2. Numerous "chains of genera" that appear to link early, primitive genera with much more recent, radically different genera (e.g. reptile - mammal transition, hyenids, horses, elephants), and through which major morphological changes can be traced. Even for the spottiest gaps, there are a few isolated intermediates that show how two apparently very different groups could, in fact, be related to each other (ex. *Archeopteryx*, linking reptiles to birds).

3. Many known species-to-species transitions (primarily known for the relatively recent Cenozoic mammals), often crossing genus lines and occasionally family lines, and often resulting in substantial adaptive changes.

4. A large number of gaps. This is perhaps the aspect that is easiest to explain, since for stratigraphic reasons alone there must always be gaps. In fact, no current evolutionary model predicts or requires a complete fossil record, and no one expects that the fossil record will ever be even close to complete. Evolutionary biologists consider gaps as the inevitable result of chance fossilizations, chance discoveries, and immigration events.

****

This "Background" packet is intended for use in conjunction with "A Cladogram of Human Evolution", by Larry Flammer (October, 1999), proposed as a lesson to be added to the ENSIweb collection. The "Background" is taken largely from the TalkOrigins Archive web site (www.talkorigins.org/faqs/faq-transitional.html), and is used here with the kind permission of its author, Kathleen Hunt.

"**Cladogenesis**": Evolution in which a daughter species splits off from a population of the older species, after which both the old and the young species coexist together. Notice that this allows a descendant to coexist with its ancestor.

PREDICTIONS: EXPECTATIONS IN THE FOSSIL RECORD:

Modern evolutionary theory holds that the living vertebrates arose from a common ancestor that lived hundreds of millions of years ago (via "descent with modification"; variety is introduced by mutation, genetic drift, and recombination, and is acted on by natural selection). Various proposed mechanisms of evolution differ in the expected rate and tempo of evolutionary change.

Predictions of evolutionary theory: Evolutionary theory predicts that fossils should appear in a progression through time, in a nested hierarchy of lineages, and that it should be possible to link modern animals to older, very different animals. In addition, the "**punctuated equilibrium**" model also predicts that new species should often appear "suddenly" (within 500,000 years or less) and then experience long periods of static equilibrium (little or no change). Where the record is exceptionally good, we should find a few local, rapid transitions between species. The "**phyletic gradualism**" model predicts that most species should change gradually throughout time, and that where the record is good, there should be many slow, smooth species-to-species transitions. **These two models are not mutually exclusive** -- in fact they are often viewed as two extremes of a continuum -- and both agree that at least some species-to-species transitions should be found.

Overview of the Transitional Vertebrate Fossil Record? The 35-page listing of transitional vertebrates offered in the TalkOrigins Archive, is a reasonably complete picture of the vertebrate record as it is now known. As extensive as it may seem, it is still just a crude summary, and some very large groups were, for convenience, left out. For instance, the list mostly includes transitional fossils that happened to lead to modern, familiar animals. This may unintentionally give the impression that fossil lineages proceed in a "straight line" from one fossil to the next. That's not so; generally at any one time there are a whole raft of successful species, only a few of which happened to leave modern descendents. The horse family is a good example; Merychippus (about 15 mya) gave rise to something like 19 new three - toed grazing horse species, which traveled all over the Old and New Worlds and were very successful at the time. Only one of these lines happened to lead to *Equus*, though, so that's the only line described in that listing. As they say, "Evolution is not a ladder, it's a branching bush."

A Bit Of Historical Background. When *The Origin Of Species* was first published, the fossil record was poorly known. At that time, the complaint about the lack of transitional fossils bridging the major vertebrate taxa was perfectly reasonable. Opponents of Darwin's theory of common descent (the theory that evolution has occurred; not to be confused with his separate theory that evolution occurs *specifically* by natural selection) were justifiably skeptical of such ideas as birds being related to reptiles. The discovery of *Archeopteryx* only two years after the publication of *The Origin of Species* was seen as a stunning triumph for Darwin's theory of common descent. *Archeopteryx* has been called the single most important natural history specimen ever found, "comparable to the Rosetta Stone" (Alan Feduccia, in "The Age Of Birds"). O.C. Marsh's groundbreaking study of the evolution of horses was another dramatic example of transitional fossils, this time demonstrating a whole sequence of transitions within a single family. Within a few decades after the *Origin*, these and other fossils, along with many other sources of evidence (such as developmental biology and biogeography) had convinced the majority of educated people that evolution *had* occurred, and that organisms *are* related to each other by common descent. (Today, modern techniques of paleontology and molecular biology further strengthen this conclusion.)

