

ANNOTATIONS FROM THE LITERATURE

BEHAVIOR: DOMESTICATION OF THE FOX

Trut LN. 1999. Early canid domestication: the farm-fox experiment. *American Scientist* 87:160-169.

Summary. In 1959, the Russian geneticist Dmitry K. Belyaev began studying the behavior of captive foxes at a fur farm. Interested in the process of domestication, he experimentally selected foxes on the basis of their reaction to humans. Individual foxes that responded with fear were removed from the experiment, while those without fear were retained. Although Belyaev died in 1985, others have continued his experiment. Considerable variation has been noted, e.g., size, color, hair texture, floppy ears and curly tail. By the 6th generation, some foxes displayed behavior resembling domestic dogs — whimpering to attract attention and licking their keepers. This domesticated behavior increased to 1 pup in 6 by the 10th generation, and to 3 pups in 4 by about the 30th generation. These changes have been accompanied by a reduction in secretion of adrenal hormones, a reduction in basal levels of blood plasma corticosteroids, and an increase in serotonin levels. Other changes have occurred in morphology and reproductive behavior. In addition to foxes, the research group has also successfully domesticated river otters and Norway rats from wild-caught ancestors.

Comment. This experiment indicates that aggressive behavior has a genetic basis, and can be reduced rapidly through selection. This suggests that aggressive behavior might also become established rapidly if a world of peaceful coexistence became dominated by competition.

BIOGEOGRAPHY: DISAPPEARING DISJUNCTION

Wen J. 1999. Evolution of Eastern Asian and Eastern North American disjunct distributions in flowering plants. *Annual Review of Ecology and Systematics* 30:421-455.

Summary. Biogeographers have noted for many years that similar plants occur in eastern Asia and eastern North America, separated by

a distributional gap. About 65 genera of seed plants have disjunct distributions between eastern North America and eastern Asia. Explanations for these disjunctions, such as long-distance dispersal, have been based on the assumption that the similar species were each other's closest relatives. Molecular studies contradict this assumption and indicate that plants in eastern North America are generally more closely related to morphologically different plants in western North America than to morphologically similar plants in eastern Asia. The proposed explanation is that the disjunctions are due to multiple factors, including convergence, vicariance, and differential extinction. Molecular-clock studies suggest that the disjunctions studied originated mostly in the Miocene.

Comment. Disjunct distributions are one of the most interesting problems for biogeography to explain, and the large number of disjuncts in eastern Asia and eastern North America have elicited considerable discussion. Now we learn that the disjunctions may not be real. This illustrates the importance of a reliable taxonomy, and the difficulty in achieving it.

CHROMOSOMAL EVOLUTION: TETRAPLOID MAMMAL

Gallardo MH, Bickham JW, Honeycutt RL, Ojeda RA, Kohler N. 1999. Discovery of tetraploidy in a mammal. *Nature* 401:341.

Summary. The red viscacha rat, *Tympanoctomys barrerae*, is a member of the family Octodontidae, endemic to South America. The genome of *T. barrerae* has twice the amount of DNA found in its closest relatives. The number of chromosome pairs is 51, compared with 28 in the other species. The most reasonable explanation is that the red viscacha rat is tetraploid, but that some of the chromosomes have been lost. These appear to include the Y chromosome and one pair of chromosomes identifiable due to a secondary constriction.

Comment. This is the first report of a tetraploid mammal, and must represent a rare situation. It has been thought that tetraploidy might be lethal in mammals, but this discovery suggests that mammals may be subject to similar karyotypic processes as other vertebrates.

GENETICS: GENE DUPLICATION WITHOUT PSEUDOGENES

Cronn RC, Small RL, Wendel JF. 1999. Duplicated genes evolve independently after polyploid formation in cotton. *Proceedings of the National Academy of Sciences (USA)* 96:14406-14411.

Summary. Current evolutionary theory predicts that new genes may arise when genes are duplicated, producing extra gene copies that are free to mutate and evolve new functions. Alternatively, the extra gene copies may degenerate into functionless pseudogenes. A third possibility is that each of the gene copies may continue to function as before the duplication event. The relative frequency of these various fates is unknown. Polyploidy produces extra copies of every gene in the genome. Polyploids may form when two slightly different species hybridize. This has happened in cotton, and the ancestral species have been identified. Sixteen genes were studied in the polyploid cotton and its ancestral species. In nearly all the comparisons, the duplicated copies continued their original function. Although the gene sequences had diverged, there was no evidence that the rate of divergence was affected by the presence of duplicated gene copies. A high rate of divergence has been previously reported among duplicated highly repetitive DNA sequences, but there are no such reports from duplicated nuclear genes.

