, monkey grade in the Oligocene, and lemur grade in the Eocene.

What does this tell us about ourselves? Are we simply the product of a "cosmic crap game," in the words of creationists? Or are we created by Wisdom, Love, and Power? These are not scientific questions, and they are not questions for science to answer. They confuse levels of being and understanding, and reflect a false dichotomy, promoted by creationists, in which spiritual and material existence are purposely confused. Church and state, our leading spiritual and material social institutions, are explicitly separated by law, and domains of spiritual and material being should be separated in education as well.

Science emerged from a philosophically motivated inquiry into the nature of our world, and it has usurped some of the mystery formerly included in religion. What we can imagine will always be greater than what we know, and we do both religion and science a disservice by confusing their respective spiritual and material realms. In the context of evolution vs. creationism, this false and sterile debate is certain to continue until creationists discover life's spiritual realm and incorporate it into their religion.

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Philip D. Gingerich received his A.B. in geology from Princeton in 1968 and his Ph.D. in vertebrate paleontology from Yale University in 1974. Since that time he has been an assistant and associate professor at the University of Michigan where he is also director of the Museum of Paleontology. His principal research interest is in the evolutionary radiation of early Cenozoic mammals, especially primates and whales.

FOOD FOR THOUGHT

We like to think of ourselves as the only species that can express the subleties of what we know and feel in that triumph of human culture, language. But one by one the sacrosanct distinctions that make our language unique are being eroded as researchers uncover in other animals astonishing abilities we thought were reserved to us.

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