Since then, *many* more transitional fossils have been found, as sketched out in the listing. Typically, the only people who still demand to see transitional fossils are either unaware of the currently known fossil record (often due to shoddy and very dated arguments they may have read) or are unwilling to recognize it for some reason.

What Does The Fossil Record Show Us Now? The most noticeable aspects of the vertebrate fossil record, those that must be explained by any good model of the development of life on earth, are:

1. A remarkable temporal pattern of fossil morphology, with "an obvious tendency for successively higher and more recent fossil assemblages to resemble modern floras and faunas ever more closely" (Gingerich, 1985) and with animal groups appearing in a certain unmistakable order. For example, primitive fish appear first, amphibians later, then reptiles, then primitive mammals, then (for example) legged whales, then legless whales. This temporal-morphological correlation is very striking, and appears to point overwhelmingly toward an origin of all vertebrates from a common ancestor.

Why don't paleontologists bother to popularize the detailed lineages and species-to-species transitions? Because they think it is unnecessary detail. For instance, it takes an entire book to describe the horse fossils even partially (e.g. MacFadden's "Fossil Horses"), so most authors just collapse the horse sequence to a series of genera. Paleontologists clearly consider the occurrence of evolution to be a settled question, so obvious as to be beyond rational dispute, so, they think, why waste valuable textbook space on such tedious detail?

What is truly amazing, given the conditions described above, is that the fossil record shows as many contiguous sequences of fossils as it does. And furthermore, as new fossils are found (and these are many per year) they always fit nicely (or closely) into the sequences already documented, both in time and morphology, and occasionally fill one of the many gaps as well. Remember, particularly in view of the overwhelming number of transitional sequences, the lack of fossils here and there does nothing to weaken the overall picture of descent with modification; the process of evolution is very much a reality.

4. Overview of the Cenozoic

As an example of patterns of fossil abundance, we'll take a look at the Cenozoic. The Cenozoic fossil record is better than the older Mesozoic record, and much better than the very much older Paleozoic record. The most extensive Cenozoic gaps are early on, in the Paleocene and in the Oligocene. From the Miocene on it gets better and better, though it's still never perfect. Not surprisingly, the very recent Pleistocene has the best record of all, with the most precisely known lineages and most of the known species-to-species transitions. For instance, of the 111 modern mammal species that appeared in Europe during the Pleistocene, **at least 25 can be linked to earlier European ancestors by species-to-species transitional morphologies** (see Kurten, 1968, and Barnosky, 1987, for discussion).

FOSSILS OF THE CENOZOIC:

Pleistocene	1.5 - 0.01 Ma	Excellent mammal record
Pliocene	5.2 - 1.5 Ma	Very good mammal record
Miocene	23.2 - 5.2 Ma	Pretty good mammal record
Oligocene	35.5 - 23.2 Ma	Spotty mammal record. Many gaps in various lineages
Eocene	56.5 - 35.5 Ma	Surprisingly good mammal record, due to uplift and exposure of fossil-bearing strata in the Rockies
Paleocene	65 - 56.5 Ma	Fair record early on, but late Paleocene is lousy

Ma = millions of years ago

WHAT IS "PUNCTUATED EQUILIBRIUM"?

What paleontologists do get excited about are topics like the average rate of evolution. When exceptionally complete fossil sites are studied, usually a mix of patterns is seen: some species still seem to appear suddenly (within a few hundred thousand years), while others clearly appear gradually (over many millions of years). Once they arise, some species stay mostly the same, while others continue to change gradually. Paleontologists usually attribute these differences to a mix of slow evolution ("**gradualism**") and rapid evolution (or "**punctuated equilibrium**": sudden bursts of evolution followed by stasis), in combination with the immigration of new species from the as-yet-undiscovered places where they first arose.