Comment. These results do not support the theory that gene duplication accelerates the process of pseudogene formation and evolution of new gene functions. Further studies are needed to see how widely these results apply.

GENETICS: INBRED VIGOR?

Visscher PM, Smith D, Hall SJG, Williams JA. 2001. A viable herd of genetically uniform cattle. *Nature* 409:303.

Summary. Inbreeding is generally considered harmful, due to accumulation of deleterious alleles. However, if inbreeding were combined with selection, deleterious alleles might be purged. Support for this idea comes from the Chillingham cattle, a feral herd of some 49 individuals living in a park in northern England. This herd is thought to have been isolated for at least 300 years, and is almost genetically uniform. The Chillingham cattle might provide a model for study of the bovine genome and the genetics of disease resistance.

Comment. This example suggests that inbreeding would not be harmful in a world without deleterious mutations. Small population sizes, such as after the creation or after the Biblical flood, would not necessarily cause genetic deterioration leading to extinction.

GENETICS: WHAT CAUSES PSEUDOGENES?

Satoh H, Inokuchi N, Nagae Y, Okazaki T. 1999. Organization, structure, and evolution of the nonadult rat beta-globin gene cluster. *Journal of Molecular Evolution* 49:122-129.

Summary. The beta-globin gene family has been characterized for both mouse and rabbit, but only incompletely for the rat. This study completes the description of the rat gene cluster by adding the embryonic globin gene sequences. The rat has three beta-globin genes expressed embryonically, in addition to the single adult gene. Two pseudogenes [non-functional degenerate genes] separate the embryonically expressed beta globin genes from the adult expressed gene. The mouse has essentially the same gene arrangement. Comparing the embryonic rat and mouse globin gene sequences shows that the functional rat genes are more similar to the corresponding mouse genes than to each other. In contrast, the rat psi-gamma-3 and mouse beta-h2 pseudogenes are more similar to functional genes of the respective species than to each other.

Comment. Similar gene arrangements are typically interpreted as inherited from a common ancestor. Similar location of pseudogenes in rat and mouse suggest possible inheritance from a common ancestor. On the other hand, the greater similarity of the rat pseudogene to the functional rat gene than to the mouse pseudogene suggests possible separate origins for the rat and mouse pseudogenes. More information is needed to clarify this situation.

Similar pseudogenes in humans and chimps have been argued as conclusive evidence for their common ancestry. The location of one or more pseudogenes between the embryonic and adult globin genes is a common feature of humans, chimps, rat, mouse, and rabbit. Could this be due to a common process of degeneration? Could it indicate a function in switching gene activity from embryonic globin forms to adult forms? These questions remain unsolved, and pseudogenes continue to present an interesting problem needing more study.

GEOLOGY: MISSOULA FLOODS OR FLOOD?

Shaw J, Munro-Stasiuk M, Sawyer B, Beaney C, Lesemann J-E, Musacchio A, Rains B, Young RR. 1999. The Channeled Scabland: back to Bretz? *Geology* 27:605-608.

Summary. The Channeled Scabland of Washington was originally described by Bretz as due to a catastrophic flood flowing from glacial Lake Missoula across the Columbia River Basalts to the Pacific Ocean. More recently, a series of floods has been proposed, extending over several centuries. This paper presents evidence indicating that there may have been only one flood, or a few, but that the water came from more than one source. Outflow from subglacial reservoirs of the Cordilleran Ice Sheet may have added to water from glacial Lake Missoula, providing sufficient water to cause the Channeled Scablands in a single flood.

Comment. The debate over the history of the Channeled Scablands provides an instructive example of the nature of science and the role of presuppositions in shaping scientific consensus. This paper adds one more chapter to the story.

MOLECULAR EVOLUTION: CAN EVOLVING PROTEINS RETAIN THEIR FUNCTIONALITY?

Bastolla U, Roman HE, Vendruscolo M. 1999. Neutral evolution of model proteins: diffusion in sequence space and overdispersion. *Journal of Theoretical Biology* 200:49-64.

Summary. A comparison of DNA sequences for homologous proteins shows a large peak at 8.5% sequence identity, which is within the range expected from a comparison of random sequences. The question that arises is whether proteins with such different sequences are connected by an evolutionary pathway of viable intermediates — a “neutral network.”