There's been a heated debate about which of these modes of evolution is most common, and this debate has been largely misquoted by laypeople. Virtually all of the quotes of paleontologists saying things like "the gaps in the fossil record are real" are taken out of context from this ongoing debate about punctuated equilibrium. Actually, no paleontologist that I know of doubts that evolution has occurred, and most agree that at least sometimes it occurs gradually, and the fossil record clearly shows this. What they're arguing about is how often it occurs gradually. You can make up your own mind about that. (As a starting point, check out Gingerich, 1980, who found 24 gradual speciations and 14 sudden appearances in early Eocene mammals; MacFadden, 1985, who found 5 cases of gradual **anagenesis**, 5 cases of probable **cladogenesis**, and 6 sudden appearances in fossil horses; and the numerous papers in Chaline, 1983. Most studies seem to show between 1/4-2/3 of the speciations occurring fairly gradually.)

"**Anagenesis**", "phyletic evolution": Evolution in which an older species, as a whole, changes into a new descendent species, such that the ancestor is transformed into the descendant.

forest-dwellers are worst. And finally, fossils from very early times just don't survive the passage of eons very well, what with all the folding, crushing, and melting that goes on. Due to these facts of life and death, there will always be some major breaks in the fossil record.

Species-to-species transitions are even harder to document. To demonstrate anything about how a species arose, whether it arose gradually or suddenly, you need exceptionally complete strata, with many dead animals buried under constant, rapid sedimentation. This is rare for terrestrial animals. Even the famous Clark's Fork (Wyoming) site, known for its fine Eocene mammal transitions, only has about one fossil per lineage about every 27,000 years. Luckily, this is enough to record most episodes of evolutionary change (provided that they occurred at Clark's Fork Basin and not somewhere else), though it misses the rapidest evolutionary bursts. In general, in order to document transitions between species, you need specimens separated by only tens of thousands of years (e.g. every 20,000-80,000 years). If you have only one specimen for hundreds of thousands of years (e.g. every 500,000 years), you can usually determine the sequence of species, but not the transitions between species. If you have a specimen every million years, you can get the order of genera, but not which species were involved. And so on. These are rough estimates (from Gingerich, 1976, 1980) but should give an idea of the completeness required.

Note that fossils separated by more than about a hundred thousand years cannot show anything about how a species arose. Think about it: there could have been a smooth transition, or the species could have appeared suddenly, but either way, if there aren't enough fossils, we can't tell which way it happened.

2. Discovery of the fossils

The second reason for gaps is that most fossils undoubtedly have not been found. Only two continents, Europe and North America, have been adequately surveyed for fossil-bearing strata. As the other continents are slowly surveyed, many formerly mysterious gaps are being filled (e.g., the long-missing rodent/lagomorph ancestors were recently found in Asia). Of course, even in known strata, the fossils may not be uncovered unless a road cut or quarry is built (this is how we got most of our North American Devonian fish fossils), and may not be collected unless some truly dedicated researcher spends a long, nasty chunk of time out in the sun, and an even longer time in the lab sorting and analyzing the fossils. Here's one description of the work involved in finding early mammal fossils: "To be a successful sorter demands a rare combination of attributes: acute observation allied with the anatomical knowledge to recognize the mammalian teeth, even if they are broken or abraded, has to be combined with the enthusiasm and intellectual drive to keep at the boring and soul-destroying task of examining tens of thousands of unwanted fish teeth to eventually pick out the rare mammalian tooth. On an average one mammalian tooth is found per 200 kg [440 pounds] of bone-bed." (Kermack, 1984.)

Documenting a species-to-species transition is particularly grueling, as it requires collection and analysis of hundreds of specimens. Typically we must wait for some paleontologist to take on the job of studying a certain taxon in a certain site in detail. Almost nobody did this sort of work before the mid-1970's, and even now only a small subset of researchers do it. For example, Phillip Gingerich was one of the first scientists to study species-species transitions, and it took him ten years to produce the first detailed studies of just two lineages (primates and condylarths). In a (later) 1980 paper he said: "the detailed species level evolutionary patterns discussed here represent only six genera in an early Wasatchian fauna containing approximately 50 or more mammalian genera, *most of which remain to be analyzed*." [Emphasis added]

3. Getting the word out

There's a third, unexpected reason that transitions seem so little known. It's that even when they are found, they're not popularized. The only times a transitional fossil is noticed much is if it connects two noticeably different groups (such as the "walking whale" fossil reported in 1993), or it illustrates something about the tempo and mode of evolution (such as Gingerich's work). Most transitional fossils are only mentioned in the primary literature, often buried in incredibly dense and tedious "skull & bones" papers, very technical and utterly inaccessible to the general public. Later references to those papers usually collapse the known species-to-species sequences to the genus or family level. The two major college-level textbooks of vertebrate paleontology (Carroll 1988, and Colbert & Morales 1991) often don't even describe anything below the family level! And finally, many of the species-to-species transitions were described too recently to have made it into the books yet.

10	Single ear bone (stapes)	Three ear bones (stapes, incus, malleus)
11	Joined external nares	Separate external nares
12	Single occipital condyle	Double occipital condyle
13	Long cervical ribs	Cervical ribs tiny, fused to vertebrae
14	Lumbar region with ribs	Lumbar region rib-free
15	No diaphragm	Diaphragm
16	Limbs sprawled out from body	Limbs under body
17	Scapula simple	Scapula with big spine for muscles
18	Pelvic bones unfused	Pelvis fused
19	Two sacral (hip) vertebrae	Three or more sacral vertebrae
20	Toe bone #'s 2-3-4-5-4	Toe bones 2-3-3-3-3
21	Body temperature variable	Body temperature constant

(*) Fenestrae are holes in the sides of the skull
(**) The presence of a dentary-squamosal jaw joint has been arbitrarily selected as the defining trait of a mammal.

5. Two Examples of Species-to-Species Fossil Sequences in Primates:

Early lemur-like primates: Gingerich (summarized in 1977) traced two distinct species of lemur-like primates, *Pelycodus frugivorus* and *P. jarrovii*, back in time, and found that they converged on the earlier *Pelycodus abditus* "in size, mesostyle development, and every other character available for study, and there can be little doubt that each was derived from that species." Further work (Gingerich, 1980) in the same rich Wyoming fossil sites found species-to-species transitions for every step in the following lineage: *Pelycodus ralstoni* (54 Ma) to *P. mckennai* to *P. trigonodus* to *P. abditus*, which then forked into three branches. One became a new genus, *Copelemur feretutus*, and further changed into *C. consortutus*. The second branch became *P. frugivorus*. The third led to *P. jarrovi*, which changed into another new genus, *Notharctus robinsoni*, which itself split into at least two branches, *N. tenebrosus*, and *N. pugnax* (which then changed to *N. robustior*, 48 Ma), and possibly a third, *Smilodectes mcgrewi* (which then changed to *S. gracilis*). Note that this sequence covers at least three and possibly four genera, with a timespan of 6 million years.

Rose & Bown (1984) analyzed over 600 specimens of primates collected from a 700-meter-thick sequence representing approximately 4 million years of the Eocene. They found smooth transitions between *Teilhardina americana* and *Tetonoides tenuiculus*, and also between *Tetonius homunculus* and *Pseudotetonius ambiguus*. "In both lines transitions occurred not only continuously (rather than by abrupt appearance of new morphologies followed by stasis), but also in mosaic fashion, with greater variation in certain characters preceding a shift to another character state." The *T. homunculus - P. ambiguus* transition shows a dramatic change in dentition (loss of P2, dramatic shrinkage of P3 with loss of roots, shrinkage of C and I2, much enlarged I1) that occurs gradually and smoothly during the 4 million years. The authors conclude "...our data suggest that phyletic gradualism is not only more common than some would admit but also capable of producing significant adaptive modifications."

B. WHY DO GAPS EXIST (OR SEEM TO EXIST)?

Ideally, of course, we would like to know each lineage right down to the species level, and have detailed species-to-species transitions linking every species in the lineage. But in practice, we get an uneven mix of the two, with only a few species-to-species transitions, and occasionally long time breaks in the lineage. Many laypeople even have the (incorrect) impression that the situation is even worse, and that there are no known transitions at all. Why are there still gaps? And why do many people think that there are even more gaps than there really are?