This question is explored with a model 36-amino acid sequence arranged in a lattice pattern. A single mutational step was taken at random, and the resulting sequence tested for whether it maintained its “phenotype,” which is analogous to its “viability” in real life. Sequences that passed the “viability test” were then mutated further. Results showed that only 6% of the sequences passed the “viability test”; 94% were rejected. Yet the small proportion of “viable” sequences

did form neutral networks in sequence space such that starting and ending points differed as much as would be expected from comparisons of random sequences. The implication is that protein function can be maintained while sequences evolve to the extent that the starting and ending sequences appear unrelated.

The model has some features that admittedly are biologically unrealistic. For example, the sequence is so short that all but two of the amino acids are on the surface of the protein. A larger number of “core” amino acids would impose greater constraints on viability of sequence changes. Other weaknesses of the model are that it considers mutations of amino acids rather than nucleotides, and does not address biological activity. However, the model does seem to provide a useful device for exploring the question.

Comment. Biologists have long been interested in the problem of viability of morphological intermediates during evolution. Less has been said about molecular intermediates, but the question is similar. The results reported by Bastolla et al. do not answer the question, but at least provide an interesting entry point into the subject. The suggestion that proteins can retain their function while undergoing major changes in amino acid sequence, if confirmed, might explain why gene duplications so rarely produce pseudogenes (see annotation on paper by Cronn et al.)

ORIGIN OF LIFE: MINIMAL COMPLEXITY

Kyrpides N, Overbeek R, Ouzounis C. 1999. Universal protein families and the functional content of the last universal common ancestor. *Journal of Molecular Evolution* 49:413-423.

Summary. Living organisms can be classified in three major groupings: eubacteria, archaea, and eukarya. Complete sequencing of the archaean, *Methanococcus jannaschii*, means that genomes of representatives of each of these groups are now available for comparison. Using the principle that shared features are ancestral, one can estimate the composition of the genome of the [hypothetical] last universal common ancestor. The number of genes shared by each of the three groupings is 324. These represent 246 unique biochemical functions. Since additional shared genes are known in other archaeans, this number represents a low estimate. This result indicates the last

universal common ancestor had a level of complexity similar to living unicellular organisms.

Comment. These conclusions have implications for origin of life theories. Scientists now have an improved basis for estimating the minimal complexity necessary in origin of life scenarios. Estimates of minimal complexity are similar to the estimate here for the “last universal common ancestor.” The degree of complexity required for even the simplest functioning cell is a strong argument for the role of intelligence in the creation of life.

PALEONTOLOGY: DINOSAUR DIVERSITY

Sereno PC. 1999. The evolution of dinosaurs. *Science* 284:2137-2147.

Summary. This paper reviews the fossil record of dinosaurs, from their first appearance in mid-Carnian (Upper Triassic) sediments to their last appearance in the Upper Cretaceous. A comprehensive, family-level phylogeny is proposed. Triassic dinosaurs are moderately diverse and include both major dinosaurian types, the Ornithischia and the Saurischia. Generic diversity waxes and wanes through the Mesozoic, reaching a maximum in the uppermost Cretaceous. Birds are linked to dinosaurs, with claims of feathered dinosaurs used in support. Dinosaurs exhibit several repeated morphological trends, e.g., increasing body size, increasing number of cervicals, increasing number of sacrals, reduction and loss of teeth, reduction of the forelimbs, etc. Dinosaurs are similar throughout the world in Triassic and Jurassic sediments, but show distinct regional differences in the Cretaceous. Biogeographic differences in dinosaur faunas seems more heavily influenced by local and regional factors than by the break-up of Pangaea into separate plates.

Comment. Dinosaurs have captured the public’s imagination, and this paper provides a valuable summary of their fossil record. Dinosaurs are notably diverse and geographically widespread at or near their first appearance in the fossil record. They have been reported from Upper Triassic sediments of North and South America, Morocco and India. Some twenty genera are known, representing ornithischians, sauropods and theropods. The failure of the dominant Mesozoic terrestrial vertebrates to exhibit phylogenetic relationships correlated with the break-up sequence of Pangaea may indicate a weakness in current interpretations of plate histories.

PALEONTOLOGY: DINOSAUR SKIN

Martill DM, Batten DJ, Loydell DK. 2000. A new specimen of the thyreophoran dinosaur cf. *Scelidosaurus* with soft tissue preservation. *Palaeontology* 43:549-559.

Summary. A fossil specimen from Great Britain with eight caudal vertebrae has been identified as a juvenile thyreophoran dinosaur. The surrounding sediments contain algal spores and bivalves that suggest the fossil came from Lower Jurassic marine sediments. Evidence of the skin is preserved, including osteoderms. Such excellent preservation of a terrestrial animal in a marine deposit is remarkable. The animal may have been washed out to sea soon after death, and sunk into the “soupy” substrate, where bacterial action contributed to mineralization of some of the skin tissue.

Comment. Taphonomy, the study of conditions of deposition and preservation of fossils, might provide important clues in improving our understanding of earth history. Data should be examined for possible trends in taphonomic conditions.

PALEONTOLOGY: FOSSIL RECORD AND PHYLOGENY

Benton MJ, Wills MA, Hitchin R. 2000. Quality of the fossil record through time. *Nature* 403:534-537.

Summary. This paper addresses the degree to which the fossil record faithfully records the history of life. It would seem obvious that older rocks are more likely to have been destroyed than younger rocks; hence, the quality of the fossil record should deteriorate as one moves downward through the geologic column. This question is tested by comparing the sequence of fossil taxa with the sequence of the branching of cladograms, where the cladograms are based on data independent of the fossil record. The results show that the degree of consistency between fossils and cladogram branching is roughly constant through the geologic column. In other words, cladograms based on Paleozoic taxa are no less consistent with the fossil record than are cladograms based on Mesozoic or Cenozoic taxa. This indicates that the fossil record, although undoubtedly incomplete, is, nevertheless, adequate for illustrating the history of diversification of living organisms.

Comment. One would expect the quality of the fossil record to increase as one moves upward through the column (the “pull of the

recent”). This paper suggests otherwise, unless the quality of the fossil record has little effect on construction of cladograms. If the quality of the fossil record is relatively uniform, the systematic pattern of morphological and genealogical gaps (fewer intermediates between higher taxa than between lower taxa) becomes all the more striking.

PALEONTOLOGY: THE INCOMPLETE RECORD

Brocks JJ, Logan GA, Buick R, Summons RE. 1999. Archean molecular fossils and the early rise of eukaryotes. *Science* 285:1033-1036. (Reaction by Knoll AH. 1999. A new molecular window on early life. *Science* 285:1025-1026.)

Summary. Archean rocks are dated as older than 2.5 billion years. There is some evidence of life in some of these rocks, but the rocks are frequently highly metamorphosed, and it has been difficult to identify the organisms. Samples of weakly metamorphosed rock from a drill core taken from northwestern Australia were analyzed and found to contain both hopanes and steranes. This extends the fossil record of biomolecules by a billion years. Hopanes are indicative of cyanobacterial activity, while steranes are derived from eukaryotes. These results indicate the presence of both bacteria and eukaryotes during deposition of these Archean sediments. They also indicate the presence of atmospheric oxygen needed for eukaryotes to produce the sterols from which the steranes were derived. These results tend to support molecular phylogenies that suggest bacteria and eukaryotes diverged long before the time suggested in the fossil record.

Comment. The presence of biomolecules unaccompanied by body fossils presents an interesting question. Why is there such a large stratigraphic gap between the biomolecules and the body fossils of the living eukaryotes that produced the molecules? Other examples of such gaps are known, although the size of the gaps is smaller. The role of depositional and taphonomic factors, including the possibility of infiltration of biomolecules into the rocks, is a topic worthy of further study.

PALEONTOLOGY: MIOCENE VERTEBRATE BURROWS

Meyer RC. 1999. Helical burrows as a palaeoclimate response. *Palaeogeography, Palaeoclimatology, Palaeoecology* 147:291-298.

Summary. Helical burrows were discovered many years ago in Miocene sediments of Nebraska. They appear to have been dug by *Palaeocastor fossor*, an extinct beaver. The burrows typically slope downward at about a 25-30 degree angle, and end in a straight, upward-sloping “living chamber” having an angle up to 43 degrees. The helical shape of the burrow is highly unusual, and it is not clear what advantage might be obtained from their peculiar shape. Calculations reported in this paper show that the helical burrows required removal of 36% to 61% more soil than would a straight burrow sloping at 43 degrees, dug to the same depth. The helical burrows do not seem to provide an advantage in closer packing of burrows within a colony, nor do they seem a good deterrent to predators. The entrance to the “living chambers” could be placed below water level to provide a refuge from predators, but the chambers lack venting. Perhaps the helical burrow shape helped conserve moisture in a dry climate. Helical burrows are also known from Permian sediments in South Africa. These burrows are thought to have been dug by *Diictodon galeops*, a therapsid. It has been suggested that the shape of the Permian burrows helped retain moisture within the living chambers. Perhaps the beaver burrows functioned in a similar way.

Comment. Burrows of terrestrial vertebrates present an interesting problem for creationists. One would not expect animals to be constructing burrows during a flood, and their presence strongly indicates that the surface was exposed to the atmosphere during the time the burrows were being constructed. This question has gotten much more attention than the question of whether the peculiar shape of these burrows might indicate some unusual environmental conditions. Perhaps future research will reveal that the answers to these two questions are related.