1. Stratigraphic gaps

The first and most major reason for gaps is "stratigraphic discontinuities", meaning that fossil-bearing strata are not at all continuous. There are often large time breaks from one stratum to the next, and there are even some times for which no fossil strata have been found. For instance, the Aalenian (mid-Jurassic) has shown no known tetrapod fossils anywhere in the world, and other stratigraphic stages in the Carboniferous, Jurassic, and Cretaceous have produced only a few mangled tetrapods. Most other strata have produced at least one fossil from between 50% and 100% of the vertebrate families that we know had already arisen by then (Benton, 1989) -- so the vertebrate record at the **family** level is only about 75% complete, and much less complete at the genus or species level. (One study estimated that we might have fossils from as little as 3% of the species that existed in the Eocene, which is a relatively fossil-rich period!) This, obviously, is the major reason for a break in a general lineage. To further complicate the picture, certain types of animals tend not to get fossilized -- terrestrial animals, small animals, fragile animals, and area showing an apparently "sudden" change. Other times, though, the transition can be seen over a very wide geological area. Many "species-to-species transitions" are known, mostly for marine invertebrates and recent mammals (both those groups tend to have good fossil records), though they are not as abundant as the general lineages.

3. Transitions to New Higher Taxa

Both types of transitions often result in a new "higher taxon" (a new genus, family, order, etc.) from a species belonging to a different, older taxon. There is nothing magical about this. The first members of the new group are not bizarre, chimeric animals; they are simply a new, slightly different species, barely different from the parent species. Eventually this new species produces a more different species, which in turn gives rise to a still more different species, and so on, until the descendents are radically different from the original parent stock. For example, the Order Perissodactyla (horses, etc.) and the Order Cetacea (whales) can both be traced back (through a series of intermediate fossils) to early Eocene animals that looked only marginally different from each other, and didn't look at all like horses or whales. (They looked rather like small foxes with raccoon-like feet and simple teeth.) But over the following tens of millions of years, the descendents of those animals became more and more different, and now we call them two different orders. This is how "**microevolution**" apparently results in apparent "**macroevolution**" (little changes accumulating over time to produce the big differences we see today).

There are now several known cases of species-to-species transitions that resulted in the first members of new higher taxa.

4. An Example of a Transition Series: from Synapsid Reptiles to Mammals

This is the best-documented transition between vertebrate classes. So far this series is known only as a series of genera or families; the transitions from species to species are not known. But the family sequence is quite complete. Each group is clearly related to both the group that came before, and the group that came after, and yet the sequence is so long that the fossils at the end are astoundingly different from those at the beginning. As Rowe recently said about this transition (in Szalay et al., 1993), "When sampling artifact is removed and all available character data analyzed [with computer phylogeny programs that do not assume anything about evolution], a highly corroborated, stable phylogeny [family tree] remains, which is largely consistent with the temporal distributions of taxa recorded in the fossil record." Similarly, Gingerich has stated (1977) "While living mammals are well separated from other groups of animals today, **the fossil record clearly shows their origin from a reptilian stock and permits one to trace the origin and radiation of mammals in considerable detail**." For more details, see Kermack's superb and readable little book (1984), Kemp's more detailed but older book (1982), and read Szalay et al.'s recent collection of review articles (1993, vol. 1).

The list of some 27 species thatbest documents the transition from mammal-like reptiles to mammals starts with pelycosaurs (early synapsid reptiles; *Dimetrodon* is a popular, advanced, example) and continues with therapsids and cynodonts up to the first unarguable "mammal". This covered some 160 million years, from the early Pennsylvanian (315 ma) to the late Jurassic (155 ma), with a 30 million year gap in the late Triassic. Most of the changes in this transition involved elaborate repackaging of an expanded brain and special sense organs, remodeling of the jaws & teeth for more efficient eating, and changes in the limbs & vertebrae related to active, legs-under-the-body locomotion. What is most striking (here, as well as in most other transitional fossils) is a mosaic mixture (existing in each species along the way) of some earlier (more primitive) traits along with newer, more derived traits, with a gradual decrease in the primitive traits, an increase in the derived traits, and gradual changes in size of various features through time. Here are some differences observed:

#	**Early Reptiles:**	**Mammals:**
1	No fenestrae (*) in skull	Massive fenestra (*) exposes all of braincase
2	Braincase attached loosely	Braincase attached firmly to skull
3	No secondary palate	Complete bony secondary palate
4	Undifferentiated dentition	Incisors, canines, premolars, molars
5	Cheek teeth uncrowned points	Cheek teeth (PM & M) crowned & cusped
6	Teeth replaced continuously	Teeth replaced once at most
7	Teeth with single root	Molars double-rooted
8	Jaw joint quadrate-articular	Jaw joint dentary-squamosal (**)
9	Lower jaw of several bones	Lower jaw of dentary bone only

TRANSITIONAL FOSSILS: BACKGROUND

This summary is taken largely from the TalkOrigins Archive web site (www.talkorigins.org/faqs/faq-transitional.html), and is used here with the kind permission of its author, Kathleen Hunt.

According to the theory of evolution, the "descent with modification" road to humans (or any other group, for that matter) is paved with a sequence of transitional fossils, spaced out in a time sequence reflected in the ages of the fossils found. Since fossils of soft-bodied animals are relatively rare (they don't fossilize easily), the record is rather spotty prior to the first appearance of vertebrates (in the form of jawless fishes), so this lesson will focus only on the fossil record of vertebrates

As we study the growing number of fossils, we find that they usually fit nicely into one group or another, and most of those groups clearly show gradual change over time, even phasing into new and different groups along the way, adding changes upon changes. Nevertheless, many of those earlier groups apparently had populations that continued to exist with very little change, producing the modern day representatives of those surviving groups. As a result, the picture painted by the fossils reveals an ongoing coexistence, of older more primitive forms continuing to live alongside the growing diversity of animals that they produced.

However, most of those groups along the way apparently failed to survive in their original forms. They became extinct. But fortunately, some members of some of those groups were fossilized, and a few of those are found from time to time, giving us the hit-or-miss, very spotty record of fossils which has lead us to hypothesize that picture of a branched tree of being which we call evolution. New fossils are being found every day, helping to fill in some of the gaps, and those fossils continue to confirm and strengthen that picture of life through time with ever-increasing detail.

In this lesson, we will peek at a very small sampling of this fossil record, focusing mainly on the forms and times when various human traits first appeared. We will build a type of "family tree" called a "cladogram", which emphasizes the first appearances of traits which are also diagnostic of particular groups living today. If you would like to see more of the transitional details, I would suggest you go to one of the documents on the well done web site of TalkOrigins Archives: "Transitional Vertebrate Fossils" (<http://www.talkorigins.org/faqs/faq-transitional.html>). Most of the following information was taken from that document. It was compiled and presented by Kathleen Hunt, a PhD candidate in zoology at the University of Washington in the mid 1990s. The references cited here can be found at the end of that 5-part document.

A. WHAT IS A TRANSITIONAL FOSSIL?

The term "transitional fossil" is used at least two different ways here. One we'll call "general lineage", and the other, "species-to-species transition".

1. "General lineage":

This is a sequence of similar genera or families, linking an older group to a very different younger group. Each step in the sequence consists of some fossils that represent a certain genus or family, and the whole sequence often covers a span of tens of millions of years. A lineage like this shows obvious morphological intermediates for every major structural change, and the fossils occur roughly (but often not exactly) in the expected order. Usually there are still gaps between each of the groups -- few or none of the speciation events are preserved. Sometimes the individual specimens are not thought to be direct ancestors to the next-youngest fossils (i.e., they may be "cousins" or "uncles" rather than "parents"). However, they are assumed to be closely related to the actual ancestor, since they have intermediate morphology compared to the next-oldest and next-youngest "links". The major point of these general lineages is that animals with intermediate morphology existed at the appropriate times, and therefore the transitions from the proposed ancestors are fully plausible. General lineages are known for almost all modern groups of vertebrates, and make up the bulk of the examples mentioned. These provide the very compelling, ever-growing "circumstantial evidence" we have for that change through time that we call "biological evolution".

2. "Species-to-species transition":

This is a set of numerous individual fossils that show a change between one species and another. It's a very fine-grained sequence documenting the actual speciation event, usually covering less than a million years. These species-to-species transitions are unmistakable when they are found. Throughout successive strata you see the population averages of teeth, feet, vertebrae, etc., changing from what is typical of the first species to what is typical of the next species. Sometimes, these sequences occur only in a limited geographic area (the place where the speciation actually occurred), with analyses from any other