PALEONTOLOGY: NEANDERTHALS AND MODERN HUMANS

Krings M, Geisert H, Schmitz RW, Krainitzki H, Paabo S. 1999. DNA sequence of the mitochondrial hypervariable region II from the Neanderthal type specimen. *Proceedings of the National Academy of Sciences (USA)* 96:5581-5585.

Summary. Recovery of mitochondrial DNA sequences from a Neanderthal skeleton permits sequencing and comparison with modern human mitochondrial DNA. A previous sequence showed that Neanderthal DNA falls outside the range of variation among living humans. This second Neanderthal sequence confirms the previous report. The Neanderthal sequence is about four times as different as the range of variation among living humans. This is interpreted to mean that Neanderthals diverged from modern humans about 465,000 years ago, compared with about 150,000 years ago for the divergence of living humans. This supports the theory that Neanderthals are genetically distinct from modern humans, and became extinct without blending with modern humans.

Comment. Even if one accepts that Neanderthals did not contribute mitochondrial DNA to the living human population, this does not necessarily indicate that Neanderthals did not intermarry with anatomically modern humans. The familiar “mitochondrial Eve” hypothesis is based on the idea that all living humans can trace their ancestry back to a single female, but this in no way requires that there were no other females living at the time. Rather, only one ancestral female has a continuous line of female descendants, all other mother-daughter lineages having terminated. Thus, Neanderthals might have interbred with anatomically modern humans, but could be among the group without a continuous mother-daughter lineage extending to the present time.

PALEONTOLOGY: PERMIAN VERTEBRATE BURROWS

Groenewald GH, Welman J, MacEachern JA. 2001. Vertebrate burrow complexes from the Early Triassic Cynognathus zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaios* 16:148-160.

Summary. Many living vertebrates dig burrows, but fossil burrows are uncommon. Several burrows of different types have been previously

identified in Permian sediments of the Beaufort Group. This paper reports a new type of burrow from Triassic sediments, also of the Beaufort Group. The burrows are branching and have terminal chambers. One burrow complex contained skeletons of 20 or more specimens of *Trirachodon*, a probably herbivorous mammal-like reptile. The cause of burial appears to be a flash flood.

Comment. These burrows are in sediments that creationists generally regard to have been deposited during the Genesis Flood. Such features seem to indicate constraints on the nature of Flood activity in South Africa during the construction of these burrows. A possible explanation might be that the area was not under water at the time, but sediment was being intermittently washed into the area from some source area. Sufficient time passed between sedimentary episodes, such as flash floods, to permit burrow construction by these animals, which were similar in size to prairie dogs.

PALEONTOLOGY: VERTEBRATES IN THE CAMBRIAN EXPLOSION

Shu D-G, Luo H-L, Conway Morris S, Zhang X-L, Hu S-X, Chen L, Han J, Zhu M, Li Y, Chen L-Z. 1999. Lower Cambrian vertebrates from south China. *Nature* 402:42-46. (Reactions: Janvier P. 1999. Catching the first fish. *Nature* 402:21-22; Zimmer C. 1999. Fossils give glimpse of old mother lamprey. *Science* 286:1064-1065.)

Summary. New fossil discoveries have confirmed the presence of vertebrates in Lower Cambrian sediments. The inch-long fossils were discovered in the area of Chengjiang, in Yunnan Province, China, an area famous for fossils in an excellent state of preservation. Two new genera of agnathan fish are described in this paper, *Mylokummingia* and *Haikouichthys*. Both genera are considered more advanced than the living hagfish, but related to both the hagfish and lamprey.

Chen J-Y, Huang D-Y, Li C-W. 1999. An early Cambrian craniate-like chordate. *Nature* 402:518-522. (Reaction: Enserink M. 1999. Fossil opens window on early animal history. *Science* 286:1829.)

Summary. More than 300 specimens of a new chordate have been discovered in the Chengjiang region of Yunnan Province, China. The new find, named *Haikouella*, appears somewhat similar to *Yunnanozoon*, found in the same region in 1995, but is more vertebrate-like. The fossils were found in fine-grained silts, which preserved such

details as the heart, brain, fins, segmented muscles, and possible eyes. The fossils are up to three centimeters in length.

Comment. The sudden appearance of most animal phyla in Cambrian sediments is one of the most compelling features of the fossil record. Previous discoveries had suggested that chordates were included in the “Cambrian Explosion,” but this point has been debated. These newly discovered fossils should settle the case, not only for chordates in general, but also for vertebrates.

PHYLOGENY: DEVELOPMENTAL PROBLEMS

Lovejoy CO, Cohn MJ, White TD. 1999. Morphological analysis of the mammalian postcranium: a developmental perspective. *Proceedings of the National Academy of Sciences (USA)* 96:13247-13242.

Summary. Phylogenetic studies based on fossils have to rely on anatomical characters for which the underlying genetic basis is largely unknown. Increased resolution is often sought by subdividing characters into finer detail, without respect for whether the finer details are genetically independent. Research in vertebrate limb development has shown that patterning in the limb is determined at the cellular level, not the larger anatomical level. Thus, there probably is not a separate gene for each anatomical detail. Rather, anatomy appears to be the result of gradients of molecules that control rates of developmental processes. The authors propose that differences in traits between taxa be classified into five categories, based on the developmental genetics of the trait. This distinction could enhance phylogenetic studies by reducing the number of non-independent characters.

Comment. It has been known for a long time that increasing the level of anatomical detail may not increase phylogenetic resolution, but information has been lacking on the relationship between genes and structure. As this information becomes available, it should become easier to evaluate hypotheses of relationships among different species groups. It would be interesting to see whether this information might be useful in identifying groups with independent origins.

PHYLOGENY: DEVELOPMENTAL PROBLEMS IN HUMANS

McCollum MA. 1999. The robust Australopithecine face: a morphogenetic perspective. *Science* 284:301-305.

Summary. The robust australopithecines are considered a side branch in human evolution. Three species are grouped into a single clade, defined by a number of morphological synapomorphies, and sometimes classified in the genus *Paranthropus*. Resolution of relationships among the three species has been difficult, with the result that anatomical features have been more finely subdivided to increase the number of characters to be analyzed. However, these features may be correlated rather than independent. A model for the development of the face and skull is described in this paper, with the suggestion that the number of independent characters is actually only two, instead of the twenty that have been proposed. The three robust species show some significant morphological differences that might indicate separate ancestries for the East and South African forms.

Comment. This example illustrates the point made in the previous paper: that splitting morphological features more finely does not necessarily improve the accuracy of evolutionary relationships.

PHYLOGENY: GALAPAGOS TORTOISES

Caccone A, Gibbs JP, Ketmaier V, Suatoni E, Powell JR. 1999. Origin and evolutionary relationships of giant Galapagos tortoises. *Proceedings of the National Academy of Sciences (USA)* 96:13223-13228.

Summary. Darwin was much interested in the giant Galapagos tortoises, *Geochelone nigra*, when he visited the islands on his famous trip. However, their closest relative has not been determined. Based on mitochondrial DNA sequences, the closest living relative is the chaco tortoise, *G. chilensis*. Somewhat surprisingly, the chaco tortoise is relatively small-bodied compared to several other South American tortoises. However, fossils are known that appear plausible ancestors of the Galapagos giants. Giantism is thought to have preceded colonization of the Galapagos islands. The study may offer renewed hope for "Lonesome George," the last of the tortoises from the island of Pinta. He has failed to mate, despite numerous efforts to induce mating. Genetic analysis indicates his closest relatives are on the islands of

San Cristobal and Espanola, which are the farthest islands from Pinta. Perhaps a more suitable mate can be found on one of those islands.

Comment. It comes as no surprise to learn that size is not a reliable indicator of relationships. The unexpected geography of “Lonesome George’s” relationship reminds us not to take too much for granted, but we can all extend our best wishes to “Lonesome George” in perpetuating his race.

PHYLOGENY: THE HOATZIN IS A TURACO?

Hughes JM, Baker AJ. 1999. Phylogenetic relationships of the enigmatic hoatzin (*Opisthocomus hoazin*) resolved using mitochondrial and nuclear gene sequences. *Molecular Biology and Evolution* 16:1300-1307.

Summary. The hoatzin is a strange bird of uncertain relationships, living in South America. The young have claws at the wrist joint of their wings, used to climb among tree branches. The hoatzin has been classified with the pheasants, but recently has been proposed to be a cuckoo. Mitochondrial studies reported here indicate it is actually related to the turacos, which are otherwise restricted to tropical Africa. A hoatzin-turaco relationship has been proposed previously, but has not been generally accepted.

Comment. Identification of the hoatzin as a turaco adds another interesting biogeographical problem of a group restricted to Africa and South America. One might be tempted to explain this disjunction as due to separation of the African and South American plates, but this is an unlikely explanation. Turaco fossils are more widely distributed than are the living members of the group, and it is likely that the ancestors of the hoatzin came through North America. Extinction of the Eurasian and North American members of the group, perhaps due to climatic changes, would leave the hoatzin isolated in South America.

PHYLOGENY: IS THERE REALLY A TREE OF LIFE?

Doolittle WF. 1999. Phylogenetic classification and the universal tree. *Science* 284:2124-2128.

Doolittle WF. 1999. Lateral genomics. *Trends in Genetics* 15:M5-M8.

Summary. Phylogenetic trees based on different gene sequences often conflict in important ways. Conflict may be caused by inadequate

analyses or oversimple assumptions about rates of change, but these problems do not explain all the observed conflicts. It appears that genes have been commonly transferred from one species to another among the three great divisions of life, Archaea, Bacteria, and Eukarya. This process may be responsible for much of the confusion in attempts to trace their phylogenetic relationships. Thus, it may never be possible to portray phylogenetic relationships as a hierarchical tree with a single root. Instead, phylogenetic relationships may take the form of a net or web.

Katz LA. 1999. The tangled web: gene genealogies and the origin of eukaryotes. *American Naturalist* 154:S137-S145.

Summary. Eukaryotes are characterized by having a nucleus and a cytoskeleton. Hopes that eukaryotic DNA might have some identifying features have not been realized. Eukaryotic genes involved in information processing are more similar to archaean genes than to bacterial genes. Other types of eukaryotic genes, however, may be more similar to bacterial than to archaean genes. Still other eukaryotic genes are equivocal. The picture is emerging that eukaryotic genes might be chimeric, composed of material from different sources. Several hypotheses have been generated to explain the apparent chimerism of eukaryotic genomes. One such hypothesis is that most lateral transfers involved a few “donor” lineages that contributed genes to many recipient lineages. Other hypotheses invoke serial endosymbiosis, “you are what you eat,” or “genetic annealing.” The latter suggests an early explosion in the frequency of gene transfer, followed by a much lower rate. These hypotheses may be difficult to test, and to evaluate statistically. Better tools of analysis are needed.

Comment. The notion of lateral gene transfer is supported by evidence that seems convincing. However, the pattern of gene distribution among different organisms might be explained in part as the result of common design. It seems unsurprising that a Creator might design different species with different combinations of genes, thus providing for a variety of environmental interactions. Some of the conflicts in phylogenies might reflect separately created lineages rather than lateral gene transfer.

PHYLOGENY: LATERAL GENE TRANSFER

Jordan IK, Matyuina LV, McDonald JF. 1999. Evidence for the recent horizontal transfer of long terminal repeat retrotransposon. *Proceedings of the National Academy of Sciences (USA)* 96:12621-12625.

Summary. Mobile genetic elements are able to move within the genome of an organism, and are a leading cause of mutations. One class of mobile elements, the long terminal repeat (LTR) retrotransposons have been linked to mutations with major phenotypic effects. Movement of an LTR element is accomplished by reverse transcription of an RNA intermediate. Evidence presented in this paper indicates that LTR retrotransposons not only can move within the genome of an individual, but can also move from one species to another. An LTR element named *copia* is common in *Drosophila melanogaster*, but is patchily distributed among a distantly related species, *D. willistoni*. The best explanation is a recent cross-species transfer of this retrotransposon.

Comment. The origin and role of mobile elements are questions that potentially have far-reaching implications for understanding relationships among organisms. For example, shared patterns of inserted elements are claimed as the strongest evidence for an evolutionary relationship of whales and artiodactyls (e.g., cattle, pigs, hippos). Demonstration of cross-species transfer could weaken that claim, while evidence refuting cross-species transfer would strengthen it. Explanations of how mobile elements originated might shed light on the nature of the mechanisms involved in morphological changes since the creation.

PHYLOGENY: LIMITS TO CHANGE?

Wagner PJ. 2000. Exhaustion of morphologic character states among fossil taxa. *Evolution* 54:365-386.

Summary. This paper reports the results of efforts to determine if new character states are added continuously in evolutionary development of a lineage. If not, then character space might become saturated, and similar character states might appear repeatedly, frustrating efforts to determine evolutionary relationships on the basis of uniquely shared derived traits. Fifty-six taxa were analyzed, representing mammals, echinoderms, arthropods and mollusks. Results showed that character

space does tend to become saturated. New species tend to repeat previous character states rather than evolving new ones. This may explain why inconsistencies (homoplasies) are so common in phylogenetic studies, and also why long branches seem to tend to cluster together. Another implication is that phylogenetic studies may lack the precision needed to evaluate completeness of the fossil record.

Comment. The results reported here have important implications for constructing phylogenetic trees. On average, 75-80% of the potential character states were observed in fossils belonging to the taxa studied (ranging from genus to class). One implication is that cladograms become more unstable when living and fossil species are added together in the same study. Another is that diversification may involve different combinations of existing character states rather than addition of new character states. This is reminiscent of the creationist prediction of limits to change.

PHYLOGENY: THE SURPRISING SHARK

Rasmussen A-S, Arnason U. 1999. Phylogenetic studies of complete mitochondrial DNA molecules place cartilaginous fishes within the tree of bony fishes. *Journal of Molecular Evolution* 48:118-123.

Summary. Sharks and their allies comprise the cartilaginous fishes, which are usually regarded as the most primitive group of jawed vertebrates. Comparison of the complete mitochondrial DNA sequence of the spiny dogfish indicates it falls between the teleosts and non-teleost bony fishes on the phylogenetic tree. This implies that cartilaginous fish have lost the swimbladder and bony skeleton. In the tree, lungfish appear to be the most primitive jawed fish, and not the outgroup to amniotes (e.g., reptiles, birds, mammals). The altered phylogenetic tree changes the polarity of several traits used to analyze vertebrate relationships, and shows amniotes diverging outside the group of living fish.

Comment. Molecular phylogenies sometimes present unexpected results, but this result, if verified, is of more than ordinary interest. It is widely held that amniotes evolved from amphibians, which evolved from certain types of fish that have living relatives. This study indicates problems with the traditional scenario. In the proposed evolutionary tree, amniotes are not descended from any known group of jawed fish with living relatives. This could negate proposals that certain fossils

represent evolutionary transitions between fish and the ancestors of the amniotes, and require creation of a new evolutionary scenario for the evolution of jawed vertebrates.

SPECIATION: DEVELOPMENTAL GENES

Ting C-T, Tsaur S-C, Wu M-L, Wu C-I. 1998. A rapidly evolving homeobox at the site of a hybrid sterility gene. *Science* 282:1501-1504.

Summary. Homeobox genes are believed to have regulatory functions in development. They generally have highly similar sequences in different species. One homeobox gene, named Odysseus (*Ods*) has been found to differ significantly between two species of fruit flies, *Drosophila mauritiana* and *D. simulans*. Males resulting from crossing these two species are always sterile, and the *Ods* gene is thought to play an important role in the sterility. The gene responsible for the sterility was sequenced and compared among the two *Drosophila* species, the mouse *uncx4.1* gene, and the *unc-4* gene of the worm *Caenorhabditis elegans*. The two species of fly differ by 15 amino acids. This compares with a difference of 17 amino acids between *Drosophila* and the mouse, and only 7 amino acids between the mouse and *C. elegans*. Further comparison of the sequences of the two flies shows that the exonic sequences differ by eight times the intronic sequences. This is interpreted as due to strong selection on the gene. One potential selective force on this gene might be sexual selection for male hybrid sterility. If so, this gene may play an important role in speciation within fruit flies.

Comment. Homeobox genes are thought to be involved in switching genes on and off during development. The sequence consistency typical of homeobox genes is commonly interpreted to reflect conservation of gene function. This example of strong difference in homeobox sequence in two closely related species of *Drosophila* suggests that the relationship between homeobox genes and development is not so simple. This discovery is also important in indicating a possible molecular basis for speciation in these flies.

SPECIATION: RIFT LAKE CICHLIDS

Ruper L, Verheyen E, Meyer A. 1999. Replicated evolution of trophic specializations in an endemic cichlid fish lineage from Lake Tanganyika. *Proceedings of the National Academy of Sciences (USA)* 96:10230-10235. [See also Stiassny MLJ, Meyer A. 1999. Cichlids of the rift lakes. *Scientific American* 280(Feb):64-69.]

Summary. Lake Tanganyika has 49 endemic genera of cichlid fishes assigned to twelve different tribes, based primarily on morphological criteria such as tooth shape. One of these tribes is Eretmodini, with three genera and four species. Comparison of mitochondrial DNA sequences from these four species shows that six lineages are present rather than the four identified from morphology. Furthermore, morphologically different individuals are frequently more closely related genetically than morphologically similar individuals. It appears that similar tooth shape has evolved several times independently. Such parallel evolution has previously been reported in other cichlids.

Comment. The Rift Lake cichlids have become one of the classical examples of speciation. Studies such as this one have shown that genetically similar individuals may exhibit significant morphological variation, sufficient to be interpreted as distinct species. However, the number of alternative morphological states may be limited. In the present case, six different lineages produced only three different morphological states (interpreted as genera). It may be that the range of variation is limited within a species or group of species.